Flying Foxes (Chiroptera: Pteropodidae): Threatened Animals of Key Ecological and Economic Importance

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Abstract: *Flying foxes are animals of extraordinary ecological and economic importance throughout forests of the Old World tropics. Nearly 200 species play an essential role as forest pollinators and seed dispersers, yet they are frequently misunderstood, intensely persecuted, and exceptionally vulnerable to extinction. Their role in the propagation of numerous important plants remains virtually uninvestigated. However, our review of already available literature demonstrates that at least 289 plant species rely to varying degrees on large populations of flying foxes for propagation. These plants, in addition to their many ecological contributions, produce some 448 economically valuable products. The fact that flying foxes are increasingly threatened, and that few baseline data exist on population trends is cause for concern. Many appear to be in severe decline, and several species are already extinct. We present initial observations on flying fox importance and survival threats in hopes of highlighting research and conservation needs.*

Resumen: *Los murciélagos frugivoros de la familia pteropodidae son animales de una importancia ecológica y económica extraordinaria en los bosques tropicales del Viejo Mundo. Casi 200 especies tienen un papel esencial como agentes polinizadores y dispersores de semillas, pero frecuentemente no se tiene una idea clara de su importancia, se los persigue intensamente, y corren un alto riesgo de extinción. Su papel en la propagación de numerosas plantas importantes casi no ha sido investigado. Sin embargo, nuestra revisión de la literatura ya publicada demuestra que por lo menos 289 especies de plantas dependen, en medida variable, de grandes poblaciones de murciélagos frugivoros para su propagación. Estas plantas, además de sus muchas contribuciones ecológicas, producen unos 448 productos de valor económico. Debe causar preocupación el hecho de que los murciélagos frugivoros están cada vez más amenazados, y que existen pocos datos de base sobre las tendencias poblacionales. Muchos aparentemente ya están disminuyendo drásticamente y varias especies ya son sido extintas. Presentamos observaciones iniciales sobre la importancia de los murciélagos frugivoros y las amenazas a su supervivencia, con la esperanza de destacar la necesidad de la investigación y la conservación.*

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Paper submitted April 20, 1989; revised manuscript accepted March 31, 1991.

Introduction

Flying foxes play a key role in tropical forests throughout the Old World and are essential to local economies valued in the millions of dollars annually. Yet these bats suffer from a generally poor public image and a lack of information documenting their values and status. Several species are already extinct, and many more are in serious jeopardy.

There are nearly 200 species of pteropodid bats. Historically, they were the most conspicuous and numerous medium-sized mammals throughout much of the Old World tropics. Single colonies included over a million individuals. Flying foxes remain relatively conspicuous in some areas, but many current populations are only a small fraction of their former size. All flying foxes feed primarily on a combination of fruit, nectar, and pollen, and many species are large, having wingspans of a meter, some nearly two. They frequently are sold as a luxury food item in commercial trade, hunted for sport and food, or killed by farmers protecting their orchards. Large roosting camps are easily found and highly vulnerable to humans. Most flying foxes remain unstudied or monitored, and many are in rapid decline.

The challenge we wish to address is how to enhance conservation efforts for flying foxes in the face of popular "blacklisting" and a shortage of information. We believe that the problem can be most effectively addressed in the short term by stressing their importance to tropical ecosystems and human economies. In this paper, we document the role of flying foxes in plant propagation. We emphasize food and commercial products derived from plants that depend on these bats to varying degrees, the economic value of bat-dependent products in several markets, and the threat to pteropodids from hunting and pest control.

We stress that the already documented ecological and economic values we present are only the proverbial "tip of the iceberg," since most interactions between these bats and plants have not yet been investigated. We hope that the information presented will be used to publicize the need for basic research and conservation measures.

Methods and Results

Bats and Plants

Botanical and zoological literature were reviewed to identify paleotropical plant species visited by pteropodid bats for fruit, nectar, or pollen. Only observations from primary references that reported direct feeding observations and identified plants to the species level were used, to enable identification of plant products. Marshall (1985) conducted a similar survey but identified bat-plant interactions only to the generic level. Our list is more circumscribed than his but permits economic extrapolations.

Most observations reviewed do not detail the extent to which a plant species relies on bats, thought it is clear that many may be highly dependent (e.g., Start 1972; Gould 1978; Faegri & van der Pijl 1979; Kress 1985; Elmqvist et al., in press).

Economic botanical literature was reviewed to identify products derived from these plants and to determine the extent of their use in domestic and export trade. Four primary references (Corner 1952; Burkill 1966; Corner & Watanabe 1969; Brouk 1975) were consulted to record the uses and economic importance of plant products. These references, though somewhat dated, are among the most comprehensive compendiums currently available for tropical ethnobotany in Southeast Asia and Africa. To obtain updated information, questionnaires accompanying the list of plant products compiled from these references were sent to appropriate specialists, or interviews were conducted. Their responses indicated that, in general, information in the primary references was accurate.

Products were classified into the following categories: fruits, drinks, foods, ornamentals, timber, fibers, tannins, dyes, medicinals, animal fodder, fuel, and other. Some plant species produce more than one product.

Market surveys conducted by Fujita included interviews with 55 vendors in 17 local markets in Malaysia, Indonesia, and Singapore; they were used to further assess the economic value of bat-plant products in domestic trade. Southeast Asia was chosen for on-site surveys because of the area's prominence in existing literature, not because bat-plant products are necessarily more important there. The surveys were conducted in June, July, and August, 1987, a period that corresponds to the peak fruiting season for the area (P. Ashton, personal communication). Because some plant species peak outside this period, and because fruiting seasons can vary significantly across the region, many plant products may have been missed entirely.

Table 1 summarizes current knowledge of the extent to which 59 plant families rely on flying foxes for pollination or seed dispersal. Nearly equal numbers of plant species were visited for nectar or pollen (141) and fruit (145). Just 12 were visited for both fruit and flowers. Some 448 products were found to be derived from 186 plant species.

In our list, the largest number of plant species utilized for fruit are in the family Moraceae (39), and the majority of those belong to the genus *Ficus*. Other families that were observed to be visited by pteropodids primarily for fruit include Anacardiaceae (7), Annonaceae (5), Ebenaceae (6), Guttiferae (5), Meliaceae (5), and Sapotaceae (8).

Plant species most strongly represented among those reliant on bats for pollination belong to the families Myrtaceae (59), Bignoneaceae (9), Bombacaceae (5), Leguminosae (12), Musaceae (4), Proteaceae (6), and Son-

Table 1. Number of plant species visited by pteropodid bats, and the products derived from 186 of these plant species. FL = number of species visited for flower resources, FR = number of species visited for fruits, LV = number of species visited for leaves, FL + FR = number of species visited for flower and fruit resources, TOT # SPP = total number of plant species within plant family visited by bats. Types and number of different products derived from plants visited by bats: DR = drinks, DY = dyes, FI = fiber, FD = animal fodder, FO = cooked foods, FR = fresh table fruits, FU = fuel wood, ME = medicines, OR = ornamental plants, OT = other types of products, TA = tannins, TI = timber and other wood products, TOT # PRO = total number of products derived from plants visited by bats within plant family.
A complete list of plant and bat species, observation locations, specific bat-plant interactions, plant products and uses, and full references can be obtained from Bat Conservation International, P.O. Box 162603, Austin, Texas, 78716, U.S.A.

Plant family	*FL*	*FR*	*FL + FR*	*LV*	*TOT # SPP*	*DR*	*DY*	*FI*	*FD*	*FO*	*FR*	*FU*	*ME*	*OR*	*OT*	*TA*	*TI*	*TOT # PRO*
Agavaceae	4				4			3	1	1			1	3	1			10
Anacardiaceae	1	7	1		7	3	3		1	4	3	1	5		3	2	2	27
Annonaceae		5			5	1	1	1			2		2	1	2	1	1	12
Apocynaceae	1	3			4					1			1		1		2	5
Bignoniaceae	9				9	1	1			2			5	2	3	1	5	20
Bombacaceae	5				5	1	2	3	2	4	1		4	1	3	1	4	26
Bromeliaceae		1			1													0
Burseraceae		1			1					1				1	2		1	5
Caricaceae		1			1					1	1		1		1			4
Casuarinaceae	1				1												1	1
Celastracaceae		1			1													0
Chrysobalanaceae	2	1			3	1	1			2			1			1	2	8
Combretaceae	1	1	1		1					1			1		1	1	1	5
Convolvulaceae	1				1													0
Cycadaceae		1			1					1			1					2
Ebenaceae		6			6		1				2		2		2	1	3	11
Eleaocarpaceae	1	1			2													0
Euphorbiaceae		2			2		1						1		1	1		4
Flacourtiaceae		1			1													0
Gramineae		1			1													0
Guttiferae	2	5	1		6		1			1		1	2	1	2		4	12
Heliconiaceae	1				1													0
Hernaniaceae		1			1								1					1
Irvingeaceae		1			1					1							1	2
Lauraceae	1	1			2					1								1
Lecythidaceae	3				3			1			1		1		1		1	5
Leguminosae	12	2		1	15	1	2	1	3	7		1	7	4	3	2	7	38
Liliaceae	1				1								1					1
Loganiaceae	1	1			2													0
Loranthacaceae	1				1													0
Meliaceae	1	5			6					2	1	1	3	3	2		4	16
Moraceae		39			39		2	6	2	10	3		9	9	12		5	58
Musaceae	4	2	1		6			3		2	1							6
Myrtaceae	59	9	5		70		1			4	5	1	4			2	45	62
Olacaceae		1			1													0
Oleaceae		1			1													0
Palmae	3	3		1	6	2	2	3		2		1	2		1	1	2	16
Pandanaceae	5				5			1			1		1		1		1	5
Passifloraceae		5			5	1				1	3		2		1			8
Proteaceae	6				6									1			1	2
Rhamnaceae		1			1													0
Rhizophoraceae	1	1			2													0
Rosaceae	1	5			5	1				2	2		1					6
Rubiaceae	2	4		1	5		1		1	1			2	1	2		3	11
Rutaceae		1			1						1							1
Salicaceae				1	1													0
Sapindaceae	1	5			6	1				2	3		2		1		2	11
Sapotaceae	2	8	1		10	1	2			2	1	1	1		3	1	3	15
Solanaceae		5			5					3			2					5
Sonneratiaceae	5				5					2	3	1	1		1	2	2	12
Sterculiaceae				1	1					1			1					2
Strelitziaceae	1				1			1		1				1				3
Theacaceae		1			1													0
Tiliaceae	1		1		2												1	1
Ulmaceae	1	1			2													0
Urticaceae		2	1		3	1		1		1	1						1	5
Verbenaceae		1			1								1					1
Vitaceae		1			1													0
Zygophyllaceae		1			1						1				1			2
TOTAL	141	146	12	5	289	15	21	24	10	64	36	8	69	28	51	17	105	448

neratiaceae (5). Flowers of many species in these families are characterized by having numerous stamens (e.g., Leguminosae, Myrtaceae, Sonneratiaceae), by having large and sturdy blooms (e.g., Bignoneaceae, Bombacaceae), and by blooming nocturnally.

One hundred and five (23% of all products) of the bat trees identified are harvested for timber production or small wood products (Table 1), primarily from wild stands. Twelve of these are of major importance in Malaysia, one of the largest timber exporters in the world. Export values were available from the Malaysian Timber Board for just one of these. The sawn timber export value of *Palaguium* spp. (Sapotaceae), whose seeds are dispersed by small pteropodid bats of the genus *Cynopterus*, was more than $5 million (U.S.) in 1985. Other important timber species that rely on bats, but for which global export values were not found, include *Diospyros melanoxylon* (Coromandel ebony), *Calophyllum inophyllum* (Borneo mahogany), *Chlorophora excelsa* (African iroko), *Castanospermum australe* (Australian black bean), and at least nine species of Australian *Eucalyptus*. The last-mentioned are used extensively in Australia for cabinetry and export (Ratcliffe 1931; Boland et al. 1984).

Medicinals accounted for 15% of all products (Table 1). The documented local uses include emetics (e.g., *Trichelia roka*), astringents (e.g., *Terminalia catappa*), and poisons and antidotes (e.g., *Antidesma bunias, Herndandia peltata*). The value of these medicinals and the extent to which they are currently used was not determined in this study. However, it is of note that of the broad array of 33 plant families that yield medicinal products, the most strongly represented (Anacardiaceae, Bignoniaceae, Bombacaceae, Leguminosae, and Moraceae) are also among those that bats frequently visit for fruit or flowers.

Food, drink, and fresh fruit products represent approximately 19% of the total products documented (Table 1). Some of these (e.g., *Butyrospermum parkii, Madhuca latifolia, Mangifera indica, Annona squamosa,* and *Durio zibethinus*) have significant economic importance in export markets. The majority are of local value; their uses include oils for cooking, masticatories, famine foods, and water sources.

Of the 24 fiber products identified in Table 1, fiber produced from the kapok tree (*Ceiba pentandra*) is of particular interest. This species now grows in nearly all tropical regions and is pollinated by a wide variety of pteropodid bats in the Old World (Marshall & McWilliam 1982) and by phyllostomid bats in the New World (Gardner 1977). Even cultivated trees are visited by bats. According to the Indonesian Bureau of Statistics (1986), fiber exports from Indonesian plantations alone earn $4.5 million (U.S.) and oil produced from seeds account for $500,000 (U.S.) annually.

A single plant species can produce a variety of different products. For example, in Southeast Asia the young leaves and flowers of the midnight horror tree (*Oroxylum indicum*) are cooked and eaten as a vegetable; the bark, roots, seeds, and leaves are used medicinally, and the pods and bark are used to produce a black dye used in basket-making (Corner 1952; Burkill 1966; van Steenis 1977). This plant is commonly found in Malaysian and Indonesian villages and is pollinated by medium-sized pteropodid bats (Start 1974; Gould 1978; Fujita, personal observation). *Pandanus tectorius* is a plant common on many Pacific islands and its primary seed dispersers are large flying foxes. Its leaves are traditionally used for weaving cloth, baskets, mats, and canoe sails. People also eat the large seeds (G. Wiles, personal communication). In Africa, the bat-pollinated shea butter tree (*Butyrospermum parkii*) produces seeds (shae nuts) that yield oil which is locally important in West Africa in cooking and making soap. The oil is also refined and exported for use in making margarine, ointments, soap, candles, and cosmetics. The tree itself is used locally as a source of fuel, timber, and charcoal (Hutchinson & Dalziel 1954–1972; Burkill 1966; Purseglove 1968; Brouk 1975).

Many of the products itemized in Table 1 are important to local economies where records seldom document their full economic values. Two such items of special significance in Southeast Asia are durian (Bombacaceae, *Durio zibethinus*) and petai (Leguminosae, *Parkia speciosa* and *P. javanica*). They were found in all markets surveyed and depend primarily on small pteropodid bats for pollination (Start & Marshall 1976). Bats visit both wild and cultivated trees and are especially important for fruit set, since mechanical or hand pollination is not efficient.

During the two- to three-month fruiting season for petai and durian, many vendors sell these products exclusively because they are popular and can command higher prices than other local produce. For example, a durian weighing about one kilo can be sold for as much as $5 (U.S.) in Malaysia. A vendor selling an average of 50 durian a day can make a substantial profit even after middlemen have been paid.

In Indonesia and Malaysia, petai seeds are eaten as a vegetable and are also highly valued for their garliclike flavor. Bunches of five pods sell for $0.50 to $1.00 (U.S.), and a vendor can sell as many as 100 bunches per day.

Mangrove charcoal, another locally important bat-plant product, is produced from trees of the families Rhizophoraceae and Sonneratiaceae, both families are important components of mangrove forests. The aseasonal, nocturnally blooming flowers of *Sonneratia* spp. are pollinated by several small pteropodid species and comprise an important part of their diet (Start 1974). The economic value of mangrove charcoal was not quantified, but the many kilns found along the coastal areas of Malaysia attest to its importance as a fuel source.

The values of products such as dyes, gums, lacquers, and tannins, which are finished materials derived from raw bat-plant sources, were not quantified because there was insufficient time to trace them through the various production processes in which they are used. Other bat plants are commonly planted as ornamentals and shade trees and are similarly difficult to quantify.

Observations on Bat Hunting

During this study, 12 market vendors, 6 plantation owners, 6 wildlife managers, and 4 professional bat hunters in Malaysia and Indonesia were interviewed to estimate the extent of bat trade, the intensity of pest control efforts, and the impact of these activities on target species.

Based on hunter descriptions of size, weight, and coloring, the flying foxes most commonly hunted are *Pteropus vampyrus* and *P. hypomelanus* ("Kalong" in the Indo-Malay language). These are the largest and most widespread species in the area and are easily identified by distinctive differences in size and color.

Market vendors prefer live bats, and the most common capture technique, especially among Iban hunters in Sarawak, is to net them. Large, fine-mesh nets are strung over waterways or around or above fruiting trees. Up to 200 bats can be netted at an especially good site in an evening. A less commonly used method employs a rope up to 300 m long, strung between bamboo poles above flowering or fruiting trees. Large metal fishing hooks are tied to vertical lines at 30 cm intervals, and bats are hooked and caught alive as they fly around a tree. The method is inexpensive, and up to 30 bats can be caught in an evening at a good site. Hooked bats sell for less than netted bats, because their wounds prevent them from being kept alive as long.

During fruiting and flowering seasons, many plantation owners employ bounty hunters to eradicate bats from their plantations. Bounty hunters receive as much as $3 U.S. per bat, and as many as 100 per night could be taken from a single plantation during peak fruiting or flowering. Although other animals (e.g., squirrels [*Ratufa* spp.], macaques [*Macaca nemstrina*], musong [*Arctitis binturong*], deer [*Cervus timorensis*], and wild pigs [*Sus barbatus*]) were often cited as being more destructive, bats were killed in disproportionately large numbers.

A professional hunter employed by Sabah Softwoods (a 32,000 ha plantation near Tawau, Sabah) reported purchasing 2000 rounds of ammunition in 1983 for "sport shooting" large flying foxes that were attracted to the flowers of *Eucalyptus deglupta*, a plantation species. The hunter reported that thousands of bats were killed annually during the 1983 and 1984 seasons, but numbers of bats were greatly reduced by 1985, and very few had been seen since.

A professional hunter in Kota Baru, Malaysia, reported that he had hunted bats in the area since 1964 and often had organized special hunts for others. He located diurnal roosts by taking compass readings on groups of bats returning to roosts at sunrise. Most could be found within a few days, usually located in hilly areas, in mangroves on the coast, or on small islands. Colonies contained an estimated 10,000 to 15,000 large flying foxes each, and 100 to 200 would be shot per hunt by a group of hunters "for personal consumption." Although he also shot bats at night in fruiting orchards, success was much higher when shooting at diurnal roosts.

Most Malaysians and Indonesians are Moslem and are thus not permitted to eat bats. However, a large trade in bat meat exists in the Chinese and Manadonese communities. During this study, vendors specializing in *Pteropus vampyrus* were found in the main wild animal markets in Jakarta, Kuala Lumpur, and Kuching, but not in Singapore. In Malaysia, bats sold for $2.50 to $3.30 (U.S.), and most vendors reported sales of 200 to 300 each per season. One vendor in Kuching, Sarawak, reported selling 150 to 200 bats weekly throughout the year. His bats were purchased from Iban hunters in the area. Chinese customers believed bat meat to be good for asthma, kidney ailments, and malaise.

In Jakarta, a Manadonese restaurant owner reported selling up to 2000 flying foxes in a good season. She claimed to be the main distributor for the area and purchased live bats from coastal villages in West Java and the Surabaya area of East Java. In the large Pasar Burung (bird market) in Jakarta, *P. vampyrus* was sold by at least two vendors for approximately $10 (U.S.) each. About five bats per vendor per week were sold, mostly for medicinal purposes. These bats were caught in East and West Java. Smaller pteropodids are eaten locally but are not generally sold in the markets.

Most hunters reported that *Pteropus* roosts are increasingly difficult to find. Hunters and vendors described a definite season of bat abundance that coincided with main fruiting peaks in the area. They also reported that many of the bats taken were pregnant or carrying young.

Discussion

Ecological and Economic Concerns

The decline of pteropodid bats raises serious ecological and economic concerns, especially when one considers their role as primary seed dispersers and pollinators throughout paleotropical forests (Start & Marshall 1976; Marshall 1983, 1985; Richards 1987). Long before a species declines to the point of endangered status, its numbers may become insufficient to service tropical forests and associated economies (Tuttle 1986).

A major reason for concern is that despite the importance of these animals, virtually no baseline population data or status monitoring exists for the vast majority of species. A complete assessment of decline and consequences is currently impossible, since the basic ecology of most species remains unstudied. Nonetheless, data documenting the role of flying foxes in pollination and seed dispersal has mounted, and it is now obvious that large populations are needed to ensure the maintenance and regeneration of paleotropical forest ecosystems.

The available chiropteran and botanical literature, though severely limited, does document varying degrees of pteropodid bat dependence for 289 plant species. One hundred eighty-six of these plant species are known to produce at least 448 products of value to humans.

Many of these plants have the diagnostic "bat syndrome" characteristics described by van der Pijl (1936) as indicative of a highly coadapted interaction between bat and plant species. In fact, some flowers are receptive for just a few hours on a single night and apparently are visited by only one species of bat (Kress 1985). Plant families especially exhibiting bat dependence characteristics, such as having numerous stamens or being large and sturdy and blooming at night, include the Leguminosae, Myrtaceae, Sonneratiaceae, Bignoneaceae, and Bombacaceae.

Although a few pteropodids are highly specialized for flower visitation, most feed extensively on both fruit and flowers (Marshall 1985). When feeding on fruit, they play a vital role in seed dispersal. Small pteropodid species can fly 38 km or more nightly in search of food (Start 1974), and the larger *Pteropus* spp. are known to fly much longer distances (Hall 1983; Fujita, personal observation). Because they defecate or drop large numbers of seeds in flight, pteropodid bats can therefore move seeds over longer distances and wider areas than any other rain-forest animals. In tropical forests of the Pacific Islands where there are high levels of plant endemism, flying foxes are often the only vertebrate seed dispersal and pollinating agents (Brautigam & Elmqvist 1990).

Seeds carried by pteropodid bats are especially important to forest regeneration in large manmade clearings where other forest animals seldom venture (Thomas 1982). In West Africa, Thomas found that bats flying over clearings dropped 90–98 percent of the first seeds of woody plants, and he concluded that these seeds have massive potential for forest regeneration. Similar bat importance is well documented for neotropical forests as well (Huber 1910; Fleming & Heithaus 1981; de Foresta et al. 1984; Charles-Dominique 1986; Foster et al. 1986; Fleming 1988).

Plant families especially reliant on pteropodid bats for seed dispersal include the Anacardiaceae, Annonaceae, Ebenaceae, Moraceae, Myrtaceae, and Sapotaceae. Even among plants whose fruits are eaten by many animals, bats still can be highly important. For example, figs (Moraceae) serve as a staple food source for a wide variety of animals (Terborgh 1986), but bats often are the primary dispersal agents (Janzen 1978; Morrison 1978; August 1981; Thomas 1982).

Through pollination of highly dependent flowers and dispersal of seeds into forest gaps and clearings, tropical bats everywhere play an essential role in forest ecology. In this review we have emphasized the role of flying foxes in maintaining plants of economic importance simply because many of these bats are known to be in especially rapid decline and because economic considerations often are of greatest interest to government decision-makers.

Among the bat-dependent tree species identified in our review, 105 are harvested for timber and small wood products, including species of major importance in all areas investigated. The exact market values for most are difficult or impossible to assess, but many, such as the African iroko, are believed to be worth many millions of dollars (U.S.) annually. Mangroves (Rhizophoraceae and Sonneratiaceae) that rely on several pteropodid bats for pollination (Start 1974) are an important source of charcoal, but perhaps even more importantly provide vital habitat in support of coastal marine fisheries.

The role of flying foxes in the maintenance of key plants in local economies cannot be ignored. Durian fruit (*Durio*), for example, is considered to be the "king" of Southeast Asian fruits and sells for at least $120 million (U.S.) annually (Myers 1985). Petai (*Parkia*), in addition to being an important timber tree, produces seeds eaten as a vegetable that sell for $15 million (U.S.) annually in peninsular Malaysia alone (Ng 1980). Market surveys in Southeast Asia point to the importance of both of these products in local trade. Both plants are highly bat-dependent for pollination of their night-blooming flowers (Start 1974; Soepadmo & Eow 1976; Start & Marshall 1976; Gould 1978), and much of the harvest comes from wild or semiwild trees.

Many of the world's most important domesticated food staples, including bananas, plantain, breadfruit, and mangoes, continue to rely on flying foxes for their propagation in the wild. For example, bananas (*Musa* spp.) are one of the world's most important aseasonal fruits. Edible varieties are derived from only a few species, which are vegetatively propagated and do not require pollination to set fruit. However, their wild progenitors rely on natural pollinators and are used to prevent genetic erosion among cultivars (Sastrapradja 1975). Since small pteropodid bats (e.g., *Macroglossus, Eonycteris*) are the primary pollinators of most wild banana species (Nur 1976), their conservation is of great significance.

Many additional products we identified, for example *Pandanus* leaves used throughout the Pacific Islands for weaving baskets and mats, are of obviously great local or regional value, though no reliable sales figures are available. These range from fuel wood and fodder to food, drinks, medicines, dyes, fibers, tannins, and ornamentals.

Status and Decline of Flying Foxes

Although reports of spectacular evening flights containing hundreds of thousands or even a million or more flying foxes were once common throughout much of the paleotropics, few large colonies remain. Most have not been monitored, but there are now reports from many areas of extirpated or rapidly declining populations (e.g., Bruner & Pratt 1979; Hill 1979; Cheke & Dahl 1981; Cox 1983; Wiles 1987; Wiles et al. 1989). Even where flying foxes are not yet listed as endangered, current populations are sometimes only a small fraction of former numbers (Pierson 1984; Heaney & Heideman 1987; K. Koopman, personal communication), and six species are now thought to be extinct (*Aproteles bulmerae:* Flannery 1989; *Acerodon lucifer* and *Dobsonia chapmanii:* Heaney & Heideman 1987; *Pteropus subniger:* Moutou 1982; *P. tokudae:* Wiles 1987; *P. pilosus:* K. Koopman, personal communication).

Poorly targeted, often inappropriate pest control is one of the most important causes of flying fox decline. Most commercial fruit is harvested at a stage too green for normal flying fox consumption (Ratcliffe 1932; Tuttle 1984*a*), though locally heavy crop damage can occur, especially to stone fruits (Fleming & Robinson 1987), during droughts when natural foods are insufficient (Ratcliffe 1931; Loebel & Sanewski 1987). Many reports of crop damage are greatly exaggerated (Ratcliffe 1932; Constantine 1970; Tuttle 1984*a*; Makin & Mendelssohn 1985).

In plantations in East Africa (Tuttle 1984*a*) and in Southeast Asia (Fujita, personal observation) damage from other animals frequently was mistakenly blamed on pteropodid bats. Flying foxes often seem to be killed out of proportion to the problems they cause, while more serious pests are relatively ignored. In Papua New Guinea, J. Smith (personal communication) reported investigating a plantation owner's complaints only to conclude that his annual cost for shotgun shells to kill flying foxes exceeded the cost of crop damage. In Malaysia and Indonesia growers of rambutan (*Nephelium lappaceum*), langsat (*Lansium domesticum*), and water apples (*Eugenia aquea*) admitted that bats presented a problem for only a few days prior to harvest and that these problems could be largely avoided by simple protective measures, such as shining bright lamps or lighting small fires below fruiting trees. Their comments were surprising, given the number of bats shot each year. The problem is reminiscent of predator control in much of the western United States.

Major campaigns have exterminated large numbers of flying foxes, using methods ranging from bounty hunting (Duff et al. 1984) and poisoning (Constantine 1970; Makin & Mendelssohn 1985), to the use of flame throwers and bombs at their diurnal roosts (Ratcliffe 1931; Gee 1952; Hall & Richards 1987).

Hunter, plantation owner, and vendor reports that there is a definite season for flying fox hunting and control coincident with fruiting peaks, and that captured or shot bats often are pregnant or carrying young, are cause for added concern. Tropical bats frequently time lactation to fruiting peaks (Fleming et al. 1972; Wodzicki & Felten 1975) and increased hunting at that time would have an exceptionally negative impact on population stability.

On many Pacific and Indian Ocean islands and in Africa, large flying foxes additionally are threatened by overhunting for human food, causing major declines (e.g., Wodzicki & Felten 1975; Cheke & Dahl 1981; Cox 1983; Tuttle 1986; Wiles & Payne 1986; Wiles 1987; D. Thomas, personal communication). Our results indicate that similar problems exist in Southeast Asia. Smaller pteropodids that live in caves are also highly vulnerable, especially in Southeast (Tuttle 1984*b*; Heaney & Heideman 1987) and Austral Asia (Craven 1988; Flannery 1989).

Despite what appears to be a dramatic decline in many pteropodid species, only four are included on the 1986 IUCN Red List, and the six now thought to be extinct were not even listed as endangered prior to their demise. Massive indiscriminant killing of flying foxes in New South Wales and Queensland, Australia, was terminated in 1986 and 1990 respectively, though farmers still can obtain permits to deal with specific, documented orchard problems (L. Hall, personal communication).

Recently, the seven species most vulnerable to commercial hunting on Pacific Islands were listed in CITES Appendix I. Additionally, all members of the genus *Pteropus* and five species of the very similar genus *Acerodon* were listed in Appendix II (Brautigam & Elmqvist 1990). This legislation provides protection only from commercial trade across international boundaries, but combined with improved law enforcement on Guam, it is greatly reducing commercial trade among Pacific Islands (Wiles 1990). Unfortunately, legal protection remains nonexistent throughout most of the remaining paleotropical distribution of these animals.

Conclusions

Due to the multifaceted ecological and economic roles of pteropodid bats, especially in reforestation, their conservation and management must be considered an essential element of sustainable development planning for tropical forests. Because many flying fox populations are already reduced, probably below threshold levels for forest maintenance, and are considered pests without legal protection, immediate population monitoring, conservation planning, and further research to document their unique roles are urgently needed. We hope that our review of current knowledge will be used to effect positive changes in their public image and conservation status.

Acknowledgments

For logistical assistance in the field, we gratefully acknowledge Chuck Darsono and family, Kamil Oesman, Cecilia and Danny Chew, Ken Scriven, the Malaysian Nature Society, the Sarawak Nature Society, and Yayasan Indonesia Hijau. We thank Paul Robertson, Rod Fujita, Sharon Leathery, John Kress, Elizabeth Pierson, and John Francis for editorial assistance, and Andrew Teare, Alan Tipton, and Laurie Bingaman for computer assistance. Gary Wiles provided unpublished data on bat-plant interactions and plant products for the Pacific Islands. Funding for this project was provided by an anonymous donor, Bat Conservation International and World Wildlife Fund—U.S.

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