

Food Plants and Economic Importance of Flying Foxes on Pacific Islands

by

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Abstract. We reviewed the zoological and botanical literature to document the food plants of flying foxes (Chiroptera: Pteropodidae) on Pacific islands. Our list of known bat foods contains 84 species of plants from 41 families, with species from the Myrtaceae, Moraceae, Anacardiaceae, Leguminosae, and Pandanaceae most common. A similar review of the products obtained from these plants was also conducted to determine the economic effect of bat-plant interactions in the region. The three largest categories of products derived from bat-visited plants are timber and other items made from wood, medicinals, and fruits. Most products are used locally within traditional societies, making it difficult to place a monetary value on their worth. Further study on bat-plant interactions is needed to determine the extent to which the region's plants depend on pteropodids for seed dispersal or pollination.

Many species of flying foxes are threatened by destruction of their habitat, overexploitation for human food, and extermination as agricultural pests (Wiles and Payne 1986; Heaney and Heide- man 1987; Pierson and Rainey 1992; Wiles 1992; Fujita and Tuttle, unpublished manuscript). Unfortunately, conservation efforts are hampered by public misconceptions about bats and a basic lack of information on their distribution, abundance, and ecology.

The ecological importance of flying foxes as seed dispersers and pollinators for a vast number of paleotropical plant species is only now being recognized (Fujita and Tuttle, unpublished manuscript). However, these services also have important economic ramifications that may directly af-

fect local and world markets. Comparatively little is known of bat-plant interactions or their economic significance on Pacific islands. In this paper, we list the known food plants of pteropodids in the region, and we present information on products derived from these plants that are used by humans. We hope that this summary will help to stimulate further research on bat-plant interactions and their economic significance and to strengthen arguments for the conservation of flying foxes in Oceania.

We have limited this review geographically to include the islands in Micronesia northward to the Ogasawara Islands and those in the southern Pacific from the Solomons to New Caledonia and eastward. Eight genera and about 36 species of flying

foxes occur in this region (Nowak and Paradiso 1983), including about 23 species of *Pteropus*, 4 of *Nyctimene*, 3 of *Pteralopex*, 2 of *Melonycteris*, and a single species of *Dobsonia*, *Macroglossus*, *Notopteris*, and *Rousettus*.

Methods

We reviewed the zoological and botanical literature to identify the food plants of flying foxes in the tropical Pacific region. Only feeding observations that identified plants primarily to species level were taken from these references. A similar literature review was conducted to determine products derived from these plants and the extent of their use, both in trade and for noncommercial purposes (Safford 1905; Wilder 1931; Christopher 1935, 1938; Yuncker 1943; Degener 1949; Stone 1963, 1970; Sykes 1970; Haddock 1974; McMakin 1975; Lessa 1977; Moore and McMakin 1979). The plant taxonomy used in this paper largely follows Fosberg et al. (1979, 1987) and Smith (1979, 1981, 1985, 1988). We have updated a number of plant names from those given in the original references to reflect current taxonomic nomenclature.

Results

Bat Food Plants

Information on the food habits of flying foxes was obtained for 13 species of bats from 16 Pacific island groups (Table). However, of these, dietary information is reasonably extensive for only two species of *Pteropus* in several localities. These are *P. mariannus* in the Mariana Islands (Safford 1905, 1910; G. J. Wiles, personal observation; P. O. Glass, U.S. Fish and Wildlife Service, Houston, Texas, personal communication; E. M. Taisacan, Division of Fish and Wildlife, Department of Natural Resources, Rota, CNMI, personal communication) and Yap (Falanruw 1988), and *P. tonganus* in Niue (Wodzicki and Felten 1975) and the Cook Islands (Wodzicki and Felten 1980). Data on foods are lacking or anecdotal for the remaining pteropodid species in the region.

In general, fruit and flower resources from a broad range of plants are eaten. Our list of bat foods contains 69 genera and 84 species of plants, including 4 species identified to genus only, from 41 plant families (Table). Plant families most

strongly represented were Myrtaceae, Moraceae, Anacardiaceae, Leguminosae, and Pandanaceae. The plant parts consumed included the fruits of 65 species, the flowers of 35 species, the leaves of 5 species, and the sap of 1 species (Table). Dietary diversity in a single species of flying fox in one island group is best exemplified by *P. mariannus* in the Marianas, where 39 species of plants are known to be visited.

Flying foxes are attracted to many of the same species or genera of plants on different islands throughout the region. Taxa that are commonly selected include *Artocarpus*, *Carica papaya*, *Ceiba pentandra*, *Cocos nucifera*, *Eugenia*, *Ficus*, *Freycinetia*, *Inocarpus fagifer*, *Mangifera indica*, *Musa*, *Pandanus tectorius*, *Syzygium*, and *Terminalia catappa* (Table). Interestingly, many of these plants are cultivated by islanders or grow semiwild near human habitations. The predominance of species associated with people is probably related to several factors, among which are that humans and flying foxes share similar taste preferences in fruits (Marshall 1983; Tidemann and Nelson 1987) and that observers are more likely to encounter bats foraging near towns, villages, and family farming plots. Records of pteropodids feeding on native forest plants in the Pacific are much more limited and are probably greatly underrepresented in the literature.

Like pteropodids in other parts of the world (Marshall 1983), *Pteropus* on Pacific islands have been successful at exploiting a number of introduced plants as food sources that also attract bats in their native ranges. These include paleotropical species such as *Artocarpus altilis*, *Cananga odorata*, *Eugenia javanica*, *E. malaccensis*, *Mangifera indica*, some *Musa*, and some *Syzygium*, and neotropical plants such as *Agave*, *Annona*, *Carica papaya*, *Ceiba pentandra*, *Cestrum diurnum*, *Persea americana*, and *Psidium guajava* (Table).

Products from Bat Plants

A thorough analysis of the products obtained from bat-visited plants in Oceania is hindered by a sparse ethnobotanical literature, particularly for Melanesia and Fiji. Several of the references used here were based on field studies conducted before 1960; some of the recorded uses of plants may no longer be widely practiced as some island societies become increasingly modernized. With these limitations in mind, we documented a variety of products that are derived from plants that depend to varying degrees on flying foxes for seed dispersal

Table. *Known food plants of Pteropus and other flying foxes in the tropical Pacific region. Products that islanders derive from these plants are listed only for the island groups where this information is known.*

Plant	Bat	Food ^a	Location	References ^b	Products ^c
Agavaceae					
<i>Agave americana</i>	<i>Pteropus pselaphon</i>	fl	Ogasawara, Iwo	9	
<i>Agave rigida</i>	<i>Pteropus mariannus</i>	fl	Marianas	20	ornamental
Anacardiaceae					
<i>Camptosperma brevipetiolata</i>	<i>Pteropus mariannus</i>	fr	Yap	6	
<i>Dracontomelon</i> sp.	<i>Pteropus tonganus</i>	fr	Vanuatu	2	
<i>Mangifera indica</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	fruits eaten; sap used medicinally ^c
	<i>Pteropus mariannus</i>	fr	Palau	23	fruits eaten
	<i>Pteropus mariannus</i>	fr	Yap	6	fruits eaten
	<i>Pteropus ornatus</i>	fr	New Caledonia	19	
	<i>Pteropus tonganus</i>	fr	Cooks	26	fruits eaten
	<i>Pteropus tonganus</i>	fr	Niue	25	
	<i>Pteropus tonganus</i>	fr	Samoa	3	fruits eaten
<i>Semecarpus atra</i>	<i>Pteropus ornatus</i>	fr	New Caledonia	19	seeds eaten
<i>Semecarpus venenosus</i>	<i>Pteropus mariannus</i>	fr	Yap	6	
<i>Spondias dulcis</i>	<i>Pteropus</i> sp.	fr	Samoa	21	fruits eaten
Annonaceae					
<i>Annona muricata</i>	<i>Pteropus mariannus</i>	fr	Yap	6	fruits eaten
<i>Annona reticulata</i>	<i>Pteropus mariannus</i>	fr	Marianas	16	fruits eaten ^c
<i>Cananga odorata</i>	<i>Pteropus samoensis</i>	fl	Samoa	5	wood used to build canoes; flowers used to make leis and scent coconut oil
	<i>Pteropus tonganus</i>	fr	Cooks	26	flowers used in garlands and to scent coconut oil
	<i>Pteropus tonganus</i>	fl	Samoa	5	
Apocynaceae					
<i>Cerbera manghas</i>	<i>Pteropus tonganus</i>	fr	Cooks	26	fruits and flowers used medicinally
<i>Neisosperma oppositifolia</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	wood used for furniture ^c
	<i>Pteropus mariannus</i>	fr	Palau	23	
	<i>Pteropus mariannus</i>	fr	Ulithi	24	seeds eaten rarely; wood used for canoes, houses, and firewood; medicinal uses
	<i>Pteropus tonganus</i>	fr	Niue	25	wood used for houses and weapons ^c ; branches carved into nose flutes
<i>Ochrosia mariannensis</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	
Araliaceae					
<i>Osmoxylon mariannensis</i>	<i>Pteropus mariannus</i>	fr	Marianas	20	
Arecaceae (Palmae)					
<i>Clinostigma ponapensis</i>	<i>Pteropus molossinus</i>	fr	Pohnpei	10	
<i>Cocos nucifera</i>	<i>Pteralopex atrata</i>	fr	Solomons	18	numerous uses among Pacific islanders (see text)
	<i>Pteropus insularis</i>	fl	Chuuk (Truk)	22	
	<i>Pteropus mahaganus</i>	fr	Solomons	18	
	<i>Pteropus mariannus</i>	fl	Marianas	22	
	<i>Pteropus mariannus</i>	sap	Ulithi	24	
	<i>Pteropus mariannus</i>	?	Yap	6	
	<i>Pteropus molossinus</i>	fl	Pohnpei	22	
	<i>Pteropus ornatus</i>	fl	New Caledonia	19	
	<i>Pteropus tonganus</i>	fl	Cooks	26	
	<i>Pteropus tonganus</i>	fl	Samoa	5	
	<i>Pteropus woodfordi</i>	fr, fl	Solomons	13, 18	

Table. Continued.

Plant	Bat	Food ^a	Location	References ^b	Products ^c
<i>Gulubia palauensis</i>	<i>Pteropus mariannus</i>	fl	Palau	23	
Bombacaceae					
<i>Ceiba pentandra</i>	<i>Pteropus mariannus</i>	fl	Marianas	7, 22	fruit fibers used as stuffing ^c
	<i>Pteropus mariannus</i>	fl	Yap	6	fruit fibers used as stuffing
	<i>Pteropus molossinus</i>	fl	Pohnpei	10	
	<i>Pteropus samoensis</i>	fl	Samoa	3, 5	fruit fibers used as stuffing
	<i>Pteropus tonganus</i>	fl	Cooks	26	fruit fibers used as stuffing
	<i>Pteropus tonganus</i>	fl	Niue	25	fruit fibers used as stuffing
	<i>Pteropus tonganus</i>	fl	Samoa	3, 5	
Caricaceae					
<i>Carica papaya</i>	<i>Pteropus mariannus</i>	fr	Marianas	7, 22	fruits eaten
	<i>Pteropus mariannus</i>	fr	Yap	6	fruits eaten
	<i>Pteropus ornatus</i>	fr	New Caledonia	19	
	<i>Pteropus samoensis</i>	fr	Samoa	3	fruits eaten; bark used medicinally
	<i>Pteropus tonganus</i>	fr	Cooks	26	
	<i>Pteropus tonganus</i>	fr	Samoa	3	
	<i>Pteropus tonganus</i>	fr	Vanuatu	2	
Casuarinaceae					
<i>Casuarina equisetifolia</i>	<i>Pteropus mariannus</i>	fl	Marianas	22	lumber; firewood
Chrysobalanaceae					
<i>Parinari</i> sp.	<i>Pteropus mariannus</i>	fl	Yap	6	
Combretaceae					
<i>Terminalia catappa</i>	<i>Pteropus mariannus</i>	fr, fl	Marianas	22	seeds eaten ^c ; wood used for small utensils ^c
	<i>Pteropus mariannus</i>	fr	Palau	23	
	<i>Pteropus mariannus</i>	fr	Yap	6	seeds eaten
	<i>Pteropus tonganus</i>	fr	Cooks	26	wood used for domestic utensils
	<i>Pteropus tonganus</i>	fr	Vanuatu	2	
<i>Lumnitzera littorea</i>	<i>Pteropus mariannus</i>	fl	Yap	6	
Cunoniaceae					
<i>Geissois ternata</i>	unidentified pteropodid	fl	Fiji	8	wood used to build homes
Cycadaceae					
<i>Cycas circinalis</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	seeds used to make flour ^c ; seeds and bracts used medicinally ^c
	<i>Pteropus mariannus</i>	fr	Palau	23	
Ebenaceae					
<i>Diospyros samoensis</i>	<i>Pteropus tonganus</i>	fr	Niue	25	fruits used as a fish poison; wood used for weapons ^c
Elaeocarpaceae					
<i>Elaeocarpus joga</i>	<i>Pteropus mariannus</i>	fr, fl	Marianas	7, 17	lumber ^c
<i>Elaeocarpus augustifolius</i>	<i>Pteropus ornatus</i>	fr	New Caledonia	19	
<i>Elaeocarpus rarotongensis</i>	<i>Pteropus tonganus</i>	fl	Cooks	26	
Ericaceae					
<i>Vaccinium</i> sp.	<i>Pteropus anetianus</i>	fr	Vanuatu	1	
Euphorbiaceae					
<i>Glochidion ramiflora</i>	<i>Pteropus tonganus</i>	?	Vanuatu	2	
<i>Glochidion</i> sp.	<i>Pteropus mariannus</i>	fl	Yap	6	
Gentianaceae (Loganiaceae)					

Table. Continued.

Plant	Bat	Food ^a	Location	References ^b	Products ^c
<i>Fagraea berteriana</i>	<i>Pteropus mariannus</i> <i>Pteropus tonganus</i>	fl fr	Marianas Cooks	7 26	
Guttiferae (Clusiaceae)					
<i>Calophyllum inophyllum</i>	<i>Pteropus mariannus</i> <i>Pteropus mariannus</i>	fr fr	Marianas Ulithi	22 24	lumber ^c wood used for tools and canoes; medicinal and ceremonial uses; other minor uses
	<i>Pteropus mariannus</i> <i>Pteropus tonganus</i>	fr, fl fr	Yap Samoa	6 5	wood used for houses, canoes, and utensils; seeds, leaves, sap, and bark used medicinally
<i>Mammea odorata</i>	<i>Pteropus mariannus</i>	fr, fl	Marianas	7, 22	wood used for houses ^c and as a dye ^c
Heliconiaceae					
<i>Heliconia solomonensis</i>	<i>Melonycteris woodfordi</i>	fl	Solomons	12	
Hernandiaceae					
<i>Hernandia sonora</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	lumber ^c ; firewood ^c ; leaves, bark, and seeds used medicinally ^c
Icacinaceae					
<i>Merrilliodendron megacarpum</i>	<i>Pteropus mariannus</i>	fr	Marianas	20	
Lauraceae					
<i>Persea americana</i>	<i>Pteropus mariannus</i> <i>Pteropus tonganus</i>	fr, fl fr	Marianas Cooks	7 26	fruits eaten
Lecythidaceae					
<i>Barringtonia asiatica</i>	<i>Pteropus mariannus</i>	fl	Marianas	7	seeds used as a fish poison ^c ; fruit and bark used medicinally ^c
Leguminosae (Caesalpiniaceae and Fabaceae)					
<i>Cynometra ramiflora</i>	<i>Pteropus mariannus</i>	lv	Marianas	20	
<i>Erythrina variegata</i>	<i>Pteropus mariannus</i>	fl	Marianas	7, 22	ornamental; lumber ^c ; leaves used medicinally ^c
<i>Inocarpus fagifer</i>	<i>Pteropus mariannus</i> <i>Pteropus tonganus</i>	fr fr	Yap Cooks	6 26	seeds eaten fruits are an important food source (? ^c); seeds eaten
	<i>Pteropus tonganus</i>	fr	Niue	25	seeds eaten; wood used; leaves used medicinally
<i>Intsia bijuga</i>	<i>Pteropus mariannus</i>	fl	Palau	23	
<i>Mucuna gigantea</i>	<i>Pteropus mariannus</i>	fl	Marianas	7, 22	leaves used medicinally ^c
Meliaceae					
<i>Aglaiia mariannensis</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	wood used for small objects ^c
<i>Dysoxylum moata</i>	<i>Pteropus samoensis</i>	fr	Samoa	3	
Melastomataceae					
<i>Melastoma denticulatum</i>	<i>Pteropus</i> sp.	fr	Fiji	4	leaves used medicinally
Moraceae					
<i>Artocarpus altilis</i>	<i>Pteropus mariannus</i>	fr	Marianas	7, 22	fruits eaten; wood used for houses and canoes ^c ; bark used to make cloth ^c ; sap used medicinally ^c , as a caulk ^c , and to make paint ^c

Table. Continued.

Plant	Bat	Food ^a	Location	References ^b	Products ^c
	<i>Pteropus mariannus</i>	fr, lv	Ulithi	24	staple food; wood used for canoe parts and houses; other minor uses
	<i>Pteropus mariannus</i>	fr	Yap	6	staple food
	<i>Pteropus samoensis</i>	fr	Samoa	5	staple food; wood used for houses; fruit paste used as a caulk
	<i>Pteropus tonganus</i>	fr	Cooks	26	staple food
	<i>Pteropus tonganus</i>	fr	New Caledonia	15	
	<i>Pteropus tonganus</i>	fr	Niue	25	fruits eaten
	<i>Pteropus tonganus</i>	fr	Samoa	3, 5	
<i>Artocarpus heterophyllus</i>	<i>Pteropus mariannus</i>	fr	Yap	6	fruits eaten
	<i>Pteropus tonganus</i>	fr	Cooks	26	seeds eaten
<i>Artocarpus mariannensis</i>	<i>Pteropus mariannus</i>	fr, lv	Marianas	7, 22	fruits and seeds eaten, ^c lumber ^c
	<i>Pteropus mariannus</i>	lv	Palau	23	
<i>Artocarpus</i> sp.	<i>Pteropus tonganus</i>	fr	Vanuatu	1, 2	
<i>Ficus copiosa</i>	<i>Pteropus tonganus</i>	fr	Vanuatu	2	
<i>Ficus prolixa</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	sap used medicinally ^c ; tree is culturally significant for Chamorros
	<i>Pteropus mariannus</i>	fr	Ulithi	24	leaves used medicinally; aerial roots used as lashings
	<i>Pteropus mariannus</i>	fr	Yap	6	
	<i>Pteropus tonganus</i>	fr	Cooks	26	bark used to make cloth and fiber
	<i>Pteropus tonganus</i>	fr	Niue	25	bark used to make tapa cloth; aerial roots used as cordage
<i>Ficus tinctoria</i>	<i>Pteropus mariannus</i>	fr	Marianas	7	firewood ^c
<i>Ficus</i> sp.	<i>Pteropus anetianus</i>	fr	Vanuatu	14	
	<i>Pteropus mariannus</i>	fr	Marianas	7, 22	
	<i>Pteropus mariannus</i>	fr	Palau	23	
	<i>Pteropus mariannus</i>	fr	Yap	6	
	<i>Pteropus samoensis</i>	fr	Samoa	3	
	<i>Pteropus tonganus</i>	fr	Vanuatu	14	
Musaceae					
<i>Musa nana</i>	<i>Pteropus tonganus</i>	fr	Niue	25	fruits eaten; a minor export
<i>Musa paradisiaca</i>	<i>Pteropus tonganus</i>	fr	Niue	25	fruits eaten; a minor export
<i>Musa</i> sp.	<i>Notopteris macdonaldi</i>	fl	Vanuatu	14	fruits eaten
	<i>Pteropus mariannus</i>	fr	Marianas	22	fruits eaten; fruits made into flour ^c
	<i>Pteropus mariannus</i>	fr, fl	Ulithi	24	fruits eaten; fiber used to make cloth; medicinal uses
	<i>Pteropus mariannus</i>	fr	Yap	6	fruits eaten
	<i>Pteropus ornatus</i>	fr	New Caledonia	19	fruits eaten
	<i>Pteropus tonganus</i>	fr	Cooks	26	fruits eaten
	<i>Pteropus tonganus</i>	fr, fl	Samoa	3, 5	fruits eaten; household uses
	<i>Pteropus tonganus</i>	fr	Vanuatu	2	
	<i>Pteropus</i> sp.	fr	Samoa	21	
Myrtaceae					
<i>Eugenia javanica</i>	<i>Pteropus mariannus</i>	fr	Ulithi	24	wood used for canoe parts, houses, and firewood; medicinal and ceremonial uses
	<i>Pteropus mariannus</i>	fr	Palau	23	
<i>Eugenia malaccensis</i>	<i>Pteropus tonganus</i>	fr, fl	Cooks	26	fruits eaten
	<i>Pteropus tonganus</i>	fl	Vanuatu	14	

Table. Continued.

Plant	Bat	Food ^a	Location	References ^b	Products ^c
	<i>Pteropus</i> sp.	fr	Samoa	21	fruits eaten
<i>Eugenia</i> sp.	<i>Pteropus mariannus</i>	fr	Yap	6	fruits eaten
<i>Melaleuca viridiflora</i>	<i>Pteropus ornatus</i>	fl	New Caledonia	19	
<i>Metrosideros villosa</i>	<i>Pteropus tonganus</i>	fl	Tonga	11	
<i>Psidium guajava</i>	<i>Pteropus mariannus</i>	fr	Marianas	16	fruits eaten ^c ; wood used for tools ^c and firewood ^c ; fruits and leaves used medicinally ^c
	<i>Pteropus ornatus</i>	fr	New Caledonia	19	
	<i>Pteropus tonganus</i>	fr	Cooks	26	
	<i>Pteropus tonganus</i>	fr	Vanuatu	2	
<i>Syzygium clusiifolium</i>	<i>Pteropus tonganus</i>	fr, fl	Niue	25	wood used for firewood
<i>Syzygium cumini</i>	<i>Pteropus tonganus</i>	fr	Cooks	26	
<i>Syzygium inophylloides</i>	<i>Pteropus tonganus</i>	fl	Niue	25	important timber tree; wood used for firewood
<i>Syzygium jambos</i>	<i>Pteropus tonganus</i>	fr	Samoa	3	
<i>Syzygium richii</i>	<i>Pteropus tonganus</i>	fr, fl	Niue	25	important timber tree
<i>Syzygium</i> sp.	<i>Pteropus anetianus</i>	fr	Vanuatu	14	
	<i>Pteropus ornatus</i>	fr	New Caledonia	19	
	<i>Pteropus tonganus</i>	fr	Vanuatu	14	
Pandanaceae					
<i>Freycinetia hombroonii</i>	<i>Pteropus</i> sp.	fr	Fiji	4	roots used to make rope
<i>Freycinetia reineckeii</i>	<i>Pteropus mariannus</i>	fr, fl	Marianas	7, 22	stems used as lashings ^c
	<i>Pteropus tonganus</i>	fl	Samoa	3	
<i>Freycinetia</i> sp.	<i>Pteropus mariannus</i>	fl	Yap	6	
<i>Pandanus tectorius</i>	<i>Pteropus mariannus</i>	fr, fl	Marianas	7, 22	numerous uses among Pacific islanders (see text)
	<i>Pteropus mariannus</i>	fr	Palau	23	
	<i>Pteropus mariannus</i>	fr	Ulithi	24	
	<i>Pteropus mariannus</i>	fr	Yap	6	
	<i>Pteropus tonganus</i>	fr, fl	Cooks	26	
<i>Pandanus</i> sp.	<i>Pteropus pselaphon</i>	fr	Ogasawara, Iwo	1, 9	
	<i>Pteropus tonganus</i>	fr	Niue	25	
Passifloraceae					
<i>Passiflora suberosa</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	
<i>Passiflora</i> sp.	<i>Pteropus ornatus</i>	fr	New Caledonia	19	
Piperaceae					
<i>Macropiper puberulum</i>	<i>Pteropus</i> sp.	fr	Fiji	4	leaves and bark used medicinally
Rubiaceae					
<i>Guettarda speciosa</i>	<i>Pteropus mariannus</i>	fl	Marianas	7	
	<i>Pteropus mariannus</i>	fr, lv	Ulithi	25	wood used for houses, paddles, and firewood; medicinal uses; flowers used in leis
Rutaceae					
<i>Citrus sinensis</i>	<i>Pteropus tonganus</i>	fr	Cooks	26	fruits eaten and exported
<i>Citrus</i> sp.	<i>Pteropus mariannus</i>	fr	Yap	6	fruits eaten
	<i>Pteropus</i> sp.	fr	Samoa	21	fruits eaten
Sapindaceae					
<i>Cupaniopsis samoensis</i>	<i>Pteropus samoensis</i>	fr	Samoa	3	
<i>Pometia pinnata</i>	<i>Pteropus tonganus</i>	fr	Niue	25	fruits eaten
<i>Tristiropsis obtusangula</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	lumber ^c
Sapotaceae					
<i>Manilkara</i> sp.	<i>Pteropus pselaphon</i>	fr	Ogasawara, Iwo	1	
<i>Planchonella torricellensis</i>	<i>Pteropus samoensis</i>	fr	Samoa	5	

Table. Continued.

Plant	Bat	Food ^a	Location	References ^b	Products ^c
	<i>Pteropus tonganus</i>	fl	Niue	25	lumber
	<i>Pteropus tonganus</i>	fr	Samoa	5	
Solanaceae					
<i>Cestrum diurnum</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	ornamental ^c
<i>Solanum lycopersicum</i>	<i>Pteropus tonganus</i>	fr	Niue	25	fruits eaten
Sonneratiaceae					
<i>Sonneratia alba</i>	<i>Pteropus mariannus</i>	fr;fl,lv	Yap	6	
Urticaceae					
<i>Dendrocnide latifolia</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	
<i>Pipturus argenteus</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	
Verbenaceae					
<i>Premna obtusifolia</i>	<i>Pteropus mariannus</i>	fr	Marianas	22	wood used for houses ^c ; leaves used medicinally ^c

^a Plant parts eaten include: fr: fruit; fl: flowers; lv: leaves; ?: not identified by author.

^b References: 1. Andersen (1912); 2. Baker and Baker (1936); 3. Cox (1983); 4. Degener (1949); 5. Engbring, unpublished manuscript; 6. Palanruw (1988); 7. P. O. Glass (personal communication); 8. Guppy (1906); 9. Imaizumi (1970); 10. Jackson (1962); 11. Jaeger (1954); 12. Kress (1985); 13. Lawrence (1945); 14. Medway and Marshall (1975); 15. Ridley (1930); 16. Safford (1905); 17. Safford (1910); 18. Sanborn (1931); 19. Sanborn and Nicholson (1950); 20. E. M. Taisacan (personal communication); 21. Whitmee (1874); 22. G. J. Wiles (personal observation); 23. Wiles and Conry (1990); 24. Wiles et al. (1991); 25. Wodzicki and Felten (1975); 26. Wodzicki and Felten (1980).

^c Denotes a plant product that is no longer widely used in the location given.

or pollination (Table). Most of these items are used locally within the region's traditional cultures. The placing of a monetary value on such products is impossible because these cultures are not strongly tied to a cash economy. We recorded 113 products; timber and other wood products (25 species), medicinals (22 species), and fruits (19 species) were the three largest categories (Table). Additional items were classified as fuels (11 species), other foods (9), cordage (4), household articles (3), fiber for cloth (3), ornamentals (3), thatching (2), fish poisons (2), personal adornments (2), and other products (8). A number of plants are used for more than one purpose, but two species, *Cocos nucifera* and *Pandanus tectorius*, are particularly valuable because of the large number of products obtained from them.

Flying foxes feed on the flowers of coconut palms (*Cocos nucifera*) on many islands (Table) and may assist in the pollination of this tree. Pacific islanders rely on this species for many vital products, including food, drink, oil, timber, thatching, mats, fuel, fiber, medicine, domestic utensils, animal fodder, and cooking ingredients (Safford 1905; Barrau 1961; Burkill 1966; Purseglove 1972; Lessa 1977). On a commercial basis, coconut products in the form of copra, coconut oil, desiccated coconut, copra meal cake, and fresh fruit are mod-

erately valuable exports for a number of Pacific island nations. Insects and wind are reported to be the main pollinators of coconut flowers (Burkill 1966; Purseglove 1972; Opeke 1982). However, because of the sizable number of records of pteropodids visiting the flowers (Table), we speculate that the value of nocturnal pollination by flying foxes, particularly the small nectivorous species, has perhaps been overlooked.

Pandanus tectorius, and perhaps other species of *Pandanus*, may rely heavily on flying foxes to disperse its large seeds on islands where both coexist (Wiles et al. 1991). On many islands, *Pandanus* is second only to the coconut palm in terms of utility to residents. The leaves are used as thatching and in making woven mats, baskets, and bags. The fruits are edible and are an important seasonal food on some Micronesian atolls (Miller et al. 1956). Other parts of the plant are used medicinally, as fuel, and for other purposes (Stone 1963). Handicrafts made of *Pandanus* leaves are produced in limited quantities on some islands and are sold locally to tourists or exported to commercial outlets on larger islands (Stone 1963; Sykes 1970; G. J. Wiles, personal observation).

Some other bat-visited plants have the potential to become important to the economies of Pacific islands, based on the value of the same species in

other areas of the world. For example, *Sonneratia alba*, which occurs in Melanesia and the Caroline Islands, is important in the wood chipping industry in tropical Asia. *Ceiba pentandra* also produces fibers and oil that are exported from the Asian region (Fujita and Tuttle, unpublished manuscript).

Discussion

Fujita and Tuttle (unpublished manuscript) reviewed the zoological literature and documented the foods of flying foxes throughout their distribution in the Old World. They recorded more than 300 plants from 59 families that were visited by bats for fruit, nectar, or pollen. Marshall (1985) also published an extensive list of known food plants for the Megachiroptera, although his identifications were limited to the generic level. Our list of food plants for flying foxes is the most complete thus far compiled for the Pacific region, with 84 species of plants recorded.

In the paleotropics, morphological similarities, or syndromes, exist among many of the food plants of pteropodids and point to the importance of bats as seed dispersal or pollination agents. A number of species, especially those in the families Moraceae, Anacardiaceae, Annonaceae, and Sapotaceae, produce fruits that appear, because of their size, color, odor, or exposed hanging position, to be adapted for dispersal by bats (van der Pijl 1957). Other species, particularly those in the Myrtaceae, Bignoniaceae, Bombacaceae, and Sapotaceae, exhibit flower morphologies and other traits that similarly suggest a strong coadaptation between the plant and bats (Faegri and van der Pijl 1979).

In this paper, we compiled the information necessary to illustrate that flying foxes can be economically important to humans on Pacific islands. However, the existing literature for this region, as for other parts of the world, is far from complete, and we can only estimate the value of the plants serviced by pteropodids.

Most Pacific economies are based on subsistence agriculture, and in general the region has few exportable crops. Timber and coconut products are the region's most important commodities that may be ecologically linked with flying foxes. The Solomon Islands, Fiji, Vanuatu, and Western Samoa are exporters of timber to Asia; however, we were unable to determine which tree species dominate the harvest or whether any of these are visited by bats. One quarter of the world's copra comes from

the Pacific, and on some islands, such as Pohnpei and Tonga, copra is the largest export item. Between 1986 and 1988, the annual income received from exported coconut products averaged U.S. \$8.7 million for Western Samoa, \$6.6 million for Vanuatu, \$5.3 million for the Solomons, and \$2.9 million for Fiji (Food and Agricultural Organization 1990). Handicrafts woven from *Pandanus* or carved from certain woods are another (much smaller) revenue earner that may be linked to bats.

Fujita and Tuttle (unpublished manuscript) identified a number of plant products that are more directly linked with flying foxes elsewhere and are commercially valuable in world markets. Mangrove species in the genus *Sonneratia*, which occur from coastal Southeast Asia to eastern Australia, are bat pollinated and are important in paper and wood chipping industries. Other bat-visited trees are among the most important timber species of the countries in which they occur, providing millions of dollars annually in exports. These include the Coromandel ebony (Ebenaceae: *Diospyros melanoxylon*), the Bornean mahogany (Guttiferae: *Calophyllum inophyllum*), several species of *Palaquium* (Sapotaceae) from Southeast Asia, the African iroko tree (Moraceae: *Chlorophora excelsa*), the Australian black bean (Leguminosae: *Castenospermum australe*), and at least nine species of Australian *Eucalyptus* (Myrtaceae; Dalziel 1937; Burkill 1966; Purseglove 1968; Boland et al. 1984).

Other plants serviced by pteropodids produce fruits that are exceptionally valuable as domestic and export products. In Southeast Asia, the durian (Bombacaceae: *Durio zibethinus*) has been estimated to be worth U.S. \$120 million annually in regional sales (Myers 1985). The durian market is now also expanding to the west and can be found in New York, Los Angeles, and Honolulu (M. S. Fujita, personal observation). In Malaysia, Indonesia, and especially Thailand, durian is increasingly cultivated on plantations, in addition to the harvesting of fruits from wild plants (M. S. Fujita, personal observation). All of these trees require natural pollinating agents, the most important of which are smaller flying foxes, to set fruit and maintain outcrossing (Soepadmo and Eow 1976).

Bananas, perhaps the most important fruit in the world, originated in Southeast Asia (Purseglove 1972). Only two species, *Musa nana* and *M. paradisiaca*, are cultivated on a large scale in the tropics, including most Pacific nations, for local use or as an export. Both of these domestic

varieties no longer depend on bats for pollination in order to set fruit because they are seedless and vegetatively propagated. However, most of the approximately 20 species of wild bananas still depend on pteropodids for pollination (Nur 1976). Wild species are important in maintaining the genetic vigor of domestic varieties. Thus, preservation of the wild ancestors and their pollinators is necessary to ensure the health and productivity of cultivars.

In the Pacific, where subsistence lifestyles are still prevalent, and the remainder of the paleotropics, most items derived from plants serviced by flying foxes are important primarily on a village or regional level (Fujita and Tuttle, unpublished manuscript). Many products are not necessarily sold in marketplaces or tied to a cash economy, and determination of their monetary value is difficult. This is particularly true for the medicinal uses that were documented. About 20% of the products recorded in both studies were used as folk medicines.

Other examples of locally valuable products from Southeast Asia include the midnight horror tree (Bignoniaceae: *Oroxylum indicum*), which is used as a food, a medicinal, and to produce a black dye for coloring rattan baskets (Burkill 1966; van Steenis 1977); and petai (Leguminosae: *Parkia speciosa* and *P. javanica*), which has garlic-flavored seeds used to spice curries and other local dishes (Burkill 1966; M. S. Fujita, personal observation). Each of these species depends on pteropodid bats for pollination (Start 1974; Start and Marshall 1976; Gould 1978). Ng (1980) estimated that domestic sales of petai in peninsular Malaysia alone at almost U.S. \$15 million per year, illustrating that such products can be a significant part of a region's economy.

On Pacific islands, pteropodid bats can also be considered to be economically important in that they are integral to the maintenance of the unique and lush rainforests that attract tourists to the region. Further, flying foxes themselves may have economic value as a tourist attraction (Wiles and Payne 1986). For example, the diurnal Samoan flying fox (*Pteropus samoensis*) is a highlighted feature of a newly legislated national park in American Samoa (Anonymous 1988).

Our information from Oceania suggests that many of the plants serviced by flying foxes produce products useful to humans. More research on bat-plant interactions is needed to ascertain the full extent to which the region's economically and ecologically important plant species depend on

pteropodid bats for seed dispersal or pollination. These data are especially needed in the Pacific, where endemism among plants and animals may be high and interactions more tightly coupled than in ecosystems with more diverse floras and faunas on larger land masses.

The economic role of flying foxes is only beginning to be recognized. Nevertheless, flying foxes are threatened by overhunting and habitat loss in many of the same areas that benefit from their interactions with plants. Public awareness campaigns that promote flying fox conservation are urgently needed to avert future extinctions of some species. To be effective such programs must point out that these bats are economically more valuable as seed dispersers and pollinators of island flora than they are as a food item. This argument can also be used to convince government officials of the need to establish protective legislation for flying foxes.

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