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Pteropus tonganus.

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Pteropus Erxleben, 1777

Flying Foxes

Pteropus Erxleben, 1777:130. Type species *Vespertilio vampyrus* Linnaeus, in part, by subsequent designation (see Hopwood, 1947).

Spectrum Lacépède, 1799:15. Type species *Spectrum vampirus* (= *Vestpertilio vampyrus* Linnaeus), by monotypy. Preoccupied by *Spectrum* Scopoli, a lepidopteran.

Eunycteris Gray, 1866:64. Type species *Pteropus phaiops* Temminck (= *Pteropus melanopogon*), by monotypy.

Pselaphon Gray, 1871:110. Type species *Pteropus ursinus* Temminck (= *Pteropus pselaphon* Layard), by monotypy.

Sericonycteris Matschie, 1899:30. Type species *Pteropus rubricollis* E. Geoffroy (= *Pteropus subniger* Kerr), by original designation.

Desmalopex Miller, 1907:60. Type species *Pteropus leucopterus* Temminck, by original designation.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Megachiroptera, Family Pteropodidae, Subfamily Pteropodinae, Genus *Pteropus*. The genus *Pteropus* contains 58 species (Koopman, 1993).

Pteropus tonganus (Quoy and Gaimard, 1830)

Pacific Flying Fox

Pteropus tonganus Quoy and Gaimard, 1830:74. Type locality Tonga Islands, Tongatapu Island.

Pteropus geddiei MacGillivray, 1860:1734. Type locality Aneitum Island, Vanuatu.

Pteropus flavicollis Gray, 1871:107. Type locality fixed as Moala Island, Fiji, by Andersen (1912).

Pteropus basiliscus Thomas, 1915:387. Type locality Karkar Island, off the northeast coast of New Guinea.

Pteropus heffernani Troughton, 1930:3. Type locality Tikopia, Santa Cruz Islands.

CONTEXT AND CONTENT. See above. Three subspecies are currently recognized:

P. t. basiliscus Thomas 1915, see above.
P. t. geddiei MacGillivray 1860, see above (*P. t. heffernani* Troughton, 1930:3 is a synonym).
P. t. tonganus Quoy and Gaimard 1830, see above.

DIAGNOSIS. The color pattern of *P. tonganus*, black back with contrasting orange or yellow mantle, is common to several sympatric species of *Pteropus*. *Pteropus tonganus* (length of forearm, 120–160 mm) is larger than *P. admiralitatum* (length of forearm, <120 mm) and smaller than *P. alecto* and *P. conspicillatus* (length of forearm, >160 mm). *P. tonganus* lacks a uropatagium, which is found in *P. giganteus*, *P. lylei*, *P. seychellensis*, and *P. vampyrus*. *P. tonganus* has a darker ventrum than *P. hypomelanus*. *P. tonganus* has shorter ears (<31 mm) than *P. macrotis* (>34 mm). *P. tonganus* is most likely to be confused with *P. mariannus*. Externally, they are quite similar in appearance, but the skulls can be distinguished by the diameter of the orbit, which is >12 mm in *P. tonganus* and <12 mm in *P. mariannus*. *P. tonganus* lacks the conspicuous paler-colored rings around the eyes of *P. ocularis* and the pale crown patch of *P. poliocephalus* (Pierson and Rainey, 1995).

GENERAL CHARACTERS. The pelage of *P. tonganus* is predominantly seal brown with a sharply contrasting mantle of cream buff to tawny ochraceous (Fig. 1; Wilson and Engbring, 1992:83, fig. 7) in both young and adult bats (Cox, 1983). Russet hairs are intermixed with the seal-brown hairs between the eyes and around the base of the ears. Cream-buff hairs are interspersed with the seal-brown coat on both the dorsal and ventral sides. The forearm and tibia are bare. The chin is covered by very short seal-brown hairs. The throat has one or two patches of tawny ochraceous or russet, which gradually give way to the mantle. Andersen (1912) noted differences between males and females in texture and color of the hairs of the mantle and neck. The stiff, short, oily hairs of the males can vary near the base from uniform buffy to blackish. The long, soft, spreading hairs of the females have concealed seal-brown bases.

Averages and ranges (in parentheses) of external measurements (in mm) for both sexes are: total length, 231 (151–262); length of hind foot, 47.2 (40.5–61); length of ear, 29.1 (20–31); length of forearm, 151.4 (114–175.4); length of tibia, 68.1 (54–76); length of calcar, 19.8 (16–23); longest hairs of back, 12.3 (10–17). Body mass averages 565 g (range, 191–1,099 g—Andersen, 1912; Baker and Baker, 1936; Sanborn and Nicholson, 1950; Wilson and Engbring, 1992; Wodzicki and Felten, 1975). Averages and ranges (in parentheses) of skull measurements (in mm) for both sexes are (Fig. 2): greatest length of skull, 68.4 (56.4–74.6); condylobasal length, 65.9 (55.7–72.2); postorbital width, 7.1 (5.3–9.2); interorbital width, 8.6 (6.6–9.9); zygomatic width, 35.4 (29.3–39.4); mastoid width, 21.6 (19.5–23.8); width of braincase, 22.6 (20.5–24.7); braincase length, 37.3 (33.8–46.9); C-M2 (alv.), 25 (21.7–30.9); rostrum length, 32.4 (29.4–36.7); orbital diameter, 12.4 (11.5–13.0—Andersen, 1912; Sanborn and Nicholson, 1950; Wodzicki and Felten, 1975, 1980).

Baker and Baker (1936) suggested that adult males (≥600 g)

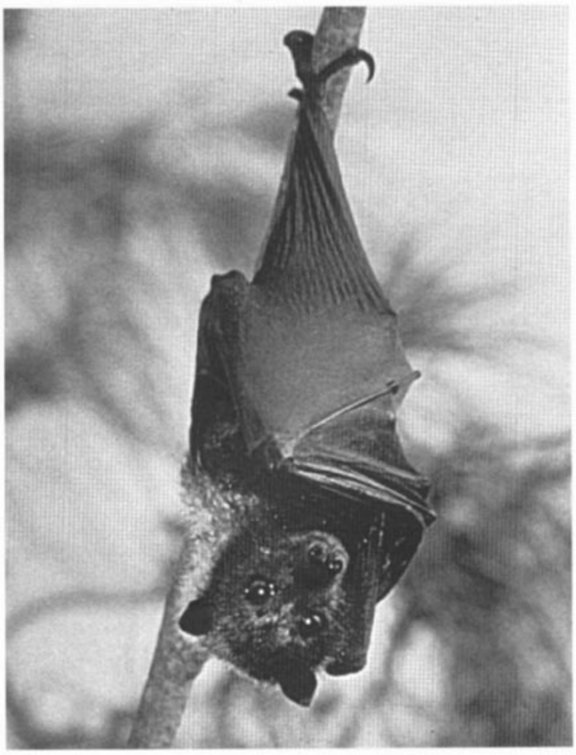

FIG. 1. *Pteropus tonganus* from Samoa. Photograph by Merlin D. Tuttle.

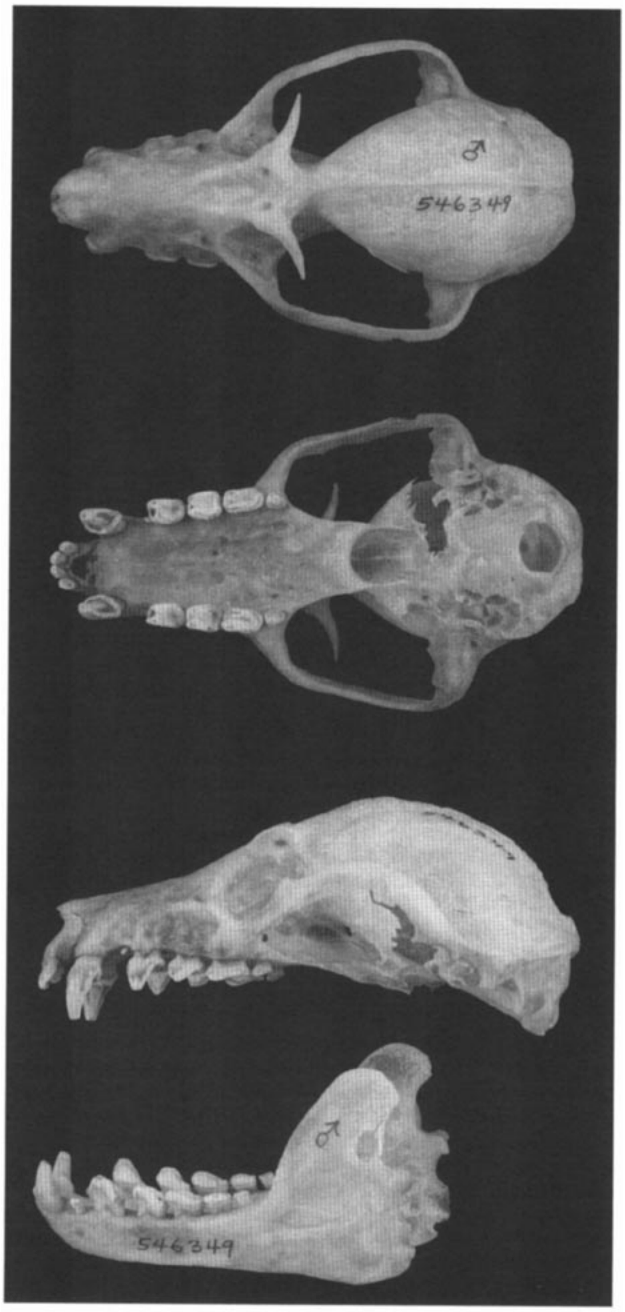

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandibles of *Pteropus tonganus* from Cook Islands (male, United States National Museum of Natural History 546349). Greatest length of skull is 66.3 mm.

grow larger than adult females (<600 g), but statistical documentation of sexual dimorphism is lacking in the literature. *P. t. geddiei* is the largest subspecies (Wilson and Engbring, 1992). There are few morphological differences among populations of *P. t. tonganus* separated by several hundred kilometers, although animals from Niue and the Cook Islands tend to be slightly smaller (Wodzicki and Felten, 1980). The pelage of *P. t. tonganus* varies depending on location, but *P. t. geddiei* is more uniform in color throughout its range (Sanborn, 1931).

FORM AND FUNCTION. The palatal-ridge formula is 5+5+3, but some individuals may have one extra ridge (Andersen, 1912). The dental formula is i 2/2, c 1/1, p 3/3, m 2/3, total 34 (Andersen, 1912). However, specimens of *P. t. geddiei* in the collection of the National Museum of Natural History have the dental formula of i 2/2, c 1/1, p 1/2, m 3/4, total 32. This difference, combined with the significantly larger size of *P. t. geddiei*, suggests trenchant differences between the subspecies that warrant further examination.

DISTRIBUTION. Similar to 86% of other species of *Pteropus*, *P. tonganus* is found only on islands (Rainey and Pierson, 1992). *P. tonganus* is found south of the equator (Fig. 3; Andersen, 1912) from the Schouten Islands (off NE New Guinea), south to New Caledonia, and east to the Cook Islands (Koopman, 1993; Kula, 1992; Marshall, 1983). The westernmost subspecies, *P. t. basiliscus*, is restricted to Karkar and the Schouten Islands, including Koi (Koopman, 1979; Laurie and Hill, 1954; Pierson et al., 1992; Rainey and Pierson, 1992).

The range of *P. t. geddiei* encompasses the Solomon Islands, New Caledonia (including the Loyalty Islands), and Vanuatu. The distribution of *P. t. geddiei* in the Solomon Islands has traditionally been restricted to Rennell and the Santa Cruz Group (Hill, 1958; Phillips, 1968); however, it was recently discovered on Malaita (Flannery, 1989), and Pierson et al. (1992) suggest that it may be widespread, but not common throughout the Solomon Islands. In Vanuatu and New Caledonia *P. t. geddiei* is common, although on New Caledonia *P. ornatus* is more common (Rainey and Pierson, 1992; Sanborn and Nicholson, 1950). In Vanuatu *P. tonganus* has been documented from Malekula, Elephant, Espiritu Santo, Efate, and Pentecost Island (Sanborn, 1931). *P. tonganus* has been reported from the Santa Cruz Islands (Vanikoro, Tapoua, and Santa Cruz), Matema (Swallow) Islands (Nupani), Duff Group (Masurers Island), and Solomon Islands (Tucopia and Rennel—Sanborn, 1931).

The easternmost subspecies, *P. t. tonganus*, occurs from Fiji, Tonga, Wallis, Futuna, and Western and American Samoa to Niue and the southern Cook Islands of Rarotonga and Mangaia (Andersen, 1912; Cox, 1983; Hill, 1979; Pernetta and Watling, 1978; Pierson et al., 1992; Rainey and Pierson, 1992; Sanborn, 1931; Wilson and Engbring, 1992; Wodzicki and Felten, 1975, 1980). In Samoa it has been found on Tutuila, Aunu'u, Ofu, Olosega, Ta'u, Savai'i, Apolima, 'Upolu, and Manono Island (Wilson and Engbring, 1992). *P. tonganus* frequently occupies small offshore islets (Wilson and Engbring, 1992). In Fiji *P. t. tonganus* has been recorded from Viti Levu, Vanua Levu, Taveuni, Ovalau, Moala, Totoya, and Naruka, and it is likely to occur on others (Degener, 1949; Pierson et al., 1992; Sanborn, 1931; Wilson and Engbring, 1992). There is no known fossil record of this species.

ONTOGENY AND REPRODUCTION. Like most *Pteropus*, *P. tonganus* has only one young per year (Baker and Baker, 1936; Pierson and Rainey, 1992). The time of year varies, depending on subspecies or location. In Samoa births have been observed in January, June, July, August, and October (Banack, 1996; Pierson and Rainey, 1992), and Banack (1996) suggested that in American Samoa, *P. tonganus* reproduces year-round. There is a synchronous breeding season for *P. t. geddiei* on Vanuatu (Baker and Baker, 1936) and New Caledonia, and for *P. t. tonganus* on the Cook Islands (Wodzicki and Felten, 1980); however, young may develop slightly later in New Caledonia (Sanborn and Nicholson, 1950). Conception does occur as late as June or July according to Baker and Baker (1936), implying a more extended breeding season. After about a six-month gestation period, bats are born in August or early September on Vanuatu (Baker and Baker, 1936) and the Cook Islands (Wodzicki and Felten, 1980). The breeding season of *P. tonganus* in Niue was between March and June, which coincides with the appearance of a favored food, *Syzygium* fruits (Wodzicki and Felten, 1975). Pierson and Rainey (1992) and Pierson et al. (1992) implied a more extended breeding season in Niue, and Grant (1994) suggested that the bats there may give birth year-round as they do in Samoa.

Parturition lasts from 11 to 55 minutes, with the baby born head first and eyes open (Banack, 1996). A female carries her infant under a wing when it is very small (Cox, 1983). Pacific flying foxes begin to fly at about 3 months of age, when they are 50–75% of adult size (Banack, 1996). About 50% of copulations observed involved females that were nursing young, suggesting postpartum estrus (Banack, 1996).

ECOLOGY. *Pteropus tonganus* is fairly adaptable, and is found in a variety of habitats and on widely dispersed islands throughout the south Pacific (Pierson et al., 1992). Koopman (1979) characterized it as a supertramp species, because it occurs on smaller, isolated, islands with few other species of bats, and is

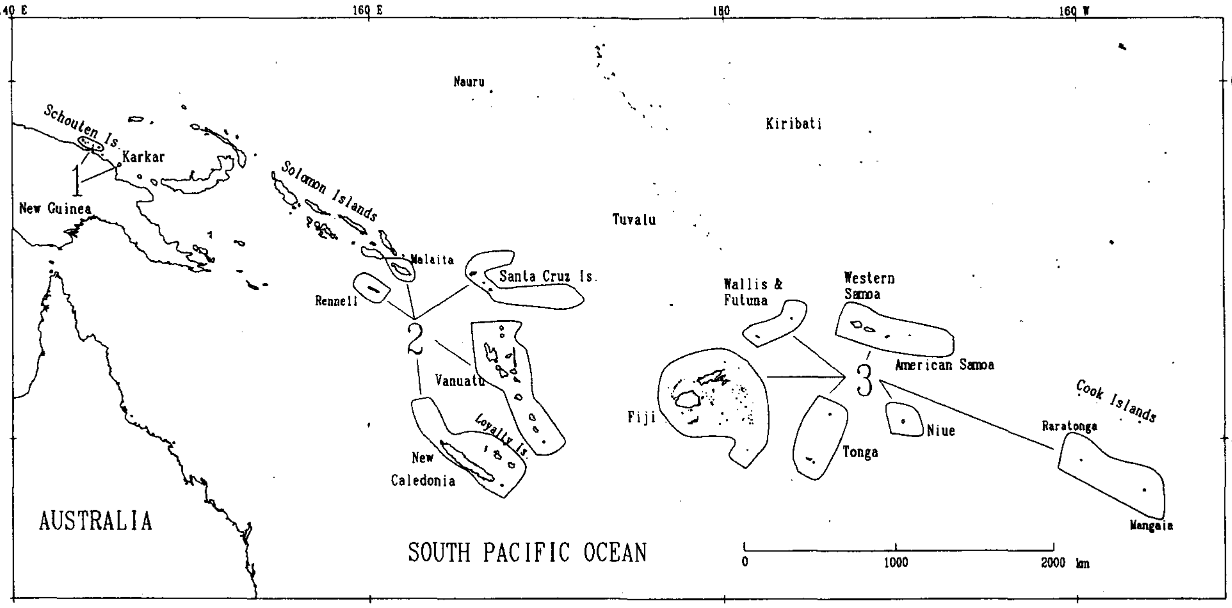

FIG. 3. Distribution of *Pteropus tonganus* (Koopman, 1993): 1, *Pteropus tonganus basilicus*; 2, *P. t. geddiei*; 3, *P. t. tonganus*.

absent from large, species-rich islands in the same region (Rainey and Pierson, 1992).

This species is primarily nocturnal and roosts colonially in montane and lowland native forests, along cliffs, islets, in intermediate zone vegetation, fresh water and inland swamps, i.e., in relatively inaccessible sites (Cox, 1983; Pernetta and Watling, 1978; Pierson and Rainey, 1992; White et al., 1988; Wilson and Engbring, 1992; Wodzicki and Felten, 1980). *P. tonganus* is occasionally found in coastal and mangrove swamps. The bats disperse from colonies to forage primarily in natural forest, although agricultural forests and residential areas are also used as foraging sites (Cox, 1983; Pernetta and Watling, 1978; Wilson and Engbring, 1992). In American Samoa *P. tonganus* used four major roosting areas, with some movement between sites (Banack, 1996). The roosts are generally found in undisturbed native forest (Wilson and Engbring, 1992) but have been reported from the Kolovai Sanctuary in Tonga and other aggregates of trees in populated areas (Pierson and Rainey, 1992).

Roosting height for *P. tonganus* ranges from 10 to 35 m (Wodzicki and Felten, 1975). Several tree species preferred for roosting on Rarotonga are *Cananga odorata* (Annonaceae), *Cerbera manghas* (Apocynaceae), *Guettarda speciosa* (Rubiaceae) and *Homalium acuminatum*, (Flacourtiaceae). These four species share the morphological features of sparse leaves and a widely spaced branching pattern (Wodzicki and Felten, 1980). Colonies are generally found on emergent trees (Pierson and Rainey, 1992) allowing for a 'free-fall take off,' which may accomodate the large size of *Pteropus* (Kingdon, 1974). In Samoa and Vanuatu, *Ficus prolixa* and *Casuarina* sp. have been cited as roosting trees (Pierson and Rainey, 1992). The bats tend to roost toward the outside of the tree, and the foliage of a roosting tree may become sparse due to the use of branches by the animals. The gregarious bats are detected most easily by audible squabbling but also by a distinct odor that emanates from inhabited roost sites (Allen, 1939; Cox 1983; Grant, 1994; Wodzicki and Felten, 1975).

Pteropus tonganus visits numerous plants for pollen, nectar, and fruit, and it acts as an important pollinator of the widespread *Ceiba pentandra* and potentially many other species (Banack, 1996). *P. tonganus* feeds on flower resources including pollen and nectar of *Rhus taitensis* (Anacardiaceae—Mickleburgh et al., 1992), *Cananga odorata* (Annonaceae—Wilson and Engbring, 1992), *Cocos nucifera* (Palmae—Wilson and Engbring, 1992), *Ceiba pentandra* (Bombacaceae—Cox, 1983), *Erythrina variegata* (Leguminosae—Banack, 1996), *Musa* sp. (Musaceae—Wilson and Engbring, 1992), *Syzygium clusiaefolium* (Myrtaceae—Wodzicki and Felten, 1975), *S. inophylloides* (Myrtaceae—Wodzicki and Felten, 1975), *S. malaccense* (Myrtaceae—Wodzicki and Felten, 1980), *S. richii* (Myrtaceae—Wodzicki and Felten, 1975), *Pandanus tectorius* (Pandanaceae—Wodzicki and Felten, 1980), and *Planchonella torricellensis* (Sapotaceae—Wodzicki and Felten, 1975).

Pacific flying foxes also feed on the fruits of *Dracontomelon* species (Anacardiaceae—Baker and Baker, 1936), *Mangifera indica* (Anacardiaceae—Wodzicki and Felten, 1975), *Cananga odorata* (Annonaceae—Wodzicki and Felten, 1980), *Cerbera manghas* (Apocynaceae—Wodzicki and Felten, 1980), *Neisosperma oppositifolium* (Apocynaceae—Wodzicki and Felten, 1975), *Carica papaya* (Caricaceae—Baker and Baker, 1936), *Terminalia catappa* (Combretaceae—Wodzicki and Felten, 1980), *Diospyros samoensis* (Ebenaceae—Wodzicki and Felten, 1975), *Elaeocarpus rarotongensis* (Elaeocarpaceae—Wodzicki and Felten, 1980), *Calophyllum inophyllum* [Guttiferae (Clusiaceae)—Wilson and Engbring, 1992], *Persea americana* (Lauraceae—Wodzicki and Felten, 1980), *Inocarpus fagifer* (Leguminosae—Wodzicki and Felten, 1975), *Fagraea berteroana* (Loganiaceae—Wodzicki and Felten, 1980), *Artocarpus altilis* (Moraceae—Wodzicki and Felten, 1975), *Artocarpus heterophylla* (Moraceae—Wodzicki and Felten, 1980), *Ficus copiosa* (Moraceae—Baker and Baker, 1936), *Ficus prolixa* (Moraceae—Wodzicki and Felten, 1975), *Ficus obliqua* (Moraceae—Banack, 1996), *Musa* sp. (Musaceae—Baker and Baker, 1936), *Myristica hypargyraea* (Myristicaceae—Banack, 1996), *Psidium guajava* (Myrtaceae—Baker and Baker, 1936), *Syzygium clusiaefolium* (Myrtaceae—Wodzicki and Felten, 1975), *S. cumini* (Myrtaceae—Wodzicki and Felten, 1980), *S. inophylloides* (Myrtaceae—Banack, 1996), *S. jambos* (Myrtaceae—Cox, 1983), *S. malaccense* (Myrtaceae—Wodzicki and Felten, 1980), *S. richii* (Myrtaceae—Wodzicki and Felten, 1975), *Cocos nucifera* (Palmae—Wodzicki and Felten, 1980), *Pandanus* sp. (Pandanaceae—Wodzicki and Felten, 1975), *Citrus sinensis* (Rutaceae—Wodzicki and Felten, 1980), *Pommetia pinnata* (Sapindaceae—Wodzicki and Felten, 1975), *Planchonella grayana* (Sapotaceae—Banack, 1996), *Planchonella samoensis* (Sapotaceae—Wodzicki and Felten, 1975), and *Lycopersicon esculentum* (Solanaceae—Wodzicki and Felten, 1975). Seasonal changes in food availability occur, and depending on the season certain foods are favored (Baker and Baker, 1936; Cox et al., 1992; Pierson et al., 1992; Wiles and Fujita, 1992; Wodzicki and Felten, 1975, 1980).

As an eclectic forager *P. tonganus* is able to find food seasonally and has the ability to respond to changes in forest structure and biomass caused by catastrophic events (Marshall, 1983; Wodzicki and Felten, 1975). The presence of a foraging generalist such as *P. tonganus* may aid plants in the colonization of an island by acting as a pollinator and seed disperser (Elmqvist et al., 1992). In contrast to its continental range where *Ceiba pentandra* flowers have a varied group of pollinators, the flower is pollinated by a single species on Samoa—*P. tonganus* (Elmqvist et al., 1992; Pierson and Rainey, 1992). *P. tonganus* helps to maintain forest diversity as seed dispersers and are important pollinators within Pacific island ecosystems (Rainey, 1990; Cox et al., 1991, 1992; Wiles and Fujita, 1992; Wodzicki and Felten, 1980).

Causes of mortality are not well known for any species in the genus. Mortality among *P. tonganus* includes predation, epidemics, hurricanes, hunting, and most importantly, habitat loss (Craig et al., 1994; Pierson and Rainey, 1992). Raptors and snakes are among the few natural predators of insular flying foxes. Due to their low reproductive rate, these animals are sensitive to overhunting, introduced predators, and catastrophic events (Cox et al., 1991). Pteropodids make up a large portion of the diet of peregrine falcons (*Falco peregrinus*) from Fiji. The range of *P. tonganus* coincides with that of peregrine falcons in New Caledonia, the Loyalty Islands, the Solomon Islands, and Vanuatu (Pierson et al., 1992; White et al., 1988). Sometime before 1949 there was an epidemic on Savu Savu, Fiji that decimated the *P. tonganus* population, leaving hundreds of bleached bones under every roost tree in the woods (Degener, 1949).

Grant and Banack (in press) documented predation by barn owls on *P. tonganus* in American Samoa. One individual was attacked in a tree while Grant and Banack were radio-tracking it, and an owl was observed attacking a second individual on the wing. Interestingly, the bats weigh about the same as the owls.

Hurricanes can cause dramatic declines in *P. tonganus* populations. In American Samoa, *P. tonganus* populations declined 80–90% following two hurricanes in 1990 and 1991 (Craig et al., 1994; Pierson et al., in press). Decreases were due to loss of habitat, scarcity of food, and subsequent overhunting. When roost sites and food were unavailable in the forest, the bats ventured into towns, sometimes even during the day, to forage on fallen fruits. They are vulnerable to attack by domestic animals (dogs, cats, pigs) because they are unable to take flight from the ground. Estimates of mortality due to pigs and cats was probably low because these animals forage in the woods and some kills may go unnoticed (Pierson and Rainey, 1992). The exposed bats were also taken by humans for food, but often only for target practice (Daschbach, 1990; Pierson and Rainey, 1992; Pierson et al., 1992).

Pteropus tonganus carries both ecto- and endoparasites (Wodzicki and Felten, 1975). Three different, and otherwise unidentified, ectoparasites were found on bats in Fiji (Degener, 1949). Sanborn and Nicholson (1950) speculated that *P. t. geddiei* was parasitized by *Cyclopodia oxycephala* Bigot, a bat tick. In American Samoa this species is heavily parasitized by wingless batflies of the family Nycteribiidae (Banack, 1996). Banack (1996) suggested that *P. tonganus* may occasionally shift its roost tree in response to ectoparasite load.

BEHAVIOR. The habits of *Pteropus* in general were described by Peale (1848:17–18). His obversations remain apt for *P. tonganus:* "The Pteropi are all more or less gregarious; most active in twilight: and when at rest, hang from the branches of trees with their heads downward, using their wings as cloaks to shelter their bodies from the wind, rain, and sun; when they fly, as they have no interfemoral membranes, they hold the two hind feet together, which makes them appear to have a tail; they climb with great facility along the under side of the branches and are very destructive to both wild and cultivated fruits, as they taste and reject until the ripest and best is found; but we never heard them accused of destroying animal life."

Pteropus tonganus is strongly colonial (Cox, 1983; Craig and Syron, 1992; Pernetta and Watling, 1978) and nocturnal (Craig and Syron, 1992; Wilson and Engbring, 1992; Wodzicki and Felten, 1975). Feeding activity commences at different times depending on location, with bats in some areas foraging well before dark. Wodzicki and Felten (1975) speculated that this diurnal behavior might indicate a larger population size, and Wilson and Engbring (1992) suggested the difference was due to hunting pressure and other human disturbance. There was little human disturbance on 'Aunu'u and Olosega, and the animals began foraging during daylight with little risk (Wilson and Engbring, 1992). Andersen (1912) suggested that those bats on Tonga that emerged before dusk were driven out by hunger or accidentally disturbed. Disturbances such as hurricanes may disrupt daily activity patterns, and resultant shortages in food supply may cause the bats to forage for longer periods and during the daytime (Craig, et al., 1994; Pierson, et al., in press).

Pteropodidae generally have distinct roosting and foraging areas. Sites may be separated in elevation or by distance across land or ocean (Marshall, 1983; Pierson and Rainey, 1992). Cox (1983) observed hundreds of *P. t. tonganus* coming in from sea at dusk, presumably to feed. *P. tonganus* congregate in noisy groups around trees with abundant fruits and flowers such as *Ficus* or *Ceiba*, and individually around trees like *Cocos nucifera* which produce only a few flowers. *P. tonganus* forages at night, often in noisy groups (Elmqvist et al., 1992; Wilson and Engbring, 1992).

Bats frequently carry their food away from the site of origin, and observations of *P. tonganus* carrying pieces of breadfruit indicate that the bats do not always remain at the foraging site to eat (Wilson and Engbring, 1992). Pacific flying foxes are known to roost on off-shore islets and islands in large numbers and to fly across open water to forage (White et al., 1988; Wilson and Engbring, 1992). Cox's (1983) observation of over 300 individuals coming in from sea may suggest group foraging. Group searching may be an effective way to capitalize on a rewarding, but temporary and scattered, resource, because the group would have experience with a more extensive region, greater perception, and additional awareness of possible threats (Marshall, 1983).

Megachiroptera use their hind feet to manipulate fruit and peel it or bite off pieces. By moving their tongue against their palate the bats are able to break up the fruit and ingest only the pulp and juices, releasing seeds (Marshall, 1985).

In one study in Samoa (Elmqvist et al., 1992) *P. tonganus* actively defended resources within flowering trees of *Ceiba pentandra*. Early in the season, before the availability of fruits and prior to anthesis, flying foxes defended areas of 1.5–2.0 m from intruding *P. tonganus* by pursuing, batting, and vocalizing. These confrontations normally finished with one animal taking flight or moving to another part of the tree (Elmqvist et al., 1992). There were two bursts of activity, the first during the initial period of nectar production early in the evening, and another just before dawn. The second was made up of smaller individuals presumed to be immature. After anthesis the animals spent considerable time crawling from one flower to another. Visits to a tree lasted from 3 to 19 minutes. During the process of foraging, 50% of *C. pentandra* flowers and developing fruits may be destroyed (Elmqvist et al., 1992).

In Vanuatu, *P. tonganus* forms large colonies from September to January, containing both sexes in large casuarina trees near the shore (Baker and Baker, 1936). The females leave in February when they become pregnant, and appear in June, when they unite in inland maternity camps to give birth to their young. Males remain in the coastal camps from January to June, but apparently disperse from June to September (Baker and Baker, 1936; MacGillivray, 1860; Pierson and Rainey, 1992).

Pteropus tonganus, like other *Pteropus* and communally roosting genera, generally has high roost-site fidelity if left undisturbed (Marshall, 1983; Pierson and Rainey, 1992). The Tongan royal family protects a colony of *P. tonganus* that can be found in the same location year after year (Pierson and Rainey, 1992). On Niue, there were reports that *P. tonganus* changes roost-sites during the year, but Wodzicki and Felten (1975) found that *P. tonganus* returned to the same trees. On Tutuila, American Samoa, colonies relocated frequently, but often in the same general area or other traditional roost sites (Pierson and Rainey, 1992). Wilson and Engbring (1992) found homogeneous colonies of *P. tonganus* in American Samoa and Fiji but did see an occasional *P. samoensis* flying in close proximity to a colony. Banack (1996) reported both species roosting in the same trees. Farther away from the colony, the two species were found flying and foraging in the same vicinity. In New Caledonia, camps moved seasonally with fluctuating numbers of *P. t. geddiei* in a given camp, and *P. t. geddiei* and *P. ornatus* were observed in the same camp but in separate areas (Sanborn and Nicholson, 1950). On one occasion a juvenile female *P. ornatus* was collected with 15 *P. t. geddiei* of both sexes and various ages (Sanborn and Nicholson, 1950). In Vanuatu, roost sites may change during the year. Once a roost has been disturbed, it may not be reoccupied for 5–10 years (Wodzicki and Felten, 1975).

Roosting patterns for some populations may be altered by human disturbance. On the island of Niue, *P. tonganus* has been observed roosting singly, in pairs, and in small groups from 20 to 100 animals (Pierson and Rainey, 1992; Wodzicki and Felten, 1980). This deviation from the regularly observed pattern has been attributed to overhunting and deforestation (Wodzicki and Felten, 1975).

CONSERVATION STATUS. *Pteropus tonganus* was listed on CITES Appendix I in 1989 and is listed in the 1990 IUCN Red Book (Brautigam, 1992; International Union for the Conservation of Nature and Natural Resources, 1990; Koopman, 1993; Pierson et al., 1992). Pierson et al. (1992) listed this species as priority grade II (not threatened), with current status unknown.

In many Pacific nations *P. tonganus* has traditionally been considered a delicacy, or consumption was limited to certain groups within society (Bani, 1992; Graham, 1992; Rainey, 1990; Sinavaiana and Enright, 1992). Recently there has been an increased demand for *P. tonganus* as a food source within the nations where it occurs, as well as on other islands such as Guam, where commercial exploitation is driven by the demands of a luxury food market (Cox, 1983; Falanruw, 1988; Graham, 1992; Wiles, 1992; Wiles and Fujita, 1992). Consequently, *P. tonganus* has suffered as a result of overhunting (Wodzicki and Felten, 1975, 1980). Another problem contributing to population declines in *P. tonganus* is habitat loss and deforestation (Robertson, 1992; Wilson and Engbring, 1992). Timber is listed as the leading natural resource in Fiji and Western Samoa (Wilson and Engbring, 1992). Much of the interior of 'Upolu (Western Samoa) has been commercially logged and converted to pasture and other agricultural land (Wilson and Engbring, 1992). On Savai'i (Western Samoa), logging is an even more important industry, although many of the logged areas are replanted or otherwise allowed to return to forest (Wilson and Engbring, 1992).

REMARKS. The name *Pteropus* is from a Greek root meaning wing-footed, an allusion to the wing membrane, which arises from the side of the back and the back of the second toe. The specific epithet, *tonganus*, refers to the type locality of the species, the Tonga Islands.

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