MAMMALIAN SPECIES No. 661, pp. 1–4, 3 figs.

Pteropus samoensis.

By Sandra Anne Banack

Published 5 June 2001 by the American Society of Mammalogists

Pteropus samoensis Peale, 1848

Samoan Flying Fox

Pteropus samoensis Peale, 1848:20–21. Type locality "Tutuila," American Samoa (*whitmeei* Alston is a synonym).

Pteropus nawaiensis Gray, 1870:107. Type locality "Fiji Islands: Nauai." As 2 specimens were labeled in Gray's handwriting, Andersen (1912:283–284) designated the specimen with the earliest catalog number as the type.

Pteropus vitiensis Gray, 1870:109. Type locality "Ovalau," Fiji Islands.

CONTEXT AND CONTENT. Order Chiroptera, suborder Megachiroptera, family Pteropodidae, subfamily Pteropodinae, genus *Pteropus*. The genus *Pteropus* contains 60 species (Nowak 1999). Andersen (1912) placed *P. anetianus* in the *samoensis* species group with *P. samoensis* and *P. nawaiensis* as separate species. Two subspecies are recognized (Wodzicki and Felten 1975).

P. s. nawaiensis Gray, 1870:107, see above.

P. s. samoensis Peale, 1848:20–21, see above.

DIAGNOSIS. *Pteropus samoensis* (Fig. 1) has a dark brown dorsum with a lighter colored mantle and a light spot on the crown. Mantle is not sharply contrasting as in *P. tonganus tonganus*, the only other sympatric *Pteropus* in its range. Length of mandible for *P. samoensis* is 44.0–49.2 mm (n = 5; Fig. 2), whereas that of *P. t. tonganus* is 49.7–53.8 mm (n = 13—Andersen 1912). Coronoid process is higher in *P. samoensis*, with a range of 25.2–28.7 mm (n = 5) in comparison with *P. t. tonganus*, which has a coronoid height of 23.5–25.8 mm (n = 13—Andersen 1912). Lower leg is bare in *P. tonganus* (Miller and Wilson 1997) in contrast to *P. samoensis*, whose lower leg is thickly haired over the proximal third (Andersen 1912). Posterior basal ledges of cheek teeth are strongly developed compared with other members of the genus. Only *P. anetianus* (from Vanuatu) has a broader, more well-defined, posterior basal ledge than *P. samoensis*. In *P. anetianus*, the ledge extends forward on lingual face of tooth as a broad, well-defined shelf (Andersen 1912; Dobson 1878). *P. anetianus* also has acutely tubercular premolars and molars, unlike *P. samoensis* (Dobson 1878).

GENERAL CHARACTERS. *Pteropus samoensis* is predominately dark brown with individual variation ranging from reddish brown to blackish gray (Alston 1874; Andersen 1912; Cassin 1858; Dobson 1878; Gray 1870; Peale 1848). Hairs are seal-brown at base with lighter tips. Longer, coarse, pale-colored (yellowish to grayish white) hairs are sprinkled throughout. Mantle varies from ocherous buffy, buffy, tawny, to yellowish white in *P. s. nawaiensis* but is darker in *P. s. samoensis*, ranging from buffy gray, tawny, dark chestnut, to a reddish brown (Alston 1874; Andersen 1912; Cassin 1858; Dobson 1878; Gray 1870; Peale 1848). In *P. s. nawaiensis*, the lighter mantle contrasts with the darker back to form a broad undefined collar (Gray 1870). Crown of *P. s. nawaiensis* is cream buff, ocherous buff, to tawny, and generally lighter than crown of *P. s. samoensis*, which varies from buff, ocherous buff, to silvery gray. Interocular space and sides of face are dark gray mixed with buffy and blackish hairs; chin and throat are dark brown to blackish, sometimes reddish brown, mixed with pale grayish and buffy hairs. Fur length for *P. s. nawaiensis* and *P. s. samoensis* is longer on mantle (17–20 mm at middle) and ventrum (18–24 mm at middle) compared with dorsum (16–18 mm at middle—Dobson 1878).

Pteropus s. samoensis is larger than *P. s. nawaiensis* and has a markedly heavier mandible with i2 and p1 larger (Andersen 1912). The i2 is 4–5 times larger than i1 in *P. s. samoensis* and 2–3 times the size of i1 in *P. s. nawaiensis*. The p1 of *P. s. nawaiensis* is ca. 1.5 times smaller than p1 in *P. s. samoensis* (Andersen 1912). *P. s. samoensis* has a more prominent posterior ledge of cheek teeth than *P. s. nawaiensis*. *P. s. nawaiensis* has no lingual ledge on lower cheek teeth, whereas posterior basal ledge of *P. s. samoensis* sometimes continues forward along lingual face of p4 and m1 as an obsolescent rim (Andersen 1912). Several teeth, p3, P4, and M1, are considerably larger in *P. s. samoensis*. The range of length and width (in mm) is as follows: *P. s. nawaiensis* (n = 6)—p3: 4.1–4.2, 2.5–2.7; P4: 4–4.5, 2.9–3.2; M1: 5–5.7, 2.9–3.2; *P. s. samoensis* (n = 2)—p3: 4.3–4.8, 2.8; P4: 4.8, 3.6–3.8; M1: 5.8–6, 3.2 (Andersen 1912).

The range of external and skull measurements for both sexes of *P. s. samoensis* (in mm; sample size in parentheses) is: length of forearm, 120–155 (31); greatest length of skull, 57.3–64.0 (8); condylobasal length, 56.0–60.8 (7); width of braincase, 21.3–22.4 (9); zygomatic width, 33.3–36.1 (6); width of rostrum, 15.6–17.5 (11); length of rostrum, 22.0–25.0 (10); length of C1–M2, 20.4–23.7 (9); interorbital width, 8.3–9.5 (10); postorbital width, 6.7–8.2 (10); length of braincase, 38.0–41.7 (6); and orbital diameter, 12.1–13.0 (10—Andersen 1912; Banack 1996; Wilson and Engbring 1992; Wodzicki and Felten 1975). Range of external measurements for both sexes of *P. s. nawaiensis* (in mm; sample size in parentheses): length of forearm, 120–135 (10); greatest length of skull, 58.4–60.7 (3); condylobasal length, 57.0–58.5 (3); width of braincase, 21.1–23.0 (9); zygomatic width, 31.2–35.5 (9); width of rostrum, 15.0–17.8 (11); length of rostrum, 22.6–24.2 (7); length of C1–M2, 20.1–22.6 (6); interorbital width, 7.7–9.4 (11); postorbital width, 6.6–7.8 (7); length of braincase, 38.0–39.7 (3); and orbital diameter, 11.8–13.1 (11—Andersen 1912; Wodzicki and Felten 1975). Body mass of *P. s. samoensis* ranges from 220 to 440 g (16) for volant animals (Banack 1996). Body mass of *P. s. nawaiensis* is not available.

DISTRIBUTION. *Pteropus s. samoensis* is found only in the Samoan archipelago (Fig. 3) on all major islands, including

FIG. 1. Juvenile *Pteropus samoensis samoensis* from Samoa. Photograph by P. A. Cox.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Pteropus samoensis samoensis* from Tutuila, American Samoa (USNM [National Museum of Natural History] 338624). Greatest length of skull is 62.2 mm. Photograph courtesy of D. E. Wilson.

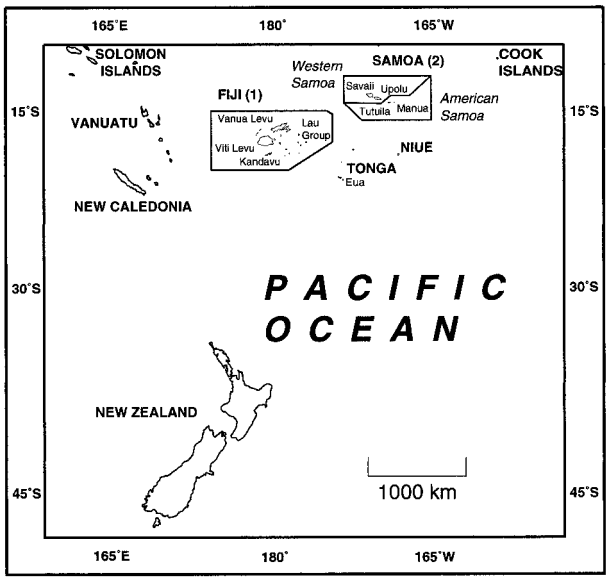

FIG. 3. Current geographic distribution of *Pteropus samoensis* in the South Pacific. Subspecies are: 1, *P. s. nawaiensis* and 2, *P. s. samoensis.*

Savaii and Upolu in Western Samoa and Tutuila, Ofu, Olosega, and Ta'u in American Samoa. *P. s. nawaiensis* occurs in Fiji on Nauai, Ovalau, Taveuni, Vanua Levu, and Viti Levu islands (Mickleburgh et al. 1992; Sanborn 1931).

FOSSIL RECORD. Remains from an extinct population of *P. samoensis* were found in Eua Island, Tonga archipelago, in both pre- and posthuman settlement strata dating from <3,000 years ago (Koopman and Steadman 1995).

FORM AND FUNCTION. Adult Samoan flying foxes have a wing span (±*SD*) of 0.86 ± 0.04 m; a wing area of 0.11 ± 0.01 m^2; an aspect ratio of 6.59 ± 0.12; and a wing loading of 33.08 ± 3.67 N/m^2 (Richmond et al. 1998). *P. samoensis* soars despite wing morphology that is not specifically adapted for this behavior. Wing morphology of *P. samoensis* is intermediate when compared with other Pteropodidae and may reflect a compromise between the selective pressures for load-carrying ability, maneuverability among vegetation, take-off ability, and soaring flight (Richmond et al. 1998). Juvenile *P. samoensis* have different wing loading and aspect ratio, suggesting that wing growth may precede increases in body mass (Richmond et al. 1998).

Brain structure of *P. samoensis* was described in the late 1880s (Zuckerkandl 1887), as was the status of milk teeth in size-specific specimens (Leche 1878). Dental formula is i 2/2, c 1/1, p 3/3, m 2/3, total 34 (Dobson 1878).

ONTOGENY AND REPRODUCTION. *Pteropus samoensis* has 1 young per year (Baker and Baker 1936; Pierson and Rainey 1992) and has a broad but seasonal reproductive period spanning from March through October with a peak of newly born animals in May and June (Banack 1996). A single reproductive period is consistent with the majority of *Pteropus* (Pierson and Rainey 1992); however, the parturition period is longer than for most *Pteropus.*

Copulations occur August–December, some with females suckling large dependent young (Banack 1996). Timing of copulation may vary from year to year. Juveniles begin to fly when they reach half the size of adults (ca. 3 months) and are still receiving some nourishment from their mothers at three-fourths the size of adults (ca. 4–6 months—Banack 1996). Young one-half the size of the mother may be carried by her (Banack 1996).

ECOLOGY. *Pteropus samoensis* depends on primary forest for roosting and foraging (Banack 1996, 1998; Cox 1983). Roosts are typically evenly spaced along ridge tops and are strategically located in trees that provide a clear drop-off exit. Occasionally, roosts are in trees offering similar understory clearance, such as along roadsides, in areas where large forest trees juxtapose plantations and low secondary growth, and in large trees in open pastureland (Banack 1996; Nicoll 1904; Wilson and Engbring 1992). *P. samoensis* has a high roost fidelity (Marshall 1983; Pierson and Rainey 1992).

Pteropus samoensis roosts singly or in male–female pairs with offspring of the current year (Banack 1996; Cox 1983; Pernetta and Watling 1978). Occasionally, larger groups of up to 9 individuals occur within a single tree (Banack 1996; Pierson et al. 1996; Wilson and Engbring 1992) or in the same trees as congeneric species (Banack 1996). They do not roost in large aggregations (Peale 1848).

Pteropus samoensis is a generalist which has fed on 32 species of plants, of which 91% grow in primary forest (Banack 1998). Fruit, leaves, and flower parts all contribute to the diet; however, fruit comprises the largest component. *P. samoensis* feeds on fruit from Eudicotyledones, Annonaceae: *Cananga odorata*; Combretaceae: *Terminalia catappa*; Ebenaceae: *Diospyros samoensis*; Elaeocarpaceae: *Elaeocarpus ulianus*; Fabaceae: *Inocarpus fagifer*; Gesneriaceae: *Cyrtandra samoensis*; Guttiferae, *Calophyllum inophyllum*; Loganiaceae, *Fagraea berteroana*; Meliaceae: *Dysoxylum maota, D. samoense*; Moraceae: *Artocarpus altilus, Ficus obliqua, F. prolixa, F. scabra, F. tinctoria, F. uniauriculata*; Myr-

taceae: *Syzygium inophylloides*; Piperaceae: *Piper graeffei*; Sapindaceae: *Cupaniopsis samoense*; Sapotaceae: *Pometia pinnata, Palaquium stehlinii, Planchonella samoensis, P. garberi, P. grayana*; and Monocotyledones, Pandanaceae: *Freycinetia reineckei* (Banack 1998). *P. samoensis* carry fruit in their mouths away from fruiting trees and, in the process, act as seed dispersers. Fruit dispersal increases with increased density of Samoan flying foxes (Banack 1996; Richards 1990). Flower resources (primarily pollen and nectar) are obtained from Eudicotyledones, Annonaceae: *Cananga odorata*; Bombacaceae: *Ceiba pentandra*; Elaeocarpaceae: *Elaeocarpus ulianus*; Fabaceae: *Erythrina variegata*; Lecythidaceae: *Barringtonia asiatica*; Myrtaceae: *Syzygium inophylloides*; Rhamnaceae: *Alphitonia zizyphoides*; Rubiaceae: *Neonauclea forsteri*; Sapotaceae: *Palaquium stehlinii, Planchonella samoensis*; Monocotyledones, Arecaceae: *Cocos nucifera*; Orchidaceae: *Eria robusta*; and Pandanaceae: *Freycinetia reineckei, Pandanus tectorius* (Banack 1998). *P. samoensis* fed preferentially on flowers with nectar or "food bodies" that were hexose-rich and well provisioned with amino acids (Cox 1984). *P. samoensis* has arguably influenced the maintenance of dioecism in *F. reineckei* through its role as a pollinator of this species (Cox 1982). In addition, *P. samoensis* feeds on leaves of Eudicotyledones, Fabaceae: *Erythrina variegata*; Elaeocarpaceae: *Elaeocarpus ulianus*; Moraceae: *Ficus tinctoria*; Monocotyledones, Orchidaceae: *Eria robusta*; and the sap of Eudicotyledones, Urticaceae: *Pipturus argenteus* (Banack 1998).

Pteropus samoensis overlaps 61% in diet with *P. tonganus* in Samoa (Banack 1998). It defends preferred food throughout the night from *P. tonganus* (Banack 1996).

The Samoan flying fox is killed by humans. In the Samoan islands *P. tonganus* is of similar size and is preyed on by owls, *Tyto alba* (Grant and Banack 1995). In Fiji, diurnal peregrine falcons (*Falco peregrinus*) regularly feed on pteropodid species, but the proportion of *P. s. nawaiensis* taken is unknown (White et al. 1988). No ectoparasites occurred on 16 *P. samoensis* netted in Tutuila, American Samoa, and Savaii, Western Samoa (Banack 1996).

The Samoan flying fox can be censused with day surveys of foraging and commuting animals (Banack 1996; Craig et al. 1994; Grant et al. 1997; Pierson et al. 1996; Wilson and Engbring 1992). They can be caught in mist nets at feeding sites and flyways and can be marked with bird bands placed on the thumb. *P. samoensis* has been radio tracked in Tutuila, American Samoa, and Savaii, Western Samoa (Banack 1996).

BEHAVIOR. *Pteropus samoensis* is unusual in being primarily diurnal, with most activity occurring in early morning and late afternoon (Cassin 1858; Cox 1983; Grant et al. 1997; Nicoll 1908; Peale 1848; Pierson et al. 1996; Thomson et al. 1998; Wilson and Engbring 1992). *P. s. nawaiensis* is less diurnal than *P. s. samoensis* and does not forage before 1600 h (Mickleburgh et al. 1992). *P. s. samoensis* is also active during the night, including large-scale movement and foraging (Banack 1996). Diurnal behavior allows *P. s. samoensis* to use soaring flight (in excess of 29 s between flaps, compared with 3 wing beats/s in flapping flight—Richmond et al. 1998) thus reducing the energetic costs of flying. Soaring occurs on thermal updrafts and wind currents along shorelines (Cassin 1858; Cox 1983; Richmond et al. 1998; Thomson et al. 1998; Whitmee 1874).

In Fiji, *P. s. nawaiensis* lacks the characteristic soaring behavior (high above the canopy) of *P. s. samoensis* (Mickleburgh et al. 1992; Wilson and Engbring 1992). *P. s. nawaiensis* feeds both in open habitat (Pernetta and Watling 1978) and in relatively dense forest (Wilson and Engbring 1992).

Pteropus samoensis is territorial. It defends and advertises its territory through aerial pursuits, vocalizations, scent marking, and wing displays. Territorial activities are more prevalent during early morning and late afternoon periods of peak foraging. Territories are ca. 2–4 km^2 (Banack 1996; Cox 1983). Most scent marking, displays, vocalizations, and aerial pursuits are performed by males. Aerial pursuits involve chases between 2 animals and attacks in which the pursing animal hits the fleeing animal with a wing or grabs the dorsum of the leading animal with its feet causing one or both animals to topple through the air and occasionally strike the vegetation below (Banack 1996). Pursuits are initiated from both perched and flying animals and continue until the lead animal exits the territory. These exit points, where the pursuing flying fox ceases pursuit and returns in the direction from which it came, generally occur at visible topographic spots in the landscape (i.e., valley contours or emergent trees such as *Ficus prolixa*—Banack 1996).

Male Samoan flying foxes typically scent mark by rubbing their neck and chin on branches or trunks of trees using secretions produced by a neck gland. Both resource trees and nonresource trees are marked (Banack 1996).

Displays and vocalizations are territorial behavior exhibited by both sexes. Only males, however, chatter and display on highly visible branches (Banack 1996). Males frequently can be seen hanging with both wings open, exhibiting an erect penis, and turning through a 45° arc on the branch. In addition, males often hang with 1 wing outstretched and dangling below the head (Banack 1996). Displays also may include grabbing a bunch of leaves in the mouth and vigorously shaking the head before releasing the leaves (Banack 1996).

CONSERVATION STATUS. *Pteropus samoensis* suffered severe population declines (50–80%) in the late 1980s and early 1990s (Craig et al. 1994; Pierson et al. 1996; Wilson and Engbring, in litt.) and even greater losses in previous decades (Cox 1983). In 1994, population size was estimated at only 500 in American Samoa, increasing to as high as 1,000 in 1996 (P. Craig, pers. comm.; National Park Service, in litt.). Population sizes of *P. samoensis* are consistently lower that those of *P. tonganus* (Pierson et al. 1996).

Pteropus samoensis may be particularly vulnerable to anthropogenic disturbance (including habitat destruction and hunting), but periodic cyclones also contributed to population declines (Cox 1983; Mickleburgh et al. 1992; Pierson et al. 1996). Posthurricane hunting also influenced population declines (Daschbach 1990).

Flying foxes are a delicacy in many Pacific islands and were exported in large numbers to Guam from 1981 to 1984. *P. s. samoensis* (and *P. tonganus*) from Samoa were popular with the Guam consumers because they tasted better and had fewer ectoparasites than other *Pteropus* species (Wiles and Payne 1986). Trade had an enormous negative impact on populations of *P. s. samoensis* in the Samoan islands (Brautigam and Elmqvist 1990).

Pteropus samoensis was listed as a category 2 Candidate Endangered Species under the U.S. Endangered Species Act (Mickleburgh et al. 1992). It was listed on CITES Appendix I in 1989 (Brautigam and Elmqvist 1990). Legislation protecting flying foxes from hunting and exporting was passed in both American Samoa and Western Samoa in 1986 and 1989, respectively (Mickleburgh et al. 1992).

REMARKS. The name *Pteropus* is derived from the Greek *pter(o)* meaning "wing" and *pus* meaning "foot" (Jaeger 1959). The specific epithet, *samoensis*, refers to the type locality of the species, the Samoan Islands.

I acknowledge the assistance of Y. Attallah, W. Z. Lidicker, R. Swamiduai, D. E. Wilson, and 2 anonymous reviewers for assistance in preparing this manuscript.

LITERATURE CITED

ALSTON, E. R. 1874. On a new species of *Pteropus* from Samoa. Proceedings of the Zoological Society of London 1874:96.

ANDERSEN, K. 1912. Catalogue of the Chiroptera in the collection of the British Museum. Second edition. British Museum (Natural History), London.

BAKER, J. R., AND Z. BAKER. 1936. The seasons in a tropical rainforest (New Hebrides). Part 3. Fruit bats (Pteropidae). Journal of the Linnean Society of London, Zoology 40:123–141.

BANACK, S. A. 1996. Flying foxes, genus *Pteropus*, in the Samoan islands: interactions with forest communities. Ph.D. dissertation, University of California, Berkeley, 281 pp.

BANACK, S. A. 1998. Diet selection and resource use by flying foxes (genus *Pteropus*). Ecology 79:1949–1967.

BRAUTIGAM, A., AND T. ELMQVIST. 1990. Conserving Pacific island flying foxes. Oryx 24:81–89.

CASSIN, J. 1858. United States exploring expedition, during the years 1838, 1839, 1840, 1841, 1842., under the command of Charles Wilkes, U.S.N. mammalogy and ornithology. C. Sherman & Son, Philadelphia 8:1–466.

COX, P. A. 1982. Vertebrate pollination and the maintenance of dioecism in *Freycinetia*. The American Naturalist 120:65–80.

COX, P. A. 1983. Observations on the natural history of Samoan bats. Mammalia 47:519–523.

COX, P. A. 1984. Chiropterophily and ornithophily in *Freycinetia* in Samoa. Plant Evolution and Systematics 144:277–290.

CRAIG, P., P. W. TRAIL, AND T. E. MORREL. 1994. The decline of fruit bats in American Samoa due to hurricanes and overhunting. Biological Conservation 69:261–266.

DASCHBACH, N. 1990. After the hurricane. Bats 8(3):14–15.

DOBSON, G. E. 1878. Catalogue of the Chiroptera in the collection of the British Museum. British Museum (Natural History), London.

GRANT, G. S., AND S. A. BANACK. 1995. Predation on *Pteropus tonganus* by a barn owl in American Samoa. Australian Mammalogy 18:77–78.

GRANT, G. S., P. CRAIG, AND P. TRAIL. 1997. Cyclone induced shift in foraging behavior of flying foxes in American Samoa. Biotropica 29:224–228.

GRAY, J. E. 1870. Catalogue of monkeys, lemurs, and fruit bats in the collection of the British Museum. British Museum (Natural History), London.

JAEGER, E. C. 1959. A source-book of biological names and terms. Third edition. Revised 2nd printing. Charles C Thomas, Publisher, Springfield, Illinois.

KOOPMAN, K. F., AND D. W. STEADMAN. 1995. Extinction and biogeography of bats on 'Eua, kingdom of Tonga. American Museum Novitates 3125:1–13.

LECHE, W. 1878. Zur Kenntniss des Milchgebisses und der Zahnhomologien bei Chiroptera. Acta Universitatis Lundensis. Lunds Universitets, Årsskrift 12:1–37.

MARSHALL, A. G. 1983. Bats, flowers and fruit: evolutionary relationships in the Old World. Biological Journal of the Linnean Society 20:115–135.

MICKLEBURGH, S. P., A. M. HUTSON, AND P. A. RACEY. 1992. Old World fruit bats an action plan for their conservation. IUCN/SSC Chiroptera Specialist Group. International Union for Conservation of Nature, Gland, Switzerland.

MILLER, C. A., AND D. E. WILSON. 1997. Pteropus tonganus. Mammalian Species 552:1–6.

NICOLL, M. J. 1904. Observations in natural history made during the voyage round the world of the R. Y. S. 'Valhalla,' 1902–3. The Zoologist: a monthly journal of natural history, 4th Series 8:401–416.

NICOLL, M. J. 1908. Three voyages of a naturalist. Witherby and Co., London.

NOWAK, R. M. 1999. Walker's mammals of the world. Sixth edition. The Johns Hopkins University Press, Baltimore, Maryland 1: 1–836.

PEALE, T. R. 1848. United States exploring expedition, during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N. mammalogy and ornithology. C. Sherman, Philadelphia 8:[17]–338.

PERNETTA, J. C., AND D. WATLING. 1978. The introduced and native terrestrial vertebrates of Fiji. Pacific Science 32:223–244.

PIERSON, E. D., T. ELMQVIST, W. E. RAINEY, AND P. A. COX. 1996. Effects of tropical cyclonic storms on flying fox populations on the South Pacific islands of Samoa. Conservation Biology 10: 438–451.

PIERSON, E. D., AND W. E. RAINEY. 1992. The biology of flying foxes of the genus *Pteropus*: a review. Pp. 1–17 in Pacific island flying foxes: proceedings of an international conservation conference (D. E. Wilson and G. L. Graham, eds.). United States Fish and Wildlife Service Biological Report 90(23):1–176.

RICHARDS, G. C. 1990. The spectacled flying fox, *Pteropus conspicillatus* (Chiroptera: Pteropodidae), in north Queensland. 2. Diet, seed dispersal and feeding ecology. Australian Mammalogy 13:25–31.

RICHMOND, J. Q., S. A. BANACK, AND G. S. GRANT. 1998. Comparative analysis of wing flight behaviour, and habitat use in flying foxes (genus: Pteropus). Australian Journal of Zoology 46:283–289.

SANBORN, C. C. 1931. Bats from Polynesia, Melanesia and Malaysia. Field Museum of Natural History 18(2):7–29.

THOMSON, S. C., A. P. BROOKE, AND J. R. SPEAKMAN. 1998. Diurnal activity in the Samoan flying fox, *Pteropus samoensis*. Philosophical Transactions of the Royal Society 353:1595–1606.

WHITE, C. M., D. J. BRIMM, AND F. CLUNIE. 1988. A study of peregrines in the Fiji Islands, South Pacific. Pp. 275–288 in Peregrine falcon populations: their management and recovery (T. J. Cade, J. H. Enderson, C. C. Thelander, and C. M. White, eds.). Peregrine Fund, Inc., Boise, Idaho.

WHITMEE, S. J. 1874. Excerpts from an untitled letter. Proceedings of the Zoological Society of London 1874:666–667.

WILES, G. J., AND N. H. PAYNE. 1986. The trade in fruit bats *Pteropus* spp. on Guam and other Pacific Islands. Biological Conservation 38:143–161.

WILSON, D. E., AND J. ENGBRING. 1992. The flying fox *Pteropus samoensis* and *Pteropus tonganus*: status in Fiji and Samoa. Pp. 74–101 in Pacific island flying foxes: proceedings of an international conservation conference (D. E. Wilson and G. L. Graham, eds.). United States Fish and Wildlife Service Biological Report 90(23):1–176.

WODZICKI, K., AND H. FELTEN. 1975. The peka, or fruit bat (*Pteropus tonganus tonganus*) (Mammalia, Chiroptera), of Niue Island, South Pacific. Pacific Science 29:131–138.

ZUCKERKANDL, E. 1887. Über das Riechcentrum: eine vergleichend-anatomische Studie. Verlag von Ferdinand enke., Stuttgart.

Editors of this account were ELAINE ANDERSON and LESLIE N. CARRAWAY. Managing editor was VIRGINIA HAYSSEN.

SANDRA ANNE BANACK, DEPARTMENT OF BIOLOGICAL SCIENCE, CALIFORNIA STATE UNIVERSITY, FULLERTON, CALIFORNIA 92834.