BIOTROPICA 32(2): 338–350 2000

Roosting Behavior of Colonial and Solitary Flying Foxes in American Samoa (Chiroptera: Pteropodidae)[1]

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ABSTRACT

We examined characteristics of roosting sites utilized by two flying fox species (*Pteropus tonganus* and *P. samoensis*) in American Samoa. The colonial roosting sites of *P. tonganus* were observed over a ten-year period, including two years when severe hurricanes devastated bat populations and destroyed roost trees. Prior to the hurricanes, roosts were located on cliff faces above the ocean or steep mountainsides, locations that were either inaccessible to people or in protected areas where hunting was not allowed. In the years immediately following the hurricanes, *P. tonganus* colonies split into smaller groups that moved frequently to different locations. Four years after the second hurricane, colonies had coalesced and returned to many of the traditional roosting sites used before the hurricanes. Common tree species in upland and coastal forest were selected as roosts. The isolated locations selected for *P. tonganus* roosts were apparently the result of hunting pressure on the colonies. The solitary roosts of *P. samoensis* were observed during 29 months. Roosting bats were well concealed and hard to detect within the forest; even bats on exposed branches were cryptic. Mature primary forest was favored as roosting habitat. Individual bats used specific branches or trees as roosts and returned to them for up to 29 months. Unlike *P. tonganus*, people did not alarm roosting *P. samoensis* easily and some roosts were located near houses and along roads.

Key words: *bat roost;* Pteropus samoensis; Pteropus tonganus; *Samoa.*

THE MAJORITY OF FLYING FOX FRUIT BATS (Pteropodidae: *Pteropus*), 48 of 56 species, are restricted to islands in the Pacific Ocean. Of these, 61 percent of the genus (35 spp.) are confined to single islands or small island groups (Mickleburgh *et al.* 1992, Rainey & Pierson 1992). Historically, flying foxes have been abundant on Pacific islands, but within recent years there have been dramatic population declines in many island countries (Wiles *et al.* 1989, Fujita & Tuttle 1991, Pierson & Rainey 1992, Bowen-Jones *et al.* 1997). Rapidly expanding human populations, deforestation of large tracts of land, and replacement of traditional hunting methods with shotguns have had drastic consequences on bat populations. While the ecological importance of pteropodid bats in maintaining native forests and agricultural crops is well recognized (Fujita & Tuttle 1991, Rainey *et al.* 1995, Banack 1998), flying foxes are hunted legally in most Pacific island countries and there are few areas where bats or roosting sites are protected.

Unlike most microchiroptera that roost in enclosed spaces such as caves, hollow trees, or buildings, flying foxes typically roost openly on the branches of emergent trees or within the forest canopy (Pierson & Rainey 1992). Most species of flying fox are highly social, forming colonies that range in size from hundreds to over a million individuals (Ratcliffe 1931, Nelson 1965, Eby 1991, Parry-Jones & Augee 1992, Tidemann *et al.*, in press). Suitable roosting sites appear ubiquitous, but flying foxes return to specific fixed sites for many years (Marshall 1983, Tidemann *et al.*, in press). For example, flying fox roosting sites in the Philippines that first were reported in the early 1900s are still in use, although the colonies have been reduced greatly in size (R. Utzurrum, pers. comm.). Other roosting sites in Australia, India, and American Samoa have been in use for at least 60 years (McCann 1934, Tidemann 1985; P. Puaga, pers. comm.).

Two similarly sized pteropodid bat species are found on the islands of American Samoa. *Pteropus tonganus*, the Tongan flying fox, is a highly social species that roosts in colonies of thousands of bats (Pierson *et al.* 1992b). Colonies are extremely noisy and have a distinct odor that makes them easy to detect. *Pteropus samoensis*, the Samoan flying fox, is a solitary and rare endemic of the Samoan and Fijian islands (Pierson *et al.* 1992a). It is one of few species that is active during the day and utilizes thermal updrafts to soar (Thomson *et al.* 1998). Both species are medium-sized pteropodids; adults

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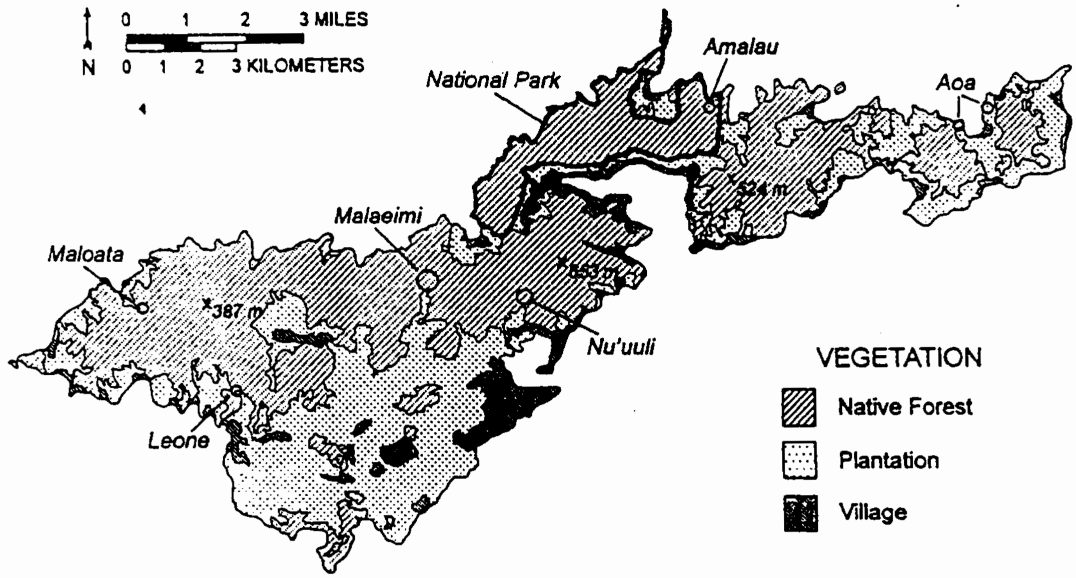

FIGURE 1. Location of *Pteropus samoensis* study valleys, native forest, agricultural forest, and the National Park of American Samoa on Tutuila island, American Samoa.

weigh *ca* 400 to 600 g with a forearm *ca* 130 to 155 mm in length (Brooke 1996). Unlike colonies of *P. tonganus*, *P. samoensis* hang solitarily and are often well hidden, high in dense canopy foliage (Cox 1983, Pierson *et al.* 1992a). The two species differ in foraging behavior: *P. tonganus* feeds within the native forest, in agricultural plantations, villages, or by houses that are at a distance from the forest, while *P. samoensis* forages within or on the immediate edge of native forest (Pierson *et al.* 1992a,b, 1996; Banack 1996; this study). Both species are resident year-round in American Samoa.

The objectives of this study were to characterize roosting sites used by *P. tonganus* and *P. samoensis* on Tutuila island, American Samoa. We wanted to know what type of forest was preferred by *P. samoensis*, why *P. tonganus* colonies preferred certain locations, and what caused colonies to move. The roosting sites of *P. samoensis* were monitored during 1995–1996 when the estimated population on Tutuila was *ca* 900 bats (Brooke 1996). Roost location and characteristics of *P. tonganus* colonies were recorded over a ten-year period (1987–1996), including two years when the island was struck by strong hurricanes: Ofa in 1990 and Val in 1991. In the months following the hurricanes, the *P. tonganus* population declined from 12,000 to 30,000 down to *ca* 1600 bats, largely as a result of overhunting (Craig *et al.* 1994, Pierson *et al.* 1996). The population increased rapidly to *ca* 5000 individuals in 1996 after the enactment of a temporary hunting ban (Brooke 1996).

MATERIALS AND METHODS

This study was conducted in the U.S. Territory of American Samoa (14°S, 170°W) in the South Pacific. Tutuila, the largest island in American Samoa, has an area of 142 km² (30 km long × 9 km across at widest point) and a maximum elevation of 653 m (Fig. 1). The climate is maritime and tropical; the daily mean temperature of 26.7°C has little seasonal variation (Nakamura 1984). Relative humidity is consistently high, between 82 and 86 percent at 1700 h year-round, and rainfall averages 3200 mm annually (Amerson *et al.* 1982). Most of the 54,000 people live along the southern coast and in the Tafuna plain (EDPO 1993). Nearly all of the flat land on Tutuila has been utilized for agricultural crops, but the mountainous interior and north coast is native forest with few villages.

Colonial roosting sites of *P. tonganus* were located for population censuses by the Department of Marine and Wildlife Resources (DMWR). A roosting site was defined as the tree or group of trees where a colony of bats were hanging. Islandwide surveys of all colonies were done from the land and from the ocean. Roosts visible from the ocean were censused in one day by three or four trained observers who circumnavigated the island in a small boat. Access to sites from the ocean was extremely difficult as the rocky shoreline prevented boats from landing. Dense forest and sheer drops restricted overland access to roosting sites. Inland colonies were censused within the same week, either by direct observation during the day or by dispersal counts at dusk. Groups of <10 individuals were not considered a colony. Dispersal counts were done whenever possible because daytime observations of bats roosting in the dense vegetation were found to underestimate colony size.

A single annual survey was done in 1987 and in 1988, a partial survey was completed in 1989, and three to four annual counts conducted from 1990 to 1996. As colonies were located for a population census, data on tree species and height were collected opportunistically. Following the hurricanes in 1990 and 1992, colony size changed rapidly as numbers increased when colonies coalesced and decreased as bats died. We were unable to determine the length of time that each site was used because of the four- to six-month intervals between counts.

Beginning in 1995, data on the solitary roosting sites of *P. samoensis* were collected from six study areas that varied in size from 0.20 to 0.94 km^2 (Fig. 1). Roosts of *P. samoensis* were defined as the tree where an individual bat was hanging. For 29 months (January 1995–May 1997), we surveyed each of the study valleys for roosts at least once a month, and single valleys were visited frequently on a daily basis. We observed *P. samoensis* with Zeiss 10 × 40 (and 10 × 50) binoculars and a Questar spotting scope from distances of 4 to 300 m. Pelage coloration varied considerably among individuals; the body fur was dark brown but the amount of pale white fur on the head and neck differed. Some individuals had only a small patch of white fur on top of the head while the heads, faces, and necks of others were entirely white or grizzled. The shoulders, necks, and heads of some males were orange to dark russet in color. Several bats had broken the terminal phalanx, the third metacarpal, which caused the wing tip to be permanently upturned. We used a combination of these unique markings to identify individuals in the field.

The elevation, slope, and distance to the nearest house for *P. tonganus* roosting sites was measured from a USGS topographic map (1: 24,000). Tree species used for roosts were identified in visits to 29 colonial roosts of *P. tonganus* and 28 individual roosts of *P. samoensis*. For both species, the type of forest where roosts were located was determined from vegetation maps in Cole *et al.* (1988) and the National Park of American Samoa Management Plan (National Park Service 1996). For *P. samoensis* roosts, we measured slope and distance to the nearest house. Since roosts of *P. samoensis* were observed only in the six study valleys, a small subset of the available habitat, the elevation of roost trees was not considered.

We were interested in how the abundance of trees that were food sources for bats differed among the six study valleys; however, the steep valley walls made it impossible to sample vegetation by transects or plots. We assumed that trees with a large canopy area produced more fruit or flowers than trees with a small canopy and thus were a more valuable resource. To quantify the differences among the valleys, we calculated the percent canopy cover of 49 tree species in 18 to 42 circular plots per valley; plots measured *ca* 6 m in diameter as defined by the field of view of a Nikon 15× spotting scope. We observed the forest from approximately the same distance to maintain a similar plot size. Three common secondary growth species that *P. samoensis* had been observed eating only once following the recent hurricanes were considered as starvation foods (rather than part of the typical diet) and were excluded from the analysis (*Hibiscus tiliaceus, Rhus taitensis, Alphitonia zizyphoides*).

RESULTS

PTEROPUS TONGANUS.—Colonies varying in size from 10 to ca 4000 individuals were found at 63 locations between 1987 and 1996 (Fig. 2; Table 1). Small groups of *P. tonganus* hanged in a single tree while large groups of several hundred or more bats were scattered through many trees encompassing entire hillsides or points protruding out into the ocean. Tall trees, but not necessarily canopy emergents, were used as roosts. The height of 90 trees in 25 roosting sites varied between 3.6 and 30.5 m ($\bar{x}$ = 15.5 m, SD = 6.5). Both the shortest and tallest trees were used following Hurricanes Ofa in 1990 and Val in 1991.

Within the thin band of coastal forest, there were a total of 21 roosting sites (Table 1). Coastal forest is a short and dense forest type found in a narrow zone at low elevations along the ocean and is limited to only 187 ha on Tutuila (Cole *et al.* 1988). Roosts in coastal forest were on cliffs or steep slopes immediately above the ocean. The mean elevation of coastal roosting sites was 67 m (range = 7–153 m) and was lower than the mean

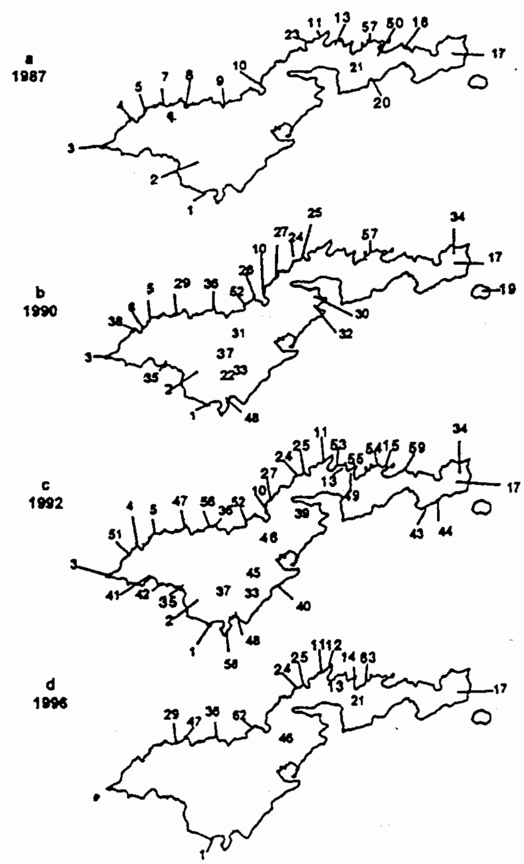

FIGURE 2. Colonial roosting sites of *Pteropus tonganus* on Tutuila island, American Samoa (1987–1996). (a) 1987; (b) 1990 (the year of Hurricane Ofa); (c) 1992 (the year following Hurricane Val); and (d) 1996.

elevation of roosting sites in upland forest (141 m, range = 14–457 m), although there was some overlap at lower elevations. The dominant species (most numerous) found in the littoral zone of coastal forest were *Barringtonia asiatica, Calophyllum inophyllum. Pisonia grandis, Erythrina variegata, Thespesia populnea, H. tiliaceus, Cocos nucifera, Hernandia nymphaeifolia,* and *Pandanas tectorius* (Cole *et al.* 1988).

Thirty-eight roosting sites were located in upland forest, the dominant vegetation type on Tutuila (Table 1). Upland forest covers *ca* 6950 ha in valleys and on ridges up to the high elevations (Cole *et al.* 1988). Prior to the hurricanes, the canopy height of some mature trees exceeded 24 m. Upland forest contained numerous species; the dominant species of montane areas included: *Dysoxolum huntii, Agaia samoensis, Arytera* spp., *Flacourtia rukam, Inocarpus fagifer, Terminalia richii, Canarium samoense, Myristica fatua, M. hypargyraea, Buchanana merrillii,* and *Syzygium samoense* (Cole *et al.* 1988). The dominant species of lowland ridges were *Syzygium inophylloides, Planchonella linggenus, Fagraea berteriana, C. samoense, Intsia bijuga, R. taitensis,* and *A. zizyphoides* (Cole *et al.* 1988).

Only after the hurricanes in 1990 and 1992 were roosting sites found in agricultural forest (N = 4; Table 2). This forest type, found near villages, along the coast, and in valleys, is a mixture of native trees and cultivated plants that include coconuts (*C. nucifera*), breadfruit (*Artocarpus altilis*), bananas (*Musa* spp.), papaya (*Carica papaya*), and mango (*Mangifera indica*) (Cole *et al.* 1988).

We found 22 tree species used by *P. tonganus* in roosts (Table 3). The most frequently used, *B. asiatica, C. inophyllum, E. variegata,* and *Dysoxylum maota,* were among the most common species in coastal and upland forests (Cole *et al.* 1988, Whistler 1994). Roost trees included a high percentage of species that were part of the bats' diet (18 of 22 spp.; Table 3).

In 1987, when the *P. tonganus* population was estimated to be 12,000–30,000 individuals, 18 roosts were located on cliff faces above the ocean or isolated mountainsides (7 in coastal forest and 11 in upland forest; Fig. 2a; Table 2). The distance from the three roosts on the southern side of Tutuila to the nearest human habitation ($\bar{x}$ = 415 m, SD = 353) was not significantly different from that of roosts on the northern coast ($\bar{x}$ = 733 m, SD = 569, Mann-Whitney rank-sums test, P = 0.4).

As the population declined to *ca* 4600 after Hurricane Ofa in 1990, colonies fractured into smaller groups and the total number of roosts increased from 18 to 26 (Fig. 2b; Table 2). Following Hurricane Val in December 1991, the population dropped to 1600 individuals and colonies again split into smaller units (Fig. 2b; Table 2). None of the roosts were used continuously during the year after Hurricane Val, and we saw colonies only once at 29 of the 41 roosting sites. In the months immediately after both hurricanes, some colonies relocated near villages. Roosts on the southern side of Tutuila were significantly closer to human habitation than roosts on the northern side of the island (1990: northern side $\bar{x}$ = 917, SD = 946, N = 13, southern side $\bar{x}$ = 190, SD = 256, N = 9. Mann-Whitney rank-sums test, P = 0.014. 1992: northern side $\bar{x}$ = 771, SD = 723, N = 20, southern side $\bar{x}$ = 337, SD = 296, N = 14, Mann-Whitney rank-sums test, P = 0.01). In 1990 and

TABLE 1. *Roosting sites of* Pteropus tonganus *colonies (1987–1996) on Tutuila island, American Samoa. Locations refer to numbered sites in Figure 2; year (no. of surveys); mean size of colony (no. of times colony present). X denotes colony present but the number of individuals was not counted. Forest type: C = coastal forest; U = upland forest; A = agricultural or plantation forest with coconuts (Cole et al. 1988).*

Fig. 2 No.	Forest type	Location	1987 (1)	1988 (1)	1989 (1)	1990 (4)	1991 (3)	1992 (4)	1993 (3)	1994 (4)	1995 (3)	1996 (3)
1	C	Fagatele Bay	4000	3000	300	130 (4)	750 (3)	280 (3)		10 (1)	1230 (3)	1730 (3)
2	U	Leone	X			45 (1)		40 (1)				
3	C	Taputapu	300	X	X	15 (1)	25 (1)	20 (2)	10 (1)			
4	C	Fagalea Pt.	400				325 (1)	80 (1)				
5	C	Leelee Pt.	450	500		110 (2)	50 (1)	30 (2)				
6	U	Fagafaga Pt.				225 (1)		70 (1)				
7	U	Oalii Cove	200									
8	U	Aoloautuai	X	1000	X							
9	C	Site Bay	X	600								
10	U	Siufaga	600	500	2000	190 (1)		85 (1)				
11	C	Polauta Ridge, W.	1000	1000	X			30 (1)	15 (1)	130 (1)	250 (2)	100 (1)
12	C	Polauta Ridge, N.						60 (1)			180 (1)	300 (3)
13	U	Amalau	X					10 (1)	400 (2)		400 (2)	200 (2)
14	U	Oa		500		840 (1)	100 (1)	50 (1)		340 (3)	270 (2)	300 (3)
15	U	Vainuu Mt.			X			X				
16	C	Masausi	X									
17	U	Olomoana Mt.	4000	3000	3000	200 (3)	185 (2)	30 (1)	300 (1)	120 (3)	140 (1)	320 (3)
18	C	Pofala Hill		100	1000		200 (1)					
19	C	Fogatia Hill			X	X	200 (2)					
20	U	Alega	X									
21	U	Mt. Pioa	X									
22	U	Faleniu				245 (1)						100 (1)
23	U	Vaaogeoge Cove	1000	X								
24	U	Puaneva Pt.				350 (1)	210 (2)	120 (1)	500 (1)	325 (2)	300 (2)	475 (2)
25	U	Nuutoga Pt.				400 (1)		220 (1)				750 (1)
26	U	Cape Larsen			X	200 (1)	250 (1)		30 (1)			
27	U	Leutu Pt.				425 (1)	275 (2)	80 (3)				
28	U	Falenili					100 (1)					
29	U	Tolotolooleoti Pt.				200 (1)	1175 (2)	200 (2)	975 (2)		600 (1)	250 (1)
30	U	Mt. Alii				30 (1)						
31	U	Tuasivitasi Ridge				200 (1)						
32	U	Utulei				15 (1)						

TABLE 1. *Continued.*

Fig. 2 No.	Forest type	Location	1987 (1)	1988 (1)	1989 (1)	1990 (4)	1991 (3)	1992 (4)	1993 (3)	1994 (4)	1995 (3)	1996 (3)
33	A	Ili'ili				60 (1)		20 (1)				
34	U	Lefutu Ridge				40 (2)	20 (1)	40 (1)				
35	A	Asili				110 (4)		20 (1)				
36	C	Siliaga Pt.			2000	275 (2)	245 (3)	100 (2)	370 (2)	560 (4)	275 (2)	850 (2)
37	U	Olavalu Crater		1000		860 (4)	395 (3)	150 (1)	875 (3)	1220 (3)		
38	U	Faga Pt.				135 (1)						
39	U	Tepatasi						50 (1)				
40	A	Fogogogo					50 (2)	75 (2)	X			
41	U	Nuamasetaga						10 (1)				
42	A	Afao						65 (2)				
43	C	Leva Pt.						30 (1)				
44	C	Mataesolo						40 (1)	350 (1)			
45	U	Tafuna Forest						85 (2)				
46	U	Fagotogo							400 (1)	360 (2)		160 (1)
47	U	Nu'uomanu Rock					25 (1)	30 (1)	375 (2)	1025 (4)	1000 (1)	880 (2)
48	C	Fogamaa Crater				X	500 (3)	40 (1)				
49	U	Gatia Pt.						80 (1)				
50	U	Masefau	500	X								
51	C	Leopard Pt.						30 (2)				
52	C	Agalua Rock				200 (1)		40 (3)	130 (1)			
53	U	Vatia Bay						100 (1)				
54	U	Lepua Pt.						30 (1)				
55	C	Tapisi Pt.						45 (1)				
56	U	Nuutavene Rock						20 (1)				
57	U	Ogetu Ridge	300	700		840 (1)	50 (1)	30 (1)				
58	C	Fagalua						75 (1)				
59	C	Tiape'a Pt.						40(1)				
60	U	Samitu'utuu Pt.							70 (1)	450 (1)		
61	U	Aunu'u West		600								
62	C	Tafaga Cove					100 (1)				250 (1)	
63	C	Vainuu Pt.									450 (1)	

TABLE 2. *Characteristics of* Pteropus tonganus *roosts on Tutuila island, American Samoa.*

Year	Estimated population	Mean colony size (range)	Roosts per forest type: Coastal	Upland	Agricultural	Mean slope (range in °)	Mean distance to nearest house (range in m)
1987	12,000–30,000	1927 (200–4000)	7	11	0	45 (26–70)	730 (70–1810)
1990	4600	261 (10–510)	18	7	2	43 (0–71)	672 (2–2784)
1992	1600	62 (10–400)	16	22	4	44 (0–71)	580 (0–2784)
1996	6000	550 (50–2100)	6	9	0	51 (30–71)	1179 (209–2784)

1992, four roosts were on flat land, two in agricultural plantation and two in upland forest. The other roosts were in coastal (N = 34) and upland forest (N = 29) on steeply sloped terrain (Table 2). Roosts closest to people were protected by cliffs (Fig. 2C, no. 11) or on privately owned land where hunting was not allowed (Fig. 2, nos. 1 and 37).

Four years after Hurricane Val, in 1996, the population had increased to *ca* 5000 individuals using 15 sites. All of the roosting sites were on slopes above the ocean in coastal forest (N = 6) or hillsides in upland forest (N = 9). Only one roost was in a location that had not been used within the past nine years. Distance to the nearest house, slope, and elevation of roosts used in 1996 were not significantly different from roosting sites used in 1986.

Distance from houses may not be as important as how accessible the roosting site is to people. Roosts that were near villages, but separated by extremely steep ridges or cliffs, were used for several years. For example, two roosting sites that were *ca* 250–300 m from Vatia village (Fig. 2, nos. 11 and 12) were protected by steep ridge and cliff.

No roosting sites were occupied constantly throughout this study or used continuously in the years after the hurricanes (Table 1); however, once a preferred site was established as a roost, colonies tended to use it repeatedly. It was difficult to document whether roost abandonment resulted from hunting, human disturbance, or was unrelated to human activity. When we approached a *P. tonganus* colony overland on foot, the bats flew long before the observers got within 50 m of the roost. The abandonment of a large colony at Olavalu crater (Fig. 1, no. 37) in 1994 and its relocation to Fagatele Bay (Fig. 1, no. 1) may have resulted from gunshots or firecrackers, which were heard regularly at dusk as bats exited to forage (S. Saucerman, pers. comm.). The colony at Olomoana Mt. (Fig. 1, no. 17) temporarily abandoned their roost after a road was constructed nearby, and an unknown number of bats were shot illegally in 1994. The colony fragmented into smaller groups of 50 to 200 individuals that moved frequently between temporary roosts but was reestablished at a less accessible site on Olomoana Mt. within two months. The colony at roost no. 11 (Fig. 1) abandoned the site after a landslide swept away the roost trees.

TABLE 3. *Tree species used by* Pteropus tonganus *and* P. samoensis *for roosting or feeding on Tutuila Island, American Samoa. Letters indicate what part of the tree was eaten: Fr = fruit; Fl = nectar and flowers; L = leaves; * = DMWR observation;* [1] *= Cox 1983;* [2] *= Rainey* et al. *1995.*

Species	Part eaten	*P. tonganus* roosts	*P. samoensis* roosts
Barringtonia asiatica	Fr, Fl (*)	15	
Calophyllum inophyllum	Fr (*)	13	1
Dysoxylum maota	Fr (1)	12	1
Erythrina variegata	L, Fl (*)	12	
Rhus taitensis	Fr (*)	9	
Alphitonia zizyphides	Fr (*)	9	
Ficus obliqua and *F. prolixa*	Fr (*)	8	3
Planchonella samoensis	Fr (*)	6	1
Myristica spp.		5	
Dysoxylum samoense	Fr (1)	4	
Cananga odorata	Fr (*)	2	
Syzygium inophylloides	Fr, Fl (*)	2	6
Pisonia grandis		2	
Fagraea berteriana		2	
Hibiscus tiliaceus		2	
Diospyros samoensis	Fr (*)	1	
Terminalia richii	Fr (2)	1	2
Inocarpus fagifer	Fr, L (*)	1	1
Canarium vitiense	Fr (2)	1	
Neonauclea forsteri		1	
Artocarpus altilis	Fr (2)	1	
Garuga floribunda	Fr (2)	1	
Unidentified dead tree		1	13

PTEROPUS SAMOENSIS.—*Pteropus samoensis* used a series of branches in different trees as roosts. Solitary bats were remarkably cryptic and hard to distinguish on any roost as they blended with the leaves and branches. The most obvious roosts were on dead branches at the top of hurricane-damaged trees, although these prominent roosts were not used on a daily basis.

Roosting bats were seen most frequently soon after dawn when they hanged from exposed dead branches ($N = 145$, d = 60). As the ambient temperature increased, bats retreated beneath the forest canopy; by midday, it was uncommon to see bats on exposed branches. In one day of dawn-to-dusk observations, we saw a male move 12 times between four trees. The bat roosted on three highly visible branches outside of the forest canopy for periods of 8 to 81 minutes ($\bar{x} = 23.2$ min, SD = 14) and roosted within the canopy for 8.7 hours.

We identified 68 roosting sites in the six study valleys and were able to distinguish 22 individual bats that returned to specific branches. We observed these 22 bats using 28 trees for varying periods: 6 bats were observed for 1 to 2 months, 5 bats for 3 to 5 months, 5 bats for 6 to 11 months, and 7 bats for 12 to 28 months ($\bar{x} = 9$ mo, SD = 8.4). The greatest number of roosts were in dead trees that we could not identify; roosts in living trees were most often in *S. inophylloides*, an abundant species with particularly dense wood that withstood hurricane damage ($N = 6$; Table 3). The 15 tree species used as long-term roosts all produced fruits that *P. samoensis* consumed (Table 3). Roosts were identified frequently along ridge crests where bats were silhouetted against the sky, although roosts also were found along the shoreline and at the bottom of valleys in relatively flat areas. The mean slope of the terrain where roost trees were located was 52° (range = 20–68°, $N = 28$). Roost branches were *ca* 5–20 m above the ground. The majority of roosts were in upland forest ($N = 26$); only two roosts were located in coastal forest. Five of the seven tree species were common in coastal and upland forest. Only *D. maota* and *Planchonella samoensis* were not among the most abundant species (Table 3; Cole *et al.* 1988). The mean distance from roosts to the nearest house was 648 m (range = 250–1125 m, $N = 28$). Houses were not present in the Amalau valley, and when it was excluded from analysis, the mean distance to the nearest house was 397 m (range: 250–625 m, $N = 14$).

Unlike *P. tonganus*, roosting *P. samoensis* were not frightened easily and did not fly quickly when approached by people. We routinely stood directly beneath roosting bats that were indifferent to our presence. A large *Ficus obliqua* that hanged over the road to Vatia village was a favored roost of an adult female and a juvenile *P. samoensis* during 1995 and 1996. The bats were not affected by vehicles, periodic roadside clearing by the village, or foot traffic passing *ca* 6–15 m below where they hanged from slender branches. Because *P. samoensis* rarely took flight when disturbed, the bats roosting in the fig were easily overlooked and few people were aware of the roost.

TABLE 4. *Percentage of canopy fruiting trees and number of* Pteropus samoensis *roosts by study valley on Tutuila island, American Samoa.*

Valley	Area of valley (km^2)	No. of Roosts	Valley area in edible tree spp. (%)
Amalau	0.26	13	54.4
Maloata	0.34	8	72.1
Leone	0.20	4	25.4
Aoa	0.61	1	35.0
Nu'uuli	0.57	0	38.9
Malaeimi	0.94	2	40.5

Roosts were most numerous in valleys with the largest percentage of trees that produced foods (Table 4). We identified 47 canopy tree species in the six valleys, of which 22 were known to be eaten by *P. samoensis*, and estimated the percentage of tree considered part of the diet (Table 4; Appendix 1; Banack 1996). The two valleys with the greatest number of roosts, Amalau ($N = 13$) and Maloata ($N = 8$), had the largest percentage of canopy food trees in the areas sampled; however, the number of roosts was not significant when compared to the other study valleys (Mann-Whitney signed-ranks test, $P = 0.68$).

We encountered several confounding factors when trying to compare study valleys. Although the forest in the Malaeimi valley was third in number of fruit-producing canopy trees (40.5%), it had the smallest number of roosting sites ($N = 2$; Table 4). We heard gunshots on several occasions and spoke with a family living in the valley who said that they routinely shot bats. The constant hunting pressure in this area was likely the cause of the low number of roosting sites. The Leone valley had the smallest number of canopy food trees (25%) but had four roosting sites (Table 4). This valley had large amounts of secondary-growth species typical of disturbed areas. The forest surrounding the study site, just over a low ridge, had not been cut and was not badly damaged by the recent hurricanes. The Leone study valley contained a large area that was not utilized by bats, while relevant habitat, mature forest to the west and north, was not included in our study.

DISCUSSION

The behavior of pteropodid bats from the isolated islands in the Pacific Ocean is poorly known. Most information on roosting sites of flying foxes comes from Australia where colonies roost near food sources and migrate seasonally to follow fruit and flower resources (Parry-Jones 1986, Eby 1991, Richards 1990, Spencer *et al.* 1991, Parry-Jones & Augee 1992, Tidemann *et al.*, in press). In Micronesia, colony size and roosting sites of *P. mariannus* vary greatly on different islands and with the amount of hunting pressure (Wiles 1987; Wiles & Conry 1990; Wiles *et al.* 1991, 1997). The natural history and ecology of solitary flying fox species is essentially unknown (Mickleburgh *et al.* 1992, Pierson & Rainey 1992, Flannery 1995).

Human disturbance at roosting sites appears to be a strong influence in the selection of roosts for *P. tonganus*. The obvious and noisy colonies rely on isolated locations, the protection of cliffs above the ocean and the steep hillsides of inland forest, to discourage people from approaching roosting sites. Bats appear to select roost trees that produce fruits that are part of the bats' diet, but the number of trees we examined may be too small to determine if this is accurate. The degree of loyalty to roosting sites is somewhat unpredictable because of hurricanes, landslides, and human intervention. Even with these disturbances, *P. tonganus* colonies returned to preferred sites for extended periods of time.

Unlike the *P. tonganus* sites, the solitary and cryptic roosts of *P. samoensis* were difficult to locate. The greatest number of *P. samoensis* roosts were in Amalau and Maloata valleys, where the least amount of hurricane and human disturbance had occurred. These two valleys and the surrounding forest contain some of the most pristine lowland forest remaining in the Samoan archipelago (Whistler 1994). The most obvious roosts on dead branches or protruding tree branches, where bats hanged in the early morning, may be used to display or advertise an individual's presence in its home range. As all of the living roost trees bore fruit that *P. samoensis* fed on, roosts may be part of the bats' defended feeding territory (Pierson, Elmquist, & Cox 1992). Roosts used during the heat of the day were typically well concealed by foliage. Long-term investigations of *P. samoensis* are lacking, but our observations suggest that favored roost trees are used for an extended time as some bats we observed returned to roosts for the duration of this study. The ease with which we approached roosting bats and the proximity of roosts to houses indicate that roosting *P. samoensis* have not been subjected to the same hunting pressure as *P. tonganus*.

Since enactment of the hunting ban in 1992, populations of both species have increased (Brooke 1996). Continued hunting pressure on *P. tonganus* roosts has been sufficient that inaccessible locations used before the hunting ban are still favored. Roosting sites on flat land and near villages were used temporarily following hurricanes only when resources were scarce (Dashbach 1990, Pierson *et al.* 1996). While roosting *P. samoensis* are cryptic or well hidden, the bats' diurnal soaring flight makes them easy targets for hunters with slingshots or shotguns. *Pteropus samoensis* was hunted regularly in the Malaeimi valley and some hunting still occurs within the National Park (on the road through Amalau valley and on the Park's boundary along the Alava Mt. Road; Brooke 1998). The new National Park of American Samoa, established in 1988, relies on community support to enforce its no-hunting regulation, but this is a novel concept not yet accepted by everyone.

In American Samoa, as throughout the South Pacific region, bat hunting is part of the culture of indigenous peoples, and bats are a traditional delicacy (Sinavaiana & Enright 1992). Since the arrival of Polynesians in the South Pacific *ca* 3000 years ago, hundreds of local populations of bats and birds have been hunted to extinction on small islands (Koopman & Steadman 1995, Steadman 1995). On Pacific islands where there is active hunting, bats are extremely wary of people, roost in inaccessible locations, and abandon roosts when disturbed (Wodzicki & Felten 1975, Wiles 1987, Falanruw 1988). Wiles and Glass (1990) watched a *P. mariannus* colony on Guam take flight after winds revealed the scent of biologists observing the bats. Hunting at *P. mariannus* roosts on Guam has caused colonies to move repeatedly (Wiles 1987). On the Yap islands, *P. mariannus* moved into mangrove swamps where roosts were difficult to reach when hunting pressure increased (Falanruw 1988). In Niue, Wodzicki and Felten (1975) reported colonies of *P. tonganus* solely from the Tapu Sanctuary of the Huvalu Forest, the only part of the island where hunting was forbidden.

Where roosting bats are not hunted, large colonial roosts are easily visible and accessible. A colony of several hundred *P. tonganus* roosts in the middle of the village of Kolovai, Tonga, where the bats are under the protection of the King of Tonga. The bats at Kolovai are habituated to people and visited daily by tour groups (Grant 1996). Another conspicuous roost is located at a private residence on a main road in Suva, Fiji (A. Brooke, pers. obs.). The roosts in Suva and Kolovai are subjected to noise and human activity but both sites are protected from hunting.

The causes of colony movements are difficult to predict because of the various disturbance factors. Traditional roosts and local movements in Australia of *P. poliocephalus*, *P. conspicillatus*, and *P. scapulatus* colonies have been linked to the availability of food resources (Nelson 1965, Parry-Jones 1986, Richards 1990, Eby 1991, Parry-Jones & Augee 1992). In American Samoa, both *P. tonganus* and *P. samoensis* commuted from roosts that were used throughout the year to foraging areas, although local abundance of fruit attracted short-term aggregations of both species. Banack (1996) credited a high density of flowering *Palaquium stehlinii* trees as the cause of one *P. tonganus* roost shift. A temporary group of *ca* 60 *P. samoensis* and *ca* 80 *P. tonganus* that roosted in adjacent trees in the Amalau valley for two days also may have been in response to an abundance of fruit or flowers (Brooke 1996).

The response of solitary and colonial bats to the destruction of roosts by hurricanes in American Samoa differed. *Pteropus samoensis* had strong site fidelity and remained within the forest valleys well away from villages (Pierson, Elmquist, & Cox 1992). In contrast, colonies of *P. tonganus* splintered into small groups that moved frequently after the major storms (Pierson *et al.* 1996). A similar pattern of colonies that fractured after hurricanes also has been noted in *P. conspicillatus* (Richards 1990). Initial roost changes were probably in response to hurricane destruction of the forest, but some later shifts were likely the result of increased hunting. In the months after Hurricane Ofa, both bat species increased the amount of time spent searching for foods in the native forest (Grant *et al.* 1997).

A potential reason for bats to shift position within a roost or move to a new location is to lessen infestations of ectoparasites that have a portion of their life cycle away from the animal host (Marshall 1982, Lewis 1996). At least three of the ectoparasties from flying foxes in American Samoa, the bat fly *Cyclopoda inclita* (Diptera: Nycteribiidae) and the bat mites *Neolaelaps spinosus* (Acarina: Laelapidae) and *Meristaspis calcarata* (Acarina: Spinturnicidae), have a life stage that does not require a host bat (N. Wilson, pers. comm.). Within a roost, bats frequently moved among trees, shifting the entire roost across hillsides over time (Grant & Banack 1995; this study). Such small-scale movements may effectively limit parasitic infestations while retaining the benefits of a protected site. Ectoparasites probably exert little influence over the major roosting movements in American Samoa. These shifts appear to be more strongly associated with human disturbance and severe storms that destroy roost trees.

Pteropus samoensis is dependent on mature forest for roosting and foraging habitat. The rarity of other solitary flying fox species suggests they may have a similar reliance on mature forests. *Pteropus tonganus* is more amenable to living with people and is not constrained by native forest for roosting or foraging habitat. Like other colonial species, roosts of *P. tonganus* are vulnerable to hunters, and colonies seek protection in isolated, inaccessible, or protected roosting sites.

ACKNOWLEDGMENTS

This paper synthesizes data collected by N. Bartley, P. Craig, H. Freifeld, G. Grant, E. Henry, P. Iose, T. Morrell, B. Ponwith, S. Samuelu, E. Seui, K. So'oto, W. Styron, P. Trail, and F. Tuilagi from the Department of Marine and Wildlife Resources, Pago Pago, American Samoa. N. Wilson kindly identified bat ectoparasites. Suggestions from H. Freifeld, E. Pierson, M. Tschapka, K. Whitman, and two anonymous reviewers greatly improved the manuscript. This study was supported by the Federal Aid to Wildlife Restoration Act administered by the U.S. Fish and Wildlife Service.

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APPENDIX 1. *Percent canopy cover of trees in* Pteropus samoensis *study valleys. Valley name is followed by the number of plots in parentheses. Species eaten by* P. samoensis *are in bold. Part eaten: Fr = fruit; Fl = flowers; L = leaves; S = sap (reviewed in Banack 1998).*

Tree species	Parts eaten	Amalau (28)	Aoa East (30) West (22)	Malaeimi (40)	Leone (18)	Nu'uli (42)	Maloata (40)
Pipturus argenteus	L, S	2.7		0.3		0.1	1.3
Buchanania merrillii		2.9		3.4	1.1	2.5	
Inocarpus fagifer	Fr, L	2.7	2.5		0.6	0.7	0.8
Ficus uniauriculata	Fr	0.7					
F. obliqua	Fr	3.8	2.7				1.3
F. prolixa	Fr	2.5	4.2				1.0
F. tinctoria	Fr					0.1	
Ficus sp.	Fr	1.6		0.1			
Hibiscus tiliaceus		4.1	25.3	12.8	1.4	8.3	3.8
Syzygium inophylloides	Fr, Fl	2.8	1.5	5.1	10.0	9.0	5.1
Barringtonia samoensis		0.4		0.3		1.7	0.5
B. asiatica	Fr, Fl	0.4	2.3			1.0	
Dysoxylum sp.		11.6	11.4	11.6	5.0	12.4	11.9
Dysoxylum maota	Fr	3.4					
Fagraea berteriana	Fr	3.0	0.3			1.2	2.0
Bischofia javanica		3.9		2.9	0.3	0.1	4.3
Rhus taitensis		11.8	19.2	20.1	42.8	18.0	0.3
Alphitonia zizyphoides		3.8	5.5	2.5	5.6	7.9	1.3
Canarium vitiense	Fr	18.0	2.3	3.3	9.2	5.0	34.6
Planchonella samoensis	Fl	6.3		13.4		7.4	12.1
P. grayana	Fr					0.6	
Palaquium stehlinii	Fr, Fl			4.5		0.7	
Cananga odorata	Fr, Fl	4.5	1.1	6.4	1.4	0.7	5.0
Kleinhovia hospita		0.8	1.3				
Elattostachys falcata		0.2					
Neonauclea forsteri	Fl	6.4	0.4	2.8	3.9	6.3	10.0
Macaranga stipulosa		0.9		0.8		1.7	
M. harveyana		1.1	0.4	0.4	6.7	0.7	1.0
Myristica fatua			2.7	1.9	5.3	2.9	2.8
Cocos nucifera	Fl		8.6			0.4	
Sterculia fanaiho			0.1	1.3			
Artocarpus altilis	Fr		0.3				
Adenanthera pavonina			1.3		5.8		
Elaeocarpus ulianus	Fr, Fl		0.3	3.0		3.9	
Terminalia catappa	Fr		2.0				
Thespesia populnea			0.2				
Cerbera manghas			0.6				
Glochidion ramiflorum			0.2				
Diospyros sp.	Fr		2.3	2.1		1.9	0.1
Crossostylis biflora			0.1				
Calophyllum neo-ebudicum			0.3			1.9	
Samanea saman				0.8			0.6
Olmolanthus nutans						0.4	
Castilla elastica							0.5
Leucosyke corymbulosa				0.5			
Paraserianthes falcataria						1.8	
Cinamonum verum					1.1		
Unidentified						0.8	