

**BIOLOGY OF THE FLYING FOXES IN AMERICAN SAMOA: *PTEROPUS*
SAMOENSIS AND *PTEROPUS TONGANUS*.**

A REPORT TO THE NATIONAL PARK OF AMERICAN SAMOA

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Introduction

The Order Chiroptera is divided into two sub-orders, the Microchiroptera which has a worldwide distribution and the Megachiroptera which is limited to the Old World tropics. The Megachiroptera consist of a single family, the Pteropodidae or old world fruit bats, found from the eastern Mediterranean, African sub-tropics throughout southeastern Asia, Australia and islands in the Pacific ocean. Within the Pteropodidae, there are 41 genera consisting of 161 species (Koopman 1993). The largest and best known genera, *Pteropus*, has 57 species commonly known as flying foxes. 55 of these species (or 96.5%) are island dwelling, with some or the entire species' range on islands in the Pacific ocean. There are a large number of island endemics, 35 species, that are confined to a single island group or a single island. Nine species are found on continental areas, five in Asia, five in Australia. Only two species are found on continents but not on islands (Mickleburgh et al. 1992).

Megachiropteran bats are generally more robust and possess a suite of physical characteristics that distinguish them from Microchiropterans including large eyes, small, simple ears lacking a tragus, a small claw on the third finger, and large, well developed thumbs. Megachiroptera rely on vision rather than echolocation for navigating at night. The diet of Megachiroptera consists primarily of fruit, nectar, pollen, and leaves (Mickleburgh et al. 1992) although there are reports of Megachiroptera occasionally eating sap (P. Craig; P. Trail personal communication), insects, (Funakoshi et al. 1993) and fish (Ghose and Ghosal 1983). The evolutionary history of bats is not well known and the fossil record scant. Whether the order has a diphyletic origin or is monophyletic is contested. (Pettigrew et al. 1989; Baker et al. 1991). The earliest known occurrence of *P. tonganus* and *P. samoensis* (subspecies unknown) are from Eua, Tonga, and predate the human colonization of Polynesia (Koopman and Steadman 1995)

Physical description

The two species of pteropodid bat found in American Samoa, *Pteropus tonganus* and *P. samoensis*, are similar in size but differ greatly in social organization, roost site choice and reproductive potential. *Pteropus samoensis*, the Samoan flying fox, is a medium sized pteropodid that weighs 300-500g and has a forearm length of 130-155 mm. Males are slightly larger than females (Brooke 1997). Body fur is dark brown while the top of the head and face of some individuals is silver-gray. The shoulders and neck of males can be dark red. Fur on the back of the neck is long and dense giving the head a rounded appearance. The white collared or Tongan flying fox, *P. tonganus*, has a distinctive white or yellow mantle that extends from behind the ears to the shoulders. The pale fur does not extend to the chest. When compared with *P. tonganus*, *P. samoensis* has a shorter rostrum, longer and denser fur. *Pteropus samoensis* has a lower aspect ratio, lower wing loading, and longer more pointed wingtips than does *P. tonganus* (Brooke 1997; Norberg et al. 1997). Distinguishing between the two species in flight can be difficult however *P. samoensis* wings appear to be broader and deeper than *P. tonganus* (Craig 1992; Wilson and Engbring 1993)

General natural history

Social behavior

Pteropus tonganus roost in colonies that may have several thousand individuals (Pierson et al. 1992b). Grant and Banack (1995) described a 'harem' type of sociality where a single male defended females roosting in his territory from other males. Young were born throughout the year.

Pteropus samoensis most commonly roosts solitarily, in pairs (male and female or female and young), or small family groups of a female, male and a single young (Cox, 83; Pierson and Rainey 92; Wilson, 1993; Banack, 1996). Each individual has a series of roost branches, some in exposed locations others within the canopy, that are used repeatedly (Cox 1983; Pierson et al. 1992a; Banack 1996; Brooke 1997).

Activity Patterns

Pteropus samoensis has been described as active diurnally or foraging mostly during the day by numerous authors (Cox 1983; Pierson et al. 1992a; Wilson and Engbring 1993; Craig et al. 1994; Morrell and Craig 1995; Banack 1996; Grant et al. 1997). The amount of diurnal activity changes throughout the year, influenced by the flowering of *Syzygium inophylloides* trees and temperature (Thomson et al. in press). In addition to foraging during the day, *P. samoensis* is also active at night (Banack 1996; see section on Foraging habitat).

Reproductive biology, development, growth, and longevity

Most bats in the genus *Pteropus* are seasonal breeders having defined times of mating and parturition (Pierson and Rainey 1992; O'Brien 1993). *Pteropus samoensis* has a broad but seasonal reproductive pattern while *P. tonganus* is one of three species known to give birth throughout the year (Pierson and Rainey 1992). Like other bats in this genus, both *P. tonganus* and *P. samoensis* give birth to a single young.

Data from wild animals on development, growth, maturity, and longevity are lacking for all Pteropodid species and inferences have been made from captive animals. The age at first reproduction for pteropodids is thought to be ca. two years and gestation for most species between 4-6 months (Pierson and Rainey 1992). Young are weaned when 3-4 months old but may remain associated with their mother for a year (Nelson 1965a; Pierson and Rainey 1992). Pteropodid bats are thought to be long lived in the wild, with a lifespan around 20 years. In captivity, a *P. giganteus* lived 31 years (Jones 1982; Pierson and Rainey 1992). The age of first flight in the wild is believed to be between two and three months. Three *P. tonganus* raised in captivity in 1996-1997 began to fly when their forearm had reached 85-95 mm. in length, around 50 days old and they were capable fliers by 80-90 days old (Brooke 1997).

Pteropus samoensis has a broad seasonal reproductive pattern that varies slightly from year to year. Between 1992-1996, females carrying young were seen in all months of the year except

February (Banack 1996; Brooke 1997). Most young were seen in June, when the number of small, medium and large pups was nearly equal. Only a single pup was observed in December and in January. Copulations have been observed only August-December although Banack attributed vocalizations to mating events in March. The timing of copulations in October 1995 and the May-June 1996 birth peak indicate gestation period of 5-6 months (Brooke 1997)

Pteropus tonganus

Species range

Pteropus tonganus has the widest range of pteropodid bats in Oceania (reviewed by Koopman and Steadman 1995). The range extends from the Schouten Islands and Karkar Island off northern Papua New Guinea (Rainey and Pierson 1992), eastward to the southern Cook Islands, including the Solomon Islands, Vanuatu, New Caledonia, Wallis and Futuna, Fiji, Tonga, Samoa, and Niue (Wodzicki and Felten 1975; Nowak 1991; Rainey and Pierson 1992). *Pteropus tonganus* is found on the outlying islands in the Solomon Islands but not the larger islands. The small populations on Rarotonga and Mangia in the Cook Islands are the easternmost limit of Pacific megachiropterans (Wodzicki and Felten 1980; Tiraa 1992). *Pteropus tonganus* is currently found on all the major islands in the Samoan archipelago: 'Upolu, Savai'i, Tutuila, Ta'u, 'Ofu, 'Olosega. Two roost sites were present on Aunu'u prior to hurricane Val (December 1991) that were abandoned after the storm. It is likely that *P. tonganus* forage on Aunu'u currently.

Wilson and Engbring (1993) reviewed the taxonomy and nomenclature of *P. tonganus* and described the three extant subspecies. The most western is *P. tonganus basiliscus*, restricted to the islands off the coast of New Guinea. *Pteropus tonganus geddiei* is found in New Caledonia, the Solomon Islands and Vanuatu. *Pteropus tonganus tonganus* is the easternmost subspecies, with a distribution covering the Samoan archipelago, the Cook Islands, Fiji, Niue, Tonga, Wallis and Futuna (Mickleburgh et al. 1992)

Archeological records from Mangaia, Cook Islands, show that *P. tonganus* was hunted and eaten since at least 1000y BP (Steadman and Kirch 1990). *Pteropus tonganus* were probably extirpated from Aitutakim, Ma'uuke, and two other islands in the Cook Island group during the early years of Polynesian settlement (Steadman and Kirch 1990). Based on this evidence, it seems likely that other populations on small and isolated islands could have been exterminated by the early Polynesians.

Europeans have written of flying foxes in the South Pacific islands since the mid-1800s. In most accounts, only a general note is given that bats were common. Peale (1848) comments: "In the Friendly (Tonga), Feejee, and Samoan or Navigator's Islands they are numerous, each group of islands having its peculiar species. Their spectral appearance is one of the characteristics in the wild and varied scenery; their strong odour taints the atmosphere of the otherwise fragrant forests...". Stair (1887) wrote of an epidemic that killed great numbers of flying foxes in Western Samoa but did not mention anything of the population size before the disease struck or the number of bats that died.

Recent and current population levels

Current population estimates are not available for all the islands within the range of *P. tonganus tonganus* and the numbers reported from most islands are from extremely limited observations (Table 1). Early population estimates were speculative but it is evident that large declines from hunting have occurred on Niue and the Cook Islands. The population in Western Samoa also seems to be much lower than in the mid-1980s, based on the number of bats that were killed following the recent hurricanes. Tonga and Fiji have the largest populations remaining. Bats are legally protected in few areas: the Tapu Forest Sanctuary on Niue, the Kolovai colony in Tonga, and throughout American Samoa. All pteropodids are listed as protected species under the International Union for the Conservation of Nature and Natural Resources (IUCN) for international trade.

Table 1. *Pteropus tonganus tonganus* abundance.

Country	Island	Date	# Observed	Reference
Tonga	Tongatapu	1986	many	Gil 1987
	‘Eua	1986	few	Gil 1987
	Tongatapu	1995	3,600	Grant 1996
	13 unnamed islands	1995	6,000	Grant 1996
Niue		1873	many	Brenchley 1873
		1968	0	Wodzicki & Felten 1975
		1994	few	Grant 1996
Fiji	Viti Levu 1 roost	1949	thousands	Pierson et al. 1992b
	Viti Levu 1 roost	1989	5,000	Wilson & Engbring 1992
	Loma Loma	1995	300	Brooke 1997
Cook Islands	Mangaia	1989	>1000	Steadman 1990
	Rarotonga	1992	>1000	Pierson et al. 1992
Wallis and Futuna			unknown	
Western Samoa	Savai’i 1 roost	1990	5,636	Pierson et al. 1996
		1995	0	Pierson et al. 1996
	‘Upolu 1 roost	1995	1,800	Brooke 1997
American Samoa	Tutuila	1987	20,000-30,000	Brooke 1997
		1992	1,600	Craig et al. 1994
		1996	6,000	Brooke 1997

Island group accounts

Tonga

In 1986, Gil (1987) noted large colonies on Tongatapu at Kolovai and Tofoa but only a few scattered individuals were found on 'Eua. Grant (1996) observed ca 10,000 individuals on Tonga; 3,600 in seven major roosts on Tongatapu, and another ca 6,000 from 25 roosts on 13 other islands. The report doesn't indicate how many of the 170 islands were visited by boat. The roost in the village of Kolovai is well known as a sanctuary where bats are legally protected. The island of Tongatapu has little if any native forest remaining and bats must forage on agricultural fruits.

Niue

Several early European records from Niue mention *P. tonganus*. In 1873, Brenchley observed "a great number flying at considerable height during daylight". In 1902, Smith (in Pierson et al. 1992b) considered bats common and noted that large flocks were seen flying overhead. In 1926 Loeb (in Pierson et al. 1992b) mentioned that bats were abundant in the early 1900s. By 1968 populations had declined severely, in 1968 and 1969, Wodzicki and Felten saw no flying bats (Wodzicki and Felten 1975; Wodzicki and Felten 1980). In 1994, Grant saw few *P. tonganus*, and found only slight evidence of other bats in the form of fruit remains and chop pellets (Grant 1996). Interviews with hunters suggest that there is a sizable population as hunting estimates ranged from 1,200 to 5,000 taken annually, although this was not quantified.

Fiji

There is no estimate of the population in Fiji. Degener (in Pierson et al. 1992b) spoke of a roost of 'thousands' in the forest at Naruka during the 1940s. Pernetta and Wattling (1978) described *P. tonganus* as widespread. A brief survey by United States Fish and Wildlife Service (USFWS) and Bat Conservation International (BCI) located a colony near Suva of ca 5,000 individuals in 1989 (Wilson and Engbring 1992). Wattling recently noted the disappearance of colonies from traditional roost sites (Pierson et al. 1992b). In 1995, Brooke located a small roost in Suva and saw several hundred bats flying to Loma Loma Island from nearby island of Vanua Balavu.

Cook Islands

Archeological records from Mangaia, Cook Islands, show that *P. tonganus* was hunted and eaten since at least 1000y BP. Bats were probably extirpated from Aitutaki, Ma'uke and two other islands in the Cook Island group during the early years of Polynesian settlement (Steadman and Kirch 1990). In recent years, Wodzicki and Felten (1980) described a population decline of 50% to 75% from hunting. Steadman speculated that fewer than 1,000 individuals remained on Mangaia in 1989 and a lesser number were present on Rarotonga (Pierson et al. 1992b). Hunting and loss of forest are credited with the low numbers of bats in the Cook Islands.

Wallis and Futuna

Nothing is known of the current or past status of bats on Wallis and Futuna although some bats were collected for the Paris Museum in the 1970s (Pierson and Rainey 1992).

Western Samoa

The population in Western Samoa was reduced by commercial hunting for export during the 1980's (Wiles 1992), habitat destruction from agricultural clearing and logging, and hunting after the recent hurricanes (Pierson 1993). There is no estimate of what the population was before the hurricanes or what it is currently. During the 1980s approximately 33,000 bats (both *P. tonganus* and *P. samoensis*, species combined) were sent to Guam to satisfy market demand (Wiles 1992). During the peak years of the trade, 1983-1986, 6,500-8,300 bats were shot annually. Prior to the hurricanes of 1990 and 1991, Wilson and Engbring (1993) watched "...a large flyway of *P. tonganus* move across the Tafua road ..." on Savaii. Pierson (et al. 1996) counted 5,636 individuals at this colony in early January 1990 just before Hurricane Ofa. Pierson also found evidence of a small colony near Falealupo. After Hurricane Ofa (January 1990) and hurricane Val (December 1991), Pierson (et al. 1996) estimated that the population at Tafua Tai declined by 90-99%. In 1995, this colony was no longer evident at Tafua Tai when Brooke visited. On 'Upolu, Cox (1983) noted *P. tonganus* flying inland at dusk over Safata Bay at Sataoa. As this site is on the southern coast, the bats were most likely moving from a roost in the adjacent forest rather than a long distance over water. At the southeastern end of 'Upolu near Vailoa, Brooke observed 1,800 *P. tonganus* exiting at dusk from a small steeply sided crater. The large number of bats that Wilson and Engbring (1993) watched flying across the road near Togitogiga were probably from this same crater.

American Samoa

The first population estimate of bats on Tutuila was made by Amerson (et al. 1982), in 1975 and 1976, who thought that only one species of pteropid was found in American Samoa. Consequently, both *P. tonganus* and *P. samoensis* were included in their estimate. The large roosts they described were undoubtedly *P. tonganus* colonies. A major roost was found at Fagatele Point and "...smaller roosts elsewhere". A large colonial roost was noted on the isolated southeast slope of Fogatia hill on Aunu'u island.

Amerson (et al. 1982) also surveyed the Manu'a islands. The colonial roost on Nu'utele islet on 'Ofu was most likely a *P. tonganus* colony. They observed bats, probably *P. samoensis*, along the cliffs along the south coast of 'Ofu, the cliffs above 'Olosega village and Sili villages, and along the east coast, north of Leala point. On Ta'u they reported bats roosting throughout the island (most likely *P. samoensis*) and noted bats above the plantation land above Fagamalo cove and in the lowland rainforest above Papaotoma point. The observations of foraging bats on Ta'u could have been either *P. tonganus* or *P. samoensis*.

The population estimates made by Amerson (et al. 1982) were taken from seasonal observations in 14 community study plots and calculated by multiplying the observed density in a habitat by the acreage of habitat on all islands on which they occur. Linear surveys were also used for abundance estimates although how the data was collected and the estimates reached is not described. They estimated that a total of 140,000 bats were present in American Samoa; 75,700 from Tutuila and 65,000 on the Manu'a islands. It is likely that they observed *P. tonganus* using flyways from roosts combined with *P. samoensis* diurnal foraging to reach this extremely large number. Wilson and Engbring (1993) questioned the validity of Amerson's bird and bat population estimates after a 1986 USFWS survey found 10 times fewer birds than the earlier

study. The later population figures are so much lower than Amerson's estimate it seems unlikely their numbers had any validity.

Several different numbers have been used as the pre-hurricane population estimate because the 1987 and 1988 Department of Marine and Wildlife Resources (DMWR) surveys include estimates from colonies that were not visited during the census. In 1987 12,750 bats were seen at eight colonies. The mean number of bats per colony was then applied to another 10 colonies that were not visited during the census count, but known to have bats, to arrive at a total island estimate of 28,000 individuals. The same methodology was used in 1988 when 13,000 bats were observed at 8 colonies and another 5,000 bats estimated at 5 colonies that were not visited. While the total population estimate for these years is highly speculative, the estimated number of bats at Fagatele Bay seems to be low; 4,000 in 1987 and 3,000 in 1988. The area used by roosting bats covered ca 400 m x 100 m on the western side of the bay. Pierson et al.s (1992b) report of ca 5,000 bats at Fagatele Bay prior to Hurricane Ofa was taken from the DMWR estimates. In 1996, the roost covered less than 100 m x 30 m. when the evening exit counts tallied 2,100. From the 1996 exit counts and Person's' observations, it seems likely DMWR underestimated the 1987 and 1988 population by several thousand animals at Fagatele Bay and potentially at other sites.

Wilson and Engbring (1992) casually gathered data on colony sizes in 1986 but made no attempt to visit all known roosts. They counted 3,169 bats in flight from a photograph of a section of the colony at Fagatele Bay. From this picture, they estimated the colony consisted of ca. 5,000 individuals. Wilson and Engbring (1992) conservatively estimated the island-wide population to be 12,000 individuals in 1986. In 1989, DMWR estimated 12,000 individuals at 8 of the 18 known colonies. It seems reasonable to assume that the *P. tonganus* population before hurricane Ofa was much larger than these estimates.

Current surveys in American Samoa

The Department of Marine and Wildlife Resources (DMWR) tries to survey the *P. tonganus* population on Tutuila four times and survey the Manu'a islands once annually. The way that bats were counted has changed during the past ten years and the methods used for the 1987-1989 counts is no longer followed. During 1987-1988, the number of roosting bats was estimated in each colony by observers with binoculars, then bats were flushed from trees by loud noises and the number of bats in flight was estimated. Only a partial island survey of roosts was done in 1989 consequently data from that year in the population estimates is not included. In 1990-1991, following Hurricane Ofa, opportunistic counts were done of colonies as they were located. Systematic quarterly surveys of Tutuila began in 1992. The number of *P. tonganus* flying over survey sites was also counted during monthly surveys for *P. samoensis*, 1990-1994, following the protocol used by (Wilson and Engbring 1992)

Pteropus tonganus typically roosts in colonies that remain at the same location for several months or years (Brooke et al manuscript). During DMWR surveys all known colonies on Tutuila are counted within a week. Observers in a small boat circumnavigate the island watching for roosts. The number of bats hanging in trees and any bats flying is estimated by 3-4 trained observers. Estimates made from the moving boat of bats hidden in foliage are probably inaccurate under the

best of circumstances. Roosts that are not visible from the ocean are visited at dusk when bats are counted as they leave the roost. Because of dense vegetation of some roosts, exit counts give a better estimate of *P. tonganus* populations than daytime roost counts. All roosts visible from the ocean are counted in one day, exit counts from inland roosts are done within the same week.

Figure 1 summarizes DMWR population estimates for Tutuila, 1987-1996. This period covers the time prior to the hurricanes when the population was large, the decline following each storm, and the ongoing recovery.

Manu'a

Little effort has been put into assessing the Manu'a *P. tonganus* population by anyone. Amerson (et al. 1982) reported an estimated population of 65,000, of both species. Wilson and Engbring (1992) did not count *P. tonganus* on Manu'a. Currently, DMWR counts the *P. tonganus* annually during the dusk and dawn *P. samoensis* surveys (Table 2). Under these conditions, sightings of *P. tonganus* are opportunistic and do not accurately reflect the population size. In 1995 was an effort made to locate colonies and estimate the number of bats at roosts. Consequently, the initial population estimates of *P. tonganus* are very low.

On Ta'u a small crater next to Judds crater, known locally as laulatiti (little crater), had a colony of ca 1,000 in July 1996. In October 1996 DMWR counted ca 500 in laulatiti and another ca 1,000 bats exiting at dusk from the Lepue crater suggesting a population of at least 1,500. It is very likely that the bats move between these two roost sites when one site is disturbed. Other roosts are likely to be found on all three islands.

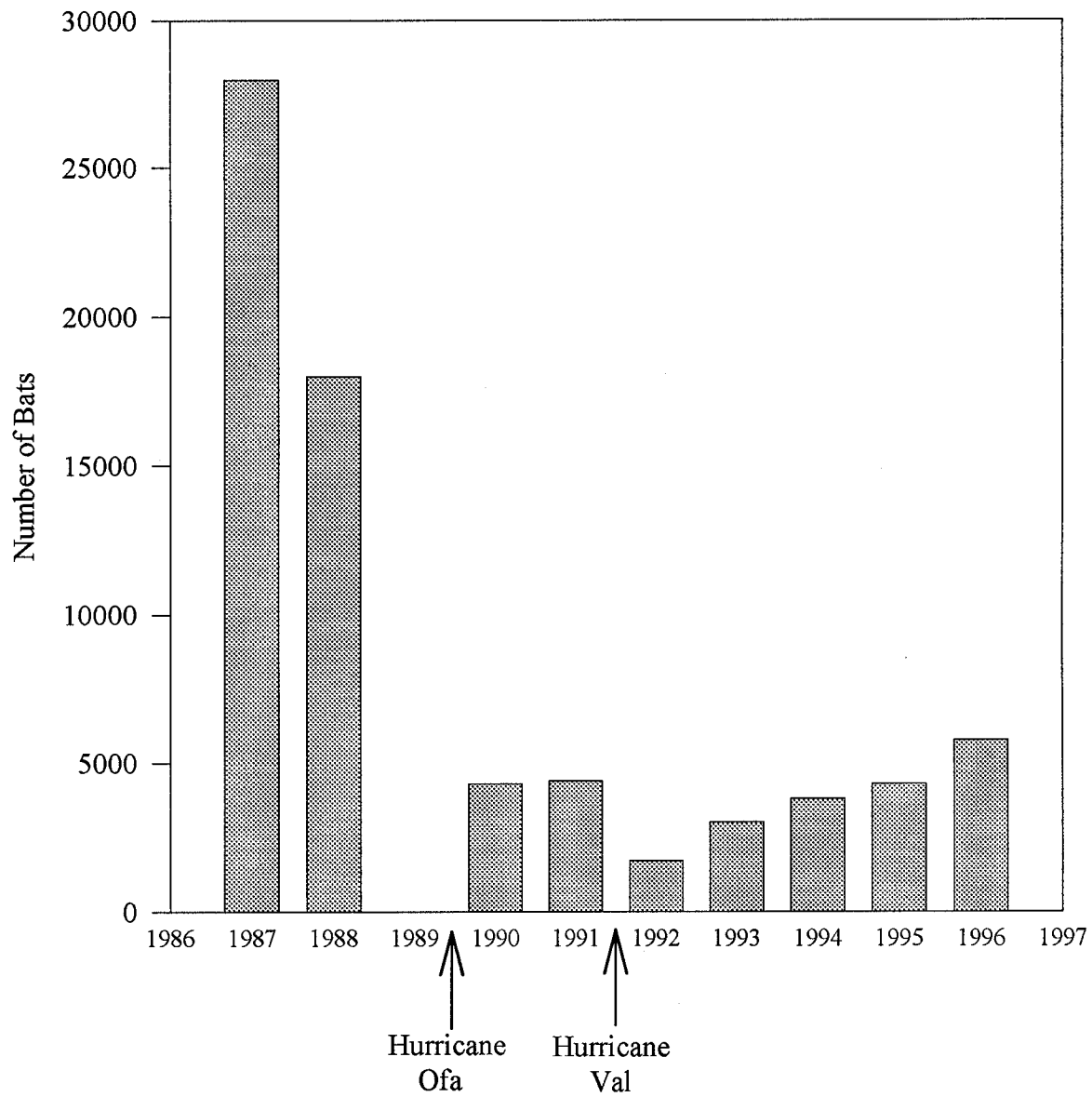
Accurate counts of the Manu'a population are complicated by the probable movement of bats among the three islands. The 11 km between Ta'u and 'Olosega is well within the nightly flight range of *P. tonganus*. In the Northern Marianas Islands, *P. mariamus* is thought to regularly travel 29-100 km between islands (Wiles and Glass 1990). Grant and Banack (1995) followed a radio collared juvenile male one night that flew from Olavalu crater to Alofau, a round trip distance of 46.7 km.

Table 2. DMWR Manu'a *Pteropus tonganus* counts.

Year	'Ofu	'Olosega	Ta'u
July 1990	9	10	14
July 1992	13	26	49
July 1993	305	15	21
Nov. 1994	250	100	40
Oct. 1996	250	20	1,500*

* combined from exit count at Lepue crater and roost estimate at laulatiti.

Fig. 1 DMWR *Pteropus tonganus* population estimate from roost counts, Tutuila island, 1987-1996

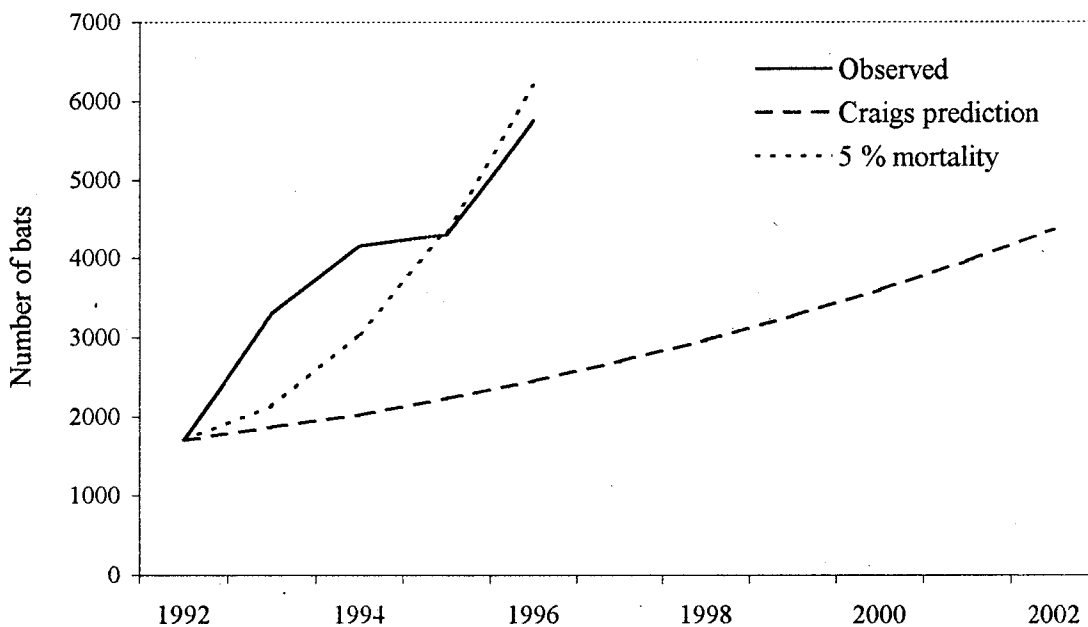


Post-hurricane population growth

There has been a rapid increase in the population following the extreme low population after hurricane Val. The hunting ban, television and radio spots immediately following the storm, and ongoing educational campaign have helped to limit the number of bats killed.

Craig (et al. 1994) predicted the post-hurricane population growth of *P. tonganus* both with and without hunting using a model developed by Pierson and Rainey (1992). The model assumes a 50/50 sex ratio at birth, one young born annually, sexual maturity at 2 years, 60% survivorship of young the first year and 80% adult survivorship annually (Fig. 2). Craig et al. predicted it would take 15-20 years to reach a population of 12,000. Four years after Hurricane Val, the population is ca 6,000 individuals. Clearly, the parameters of the model are not a good representation of the current situation. The closest fit line to the observed population growth 1992-1996 is a model with one year to sexual maturity (not two), one pup born annually, and 5% mortality for the entire population. There is no data on longevity for any wild pteropodid bat. The rapid population increase suggests there has been little mortality and that many bats have been added to the population.

Figure 2 Projected and observed population growth for *P. tonganus*, Tutuila



Craig et al (1994) model using 60% survival at year 1, 80% survival at year 2 and above.
Total population in year $t = (2)[(\text{number of mature females in year } t-1)(0.8) + (\text{number of mature females in year } t-2)((0.5) (0.6) (0.8))]$, where 0.5 = female births

Grant and Banack (1995) frequently observed post-partum copulations where the female had dependent young and suggested that *P. tonganus* may reproduce more than once a year as has been predicted for *P. marianus yapensis*. Falanruw (1988a) found that body weight was a factor in the age at which *P. marianus yapensis* reached sexual maturity. She found pregnant females weighed greater than 291g while those with a smaller body weight but larger forearm length were still immature and not pregnant. Like *P. tonganus*, *Pteropus marianus yapensis* breeds continuously throughout the year and Falanruw's observations of matings with females carrying dependent young is similar to the observed behavior of *P. tonganus*. Falanruw (1988a) speculated that females go into post-partum estrous when their offspring are 3 months old. Female *P. marianus* could produce a pup at nine month intervals if they have a six month gestation period and care for the young for three months. In Australia, female *P. melanotis* mature rapidly and can become pregnant at 6 months old while males take up to 18 months to reach sexual maturity (Tidemann 1992).

There is very little known of the reproductive capabilities of female *P. tonganus*: the age or size of females' first successful pregnancy, if females reproduce at less than one year intervals, and if a female is able to continue to reproduce that frequently. Females may give birth to two pups within an 18 month period but not conceive again for a time.

It seems likely that where bats have abundant food resources they can reach the minimal size needed for reproduction at an earlier age than when resources limited. The 'founding' population after Hurricane Val had little competition from other bats and a plentiful supply of foods several months after the storms, an optimal time to realize maximal reproductive potential. Because there is no estimate of what the population size was prior to the hunting in the 1980s, there is no estimate of the population that can be supported on Tutuila. Limited resources should slow population growth but it is unknown if that will occur with a population of 10,000 or 100,000 individuals. If the current population growth continues on Tutuila, the *P. tonganus* population is likely to exceed 12,000 individuals by the year 2,000. This is the most conservative population estimate from 1987.

Immigration from Western Samoa or the Manu'a islands can not be completely ruled out as a possible explanation for the rapid population increase although it seems unlikely that large numbers of individuals immigrated to Tutuila. While there were no sightings of bats flying over the ocean or of bats coming in from the ocean, a small amount of immigration from Western Samoa is expected and nocturnal movements may not be observed. Inter-population mtDNA testing is in progress and will provide a quantitative assessment of the similarity of the bats throughout the Samoan archipelago.

Monitoring

Past programs, problems and limitation

The two methods used by DMWR to estimate *P. tonganus* colony size both are problematical. More accurate estimates are obtained by counting bats as they exit the roost at dusk. This requires a good vantage point of a well used flyway, where flying bats are silhouetted against the sky.

Estimating the number of roosting *P. tonganus* from a moving boat is extremely difficult and estimates can differ greatly among observers. To get the best island-wide estimate, all roosts should be monitored within a few days so that bats are not counted twice at different roosts. Maintaining consistency in observers helps to minimize variation in counts but changes in personnel at DMWR make year to year continuity difficult.

Roosts of *P. tonganus* within the National Park are currently on the north coast of Tutuila. Exit counts at these sites would be very difficult so the best way to monitor the colonies is from a small boat. Currently, DMWR makes a quarterly trip along the north coast to look for new roosts and count bats at known roosts.

DMWR attempts to survey all *P. tonganus* roosts quarterly, including all roosts within the National Park. As long as DMWR continues the surveys, it seems sensible to coordinate with them when possible. The *P. samoensis* dawn surveys that are done by DMWR include Amalau but not other sites within the National Park. Coordinating surveys of other park areas when DMWR survey Amalau would enhance both agencies data collection. Because DMWR visits Manu'a only once a year, both agencies would benefit from any surveys done by National Park staff on a regular basis. Three of the six *P. samoensis* survey sites on Ta'u are within the National Park.

Roost Sites

Trends in numbers and size of roosts

Pteropus tonganus colonies roost in traditional sites that are used for long periods of time. Tree species and height are less important than steep slopes, and a location that's protected from human intervention. It is not uncommon for small groups of *P. tonganus* to form temporary aggregations and single bats may also roost near fruiting trees they defend (Wodzicki and Felten 1975; Banack 1996; Brooke 1997). Roost movements can be initiated by human disturbance, the loss of habitat from hurricanes, or bats may shift roosts temporarily to take advantage of a temporary food resource (Banack 1996; Brooke et al. manuscript).

The movement of *P. tonganus* colonies before, following each hurricane, and four years after hurricane Val was described by Brooke et al. (manuscript). Prior to hurricane Ofa (January 1990) a population of ca 20,000-30,000 bats was found in 27 roosts on Tutuila. The two largest colonies in 1987, Fagatele Bay and Olomoana mountain, each had 4,000 or more bats (mean number of bats/roost = 1,927, range = 200-4,000, Table 3 and Fig. 3). All roosts were located in coastal or upland forest (Cole et al, 1988) and were on hillsides or cliff faces (mean slope = 30°, range 26°-71°). The distance from the three roosts on the southern side of Tutuila to nearest human habitation was not significantly different from that of roosts on north coast.

The year following hurricane Ofa, 1990, the population dropped to ca 4,600. Bats were observed at 26 roosts (mean of 261 bats/roost, range = 10-510). In late December 1991, hurricane Val struck Tutuila. During 1992 the population declined to ca 1,600 bats and 37 roosts were observed (mean of 62 bats/roost, range = 10-400). Most roosts (33 of the 37 roosts) were used for less than 3 months and none were used continuously in 1992. The number of roost sites on the

southern side of the island, increased from 3 in 1987, to 9 in 1990, and to 15 in 1992 (Table 3 and Fig. 3). Following both hurricanes, roosts on southern side of Tutuila were located significantly closer to human habitation than roosts on the northern side of the island.

By 1996, four years after hurricane Val, the population had increased to ca 6,000 and 13 roosts were observed (mean of 550 bats/roost). Colonies ranged in size 50-2,100. All roosts were located in native forest and were on steep hillsides or cliffs (mean slope 54°, range 39°–71°). Eleven roost sites had been used previously within the past nine years and four of these sites had large colonies prior to the hurricanes. Fagatele bay had the largest colony and was also the closest to people but the area is protected from hunting and marine traffic is restricted. Distance to the nearest house, slope, and elevation of roosts used in 1996 was not significantly different from roost sites used in 1986.

Characteristics of roosts and roost sites

Colonies consisted of both small groups in a single tree and large groups of 1,000-5,000 individuals spread out across hillsides. The greatest number of roosts have been found in upland forest (n=36). Upland forest is the dominant climax vegetation on Tutuila where the forest canopy can exceed 24 m and trees reach up to 1 m dbh (Cole et al. 1988). 21 roosts were located in coastal forest, a shorter and more tightly spaced forest prevalent on steep coastal slopes (Cole et al. 1988). After hurricanes Ofa and Val, four roosts were located in mixed native forest and agricultural food-producing trees (coconut *Cocos nucifera*, breadfruit *Artocarpus altilis*, and bananas *Musa* spp.). One roost was in the scrub forest on a steep point over the ocean.

Bats were observed roosting in 22 tree species at 29 roost sites between 1989-1996. Roost trees were common forest species that attain large size, with the exception of one secondary growth species, *Hybiscus tiliaceus*, found at two roosts (Table 4). Bats roosted in these shortest trees, 3 m, in the years immediately following the hurricanes. Both the tallest and shortest trees in roosts were found at the same site, Olavulu crater, suggesting that tree height was less important than the roost site. Eighteen tree species (75%) that bats used as roosts were also used for food (Table 4).

The selection of roost trees is different on the various islands and may well reflect the islands vegetation more than a preference for tree species. On Niue, *P. tonganus* preferred to roost in *Planchonella torricellensis*, *Ficus prolixa*, and *Syzygium richii* trees (Wodzicki and Felten 1975). On Rarotonga, bats roosted in *Cananga odorata*, *Cerbera manghas*, *Guettarda speciosa*, *Homalium acuminatum* (Wodzicki and Felten 1980). Roosts of 20-100 bats were rare and only found in the Tapu Sanctuary where hunting was restricted (Wodzicki and Felten 1980).

The village of Kolovai, on the island of Tongatapu, Tonga, has a well known colony that is protected from hunting by the King of Tonga. When visited in 1995 by Brooke, bats roosted in Australian pine (*Casuarina equisetifolia*) and mango trees along roads and in the village.

Table 3 *Pteropus tonganus* roost sites.

Monitored colony roost sites from 1987, 1990, 1992, 1996 (Brooke et al. manuscript).

Map # Fig. 3	Location	Elev. (m)	Slope (degrees)	Distance to nearest house (m)
1	Fagatele bay	56	50	766
2	Leone	70	40	70
3	Taputapu	70	64	1322
4	Fagalea point	70	45	731
5	Leelee point	70	64	174
6	Fagafaga point	70	51	244
7	Oalii cove	61	46	1392
8	Aolautai	63	50	1810
9	Site bay	50	40	1500
10	Fagasa, Siufaga	63	42	244
11	Polauta ridge, west	70	45	244
12	Polauta ridge, north	104	52	313
13	Amalau	335	71	900
14	Oa	139	55	487
15	Vainuu Mt	90	53	244
16	Masausi	20	26	150
17	Olomoana Mt	213	51	696
18	Pofala hill	70	35	661
19	Fogatia hill	70	45	766
20	Alega	120	43	400
21	Mt Pioa	457	43	1100
22	Falenu	14	0	70
23	Vaaogeoge cove	63	26	557
24	Puaneva point	104	71	1531
25	Nuutoga point	70	64	2018
26	Cape Larsen, Tafaga cove	70	45	244
27	Leutu point	97	45	56
29	Tolotolooleoti point	111	60	2366
30	Mt Alii	14	32	21
31	Tuasivitasi ridge	456	35	418
32	Utulei	42	45	2
33	Ili'ili	14	0	10
34	Lefutu ridge	139	31	278
35	Asili	70	64	139
36	Siliaga point	56	39	2784
37	Olavalu crater	70	40	209
38	Faga point	60	42	200

Map # Fig. 3	Location	Elev. (m)	Slope (degrees)	Distance to nearest house (m)
39	Tepatasi ridge	174	31	175
40	Fogogogo	174	31	180
41	Nuamesetaga	153	24	0
42	Afao	56	34	0
43	Leva point	30	45	900
44	Mataesolo	12	45	300
45	Tafuna forest	21	0	170
46	Fogotogo bird transect	278	46	487
47	Nu'uomanu rock	70	64	1740
48	Fogma crater	97	45	418
49	Gatia point	30	27	200
50	Masefau, south of village	130	32	300
51	Leopard point	30	25	300
52	Agalua rock	91	45	1000
53	Vatia bay	36	60	700
54	Lepua point	30	47	600
55	Tapisi point	104	40	800
56	Nuutavene rock	36	45	300
57	Ogetu ridge	61	45	800
58	Fagalua	30	65	700
59	Taipe'a point	30	45	600
60	Samitu'utuu point	66	50	1800
61	West of Pofala hill	40	25	700
62	Tafaga cove	122	63	800
63	Vainuu point	30-60	30	1000

Figure 3. *Pteropus tonganus* roosts sites on Tutuila, 1987, 1990, 1992, 1996.
Roost locations identified in Table 3 (Brooke et al. manuscript.) Four roosts located in
other years are not included

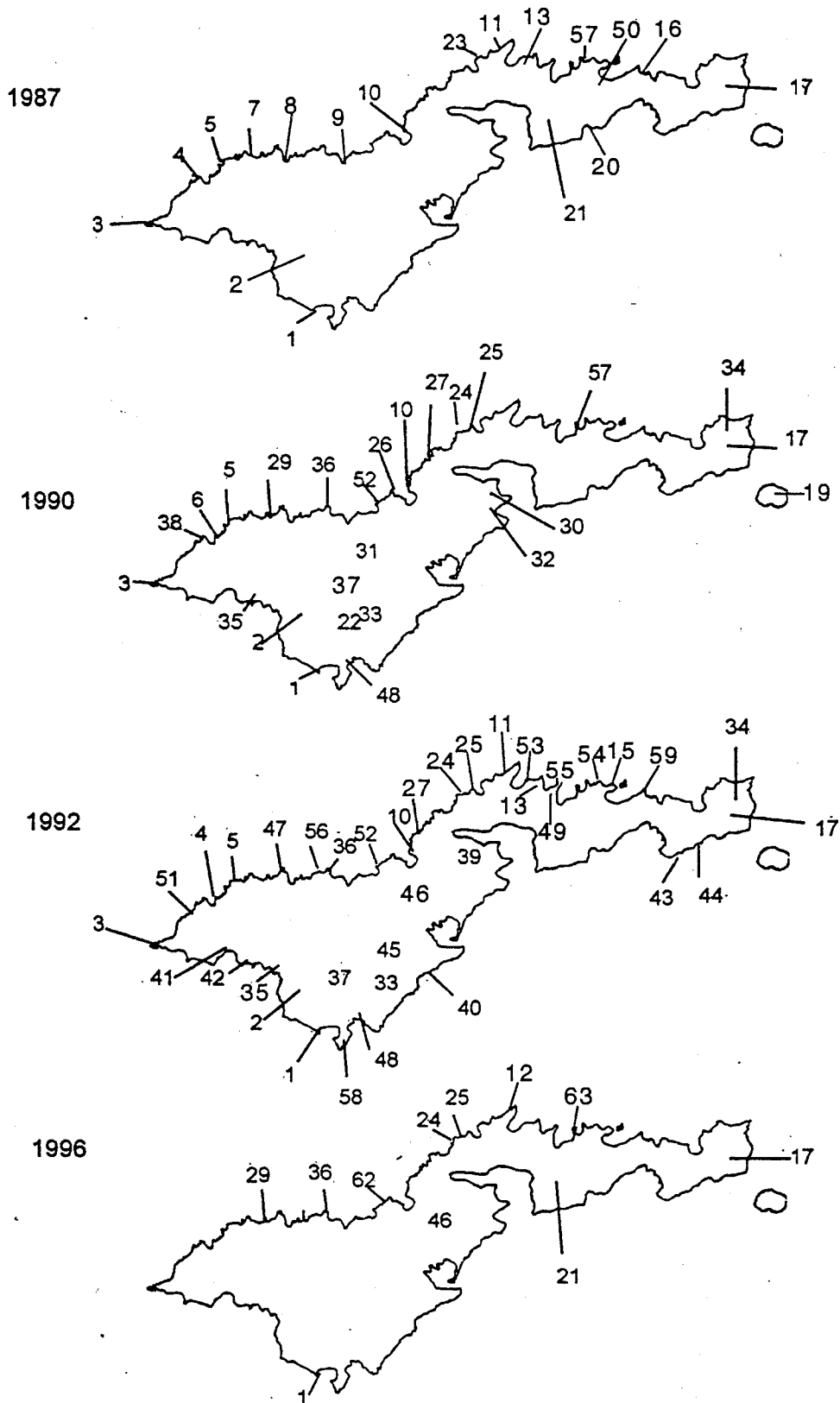


Table 4. Tree species *Pteropus tonganus* use as roost trees and parts eaten.

Parts eaten F = flowers, L = leaves, N = nectar and flowers; (*) = DMWR observation, (1) Cox 1983, (2) Mickleburgh et al. 1992, (3) Rainey et al. 1995.

Species	Parts Eaten	# Roosts	# Trees
<i>Barringtonia asiatica</i>	F, N (*)	15	26
<i>Calophyllum inophyllum</i>	F (*)	13	20
<i>Dysoxylum maota</i>	F (1)	12	37
<i>Erythrina variegata</i>	L, N (*)	12	17
<i>Rhus titiensis</i>	F (*)	9	25
<i>Alphitona zizypoides</i>	F (*)	9	45
<i>Ficus obliqua</i> and <i>F. prolixa</i>	F (*)	8	10
<i>Planchonella samoensis</i>	F (*)	6	15
<i>Myristica spp.</i>		5	17
<i>Dysoxylum samoense</i>	F (1)	4	5
<i>Canaga odorata</i>	F (*)	2	30
<i>Syzygium inophylloides</i>	F, N (*)	2	5
<i>Pisonia grandis</i>		2	3
<i>Fagraea berteriana</i>		2	2
<i>Hibiscus tiliaceus</i>		2	2
<i>Diospyros samoensis</i>	F (*)	1	1
<i>Ternstroemia richii</i>	F (4)	1	1
<i>Inocarpus fagifer</i>	F, L (*)	1	1
<i>Casuarina vitiense</i>	F (3)	1	1
<i>Neomuclea forsteri</i>		1	1
<i>Artocarpus altilis</i>	F (*)	1	1
<i>Garuga floribunda</i>	F (3)	1	1
<i>Stirculicia fanaio</i>		1	1

Importance of sites

Traditional roost locations in American Samoa have steep to vertical walls, are difficult for people to reach, or are in protected areas such as Fagatele Bay and Olavulu crater. Three old volcanic craters are traditional roosts; laulatiti on Ta'u, Olavulu crater, and Fagatele Bay. Other important traditional roost locations are the ridge top at Olomoana mountain, and numerous bays and cliff faces the north coast. There are at least four traditional roost sites within the National Park on Tutuila that are currently in use: Nuutoga point, Puaneva point, Leutu point, and Poluata ridge near the Pola. These roosts should not be visited by people on foot or have boats land near them.

Laulatiti on Ta'u can be approached on foot but any intrusion into the vegetation surrounding the crater causes bats to fly. Access to this should be limited to trained personnel and visits should be infrequent. A roost at the Lepue crater, outside of the National Park, was observed from the road but not visited. Several other potential roosts at the Olomanu, Olotania, and Olomatimu craters should be investigated. (See section on Impacts of proposed Park development.)

Diet

Pteropus tonganus eats native forest fruits as well as agricultural fruits, breadfruit, papaya, coconut, and banana flowers. The extent that *P. tonganus* relies on native as opposed to agricultural fruits in the diet is unknown. A listing of fruits, flower and leaves eaten by both bat species in Samoa is given in Appendix 1. These records list 14 plant species observed eaten only by *P. samoensis*, ten species seen eaten only by *P. tonganus* and 19 species that both bat species eat. Banack (1996) included another 13 plant species found in Samoa that *P. tonganus* has been reported to eat on other islands

Banack (1996) presents the most information on the diet of *P. tonganus* and *P. samoensis*. She found that both bat species consume fruit, flowers, or leaves from 60% of the tree species in the Amalau valley. Banacks' work showed that a large dietary overlap exists between the two species at this site. In this predominantly forested area, both bat species consume fruits from the primary forest and agricultural crops. The extent that *P. tonganus* relies on agricultural crops throughout Tutuila is unknown.

Banack investigated the amount and frequency of ten of the most commonly used species in the bats diet of bats in the Amalau valley (excluding *Ficus* spp.) by examined ejecta pellets collected from tarps beneath fruiting trees. The dental imprints of the two bat species were not sufficiently different to identify which species produced an ejecta pellet so the following information is for both species. She ranked the six native forest fruits by a preference index according to whether fruits were eaten in greater, lesser or equal proportion to abundance. The six fruits, in rank order were *Planchonella samoensis*, *P. garberi*, *Terminalia catappa*, *Syzygium inophylloides*, *P. grayana*, *Palaquium stehlinii*. The last four species in the preference ranking were from secondary growth and agricultural plantations: *Carica papaya*, *Artocarpus altilus*, *Inocarpus fagifer*, *Canaga odorata*. Dietary shifts were evident as different fruit became available seasonally. *Planchonella samoensis*, *S. inophylloides* and *A. altilus* made up 69% of the total biomass found in the diet November-October, *Inocarpus fagifer* made up 58% in March and *Palaquium stehlinii* made up 39% in January. was estimated by a preference index. Three species, *Planchonella samoensis*, *P. garberi* and *Terminalia catappa* were consumed preferentially to the amount of fruit on trees.

Nelson (1997) examined the organic components and mineral nutrients of ripe and unripe native and agricultural fruits in the diet of the Samoan bats (Appendix 1). Native forest species had higher values for several nutrients than agricultural fruits and the leaves of several trees were found to be high in proteins. Nelsons' analysis suggest that agricultural fruits are not as valuable food sources as native species. Unripe fruits and leaves, mainstays of the diet after hurricanes,

contain less sugars and more secondary compounds making them less palatable but were high in nutrients.

Serial use of particular forest areas may depend on fruit and flower availability. Different plants may be favored depending on resources available on that island. For example, Cox (1984b) found that only *P. samoensis* and not *P. tonganus* visited *Freycinetia rickettii* flowers on Savai'i. However, on Ofu numerous *P. tonganus* were seen foraging in *F. rickettii* flowers above the Vaoto Lodge in 1996 (Brooke personal observation). Flowering kapoc (*Ceiba pentandra*) were visited only by *P. tonganus* on Savai'i (Cox et al. 1991) although *P. samoensis* visit the flowers on Tutuila (Brooke personal observation).

Forging behavior

Pteropus tonganus forage in both agricultural and native forest but it is not known how much of the diet consists of introduced versus native fruits. Most observations of foraging bats are from residential areas where they are easily seen feeding and heard fighting with each other in ripe breadfruit, mango trees, and flowering kapoc. Pierson (1993) watched from Mt Alava as *P. tonganus* flew from the north coast over the native forest to plantation forest on the south side of Tutuila. Within the Amalau valley, *Pteropus tonganus* often foraged in the early evening on banana flower nectar then moved to other locations later in the evening (Banack 1996). The same plantations were often visited by bats returning to the roost the following morning.

Bats are highly defensive of foods and fight with others foraging in the same tree. Fruit defense was taken to an extreme by an adult male radio tracked by Brooke (unpublished data) that foraged exclusively in a stand of breadfruit for over a month. The bat remained within 10 m of the trees during the day over two week period, possibly to defend the trees from other bats at dawn and dusk. The bat then moved to roost at one of the large colonies but returned nightly to the breadfruit trees for another 4 weeks before starting to forage more widely.

The 16 individuals Banack (1996) followed by telemetry foraged at more than a single site. Radio collared adult males tracked within the Amalau valley typically remained at a single plantation during the night. A radio tracked juvenile male showed a very different foraging strategy as it was followed to different areas during four nights of monitoring. From the day roost at Olavalu crater, the bat flew west to Maloata, north toward Nuumanu rock, and east as far as Alofau. The greatest distance this bat flew in one night was 46.7 km. It is unknown if this animal was acting normally as the transmitter package this individual carried was 16% of its body weight attached as a collar. The recommended weight limit is 5% or less of the animals mass to avoid atypical behavior (Barclay and Bell 1988; Hickey 1992). Consequently, the value of the telemetry data collected is questionable.

Foraging habitat

Pteropus tonganus utilize most all of the plant communities on Tutuila as foraging habitat: agricultural forest, urban and residential areas, high montane forest and littoral forest. Cox (1983) thought that *P. tonganus* foraged predominantly in agricultural areas. Pierson (et al. 1992)

observed foraging *P. tonganus* in highly altered habitats and plantations. Banack (1996) found that *P. tonganus* were most commonly seen in coconut plantations and in close proximity to villages (n=57) more frequently than in primary forest (n=21). However she found that it was much easier to locate bats in agroforest than in native forest. Within the Amalau valley, an area that contains some plantations but is predominantly native forest, *P. tonganus* foraged most frequently in native forest (Banack 1996).

Factors influencing population trends

Bat populations have historically been reduced by disease or predation. Western Samoa experienced a serious epidemic of an undescribed illness in 1839 that killed people then "...devastated flying foxes in great numbers; so much that scarcely a bat could be seen." (Stair 1887). There is a similar report from Kosrae in the early part of the 20th century (Coultas 1931). Descriptions of epidemics speak of incapacitated bats dropping from the sky and dead bats accumulating beneath colonial roosts (Pierson and Rainey 1992). As travel becomes easier for people, its likely that new human-borne diseases will be introduced into the bat population.

The most significant factor that has influenced bat populations recently was the kill following Hurricane Ofa. Few dead bats were seen in the wild after the storms, however mortality from domestic animals was enormous (Pierson et al. 1996). Craig (et al. 1994) found that twice as many bats were killed by hunters in the year following Hurricane Ofa than previously. They estimated a 80-90% population decline for both species over 5 years following Hurricanes Ofa and Val. Pierson (et al. 1996) found that *P. samoensis* was better adapted at surviving storms than *P. tonganus* because they do not come into villages where *P. tonganus* were killed in great numbers. In the years since hurricane Val, the *P. tonganus* population has increased rapidly (Fig. 1).

Pacific pigeons, a highly prized food in Samoa, are traditionally hunted in October when they appear to be most abundant (Solek 1997). At this same time, mating *P. samoensis* are also highly visible (Brooke personal observation). There is increasing pressure on the director of DMWR to open a pigeon hunt and when people can legally hunt pigeons, bats will also be shot. DMWR has a limited number of personnel to monitor the hunt and there will be little enforcement. Increased trails through the National Park will provide greater access for hunters to shoot both pigeons and bats and illegal hunting activity will need to be monitored.

Sensitivity to Human Affairs

Roosts of *P. tonganus* on Tutuila are currently located in areas of the National Park that will not be affected by trails and facilities proposed in the general management plan (Anon. 1996). Foraging by *P. tonganus* is mostly nocturnal and should not be affected by the proposed facilities.

The causes of roost abandonment are difficult to document. Wiles and Glass (1990) found inter-island roost shifts of *P. marianus* after human disturbance and a storm. The *P. marianus* colony on Guam is sensitive to human smell and will fly when the wind blows from where people observe the colony, a distance of several hundred meters (Wiles 1987).

The *P. tonganus* colony at Olomoana Mt. abandoned the roost site after the line crew for ASPA shot an unknown number bats in October 1994. The colony split into several smaller groups for several months then recolonized a different location on the side of Olomoana. Olavalu crater and Fagatele bay seem to be alternate roosts for a single large colony. Fagatele bay was used prior to the hurricanes. Olavalu crater was used after the storms from 1992-1994, possibly because there was less tree damage from the storms. The colony left Olavalu temporarily October – November during 1992, 1993, and 1994 but returned each year the following January. In January 1995 the colony failed to return to Olavalu. Whether this was due to disturbance caused by gunshots or similar sounds, or whether the forest at Fagatele Bay had regrown sufficiently since hurricane Val is unknown.

Pteropus tonganus return to traditional sites after disturbance caused the roost to be abandoned. Loss of forest from hurricanes caused *P. tonganus* to abandon several sites on the north coast used before the storms. Some of these roosts have now been recolonized although others, such as Taputapu island and Tiape'a point (between Masefau and Masausi) have not been reestablished.

Pteropus tonganus also return to roosts that have been abandoned due to human disturbance. Both major disturbance of hunting at Olomoana Mt. and relatively minor disturbances of a boat approaching the roost on a DMWR survey or people on foot approaching the Laulatiti crater cause temporary roost abandonment. Repeated disturbance may cause permanent or long term roost changes. Because the cost of such moves to a colony is unknown, unnecessary visits should be avoided to limit disturbance.

Impacts of proposed park development

There should be little impact of National Park management activities on *P. tonganus* if roosts are avoided. Repeated visits to the colony at laulatiti on Ta'u may cause the site to be abandoned. The laulatiti crater appears to be a preferred roost, for whatever reason, and this should be considered in determining how frequently people visit the roost.

The National Park is less critical to the survival of *P. tonganus* than it is for *P. samoensis*. Although population estimates are not available for most of the range of *P. tonganus tonganus* large colonies are present in Tonga and Fiji. (Wilson and Engbring 1993; Grant 1996). Roost habitat less critical for *P. tonganus* on Tutuila as the largest traditional roosts are not located in the National Park.

Roosts used traditionally by *P. tonganus* have steep to vertical walls and are extremely difficult for people to reach on foot or are in protected areas such as Fagatele Bay. In American Samoa three old volcanic craters are prime traditional roosts; laulatiti on Ta'u, Olavalu crater and Fagatele Bay. Other prime traditional roost locations are the ridge top at Olomoana mountain, and Puaneva point, Siliaga point, and the ridge at Oa on the north coast.

Pteropus samoensis

Historic range and populations

Pteropus samoensis is endemic to the Samoan and Fijian archipelagos. The first report of *P. samoensis* was from Tutuila and the species was noted on "...all the islands in the Samoan group..." (Peale 1848). The only record of abundance is Peale's mention that the bats were "...common everywhere on the islands of Manua, Tutuila, Upolu and Savaii." Because of the similar appearance of *P. samoensis* and *P. tonganus* confusion between the species is evident in most of the early reports with *P. samoensis* reported as colonial and as abundant as *P. tonganus* (Gray 1870; Alston 1874; Whitmee 1875; Nicoll 1908). As recently as 1982, (Amerson et al. 1982) didn't realize that two different species were present in American Samoa and called all bats *P. tonganus*. Wilson and Engbring (1992) reviewed the taxonomy and clarified the early observations. In spite of the problems with species identification, the overall inference is that *P. samoensis* has never been as abundant as *P. tonganus*.

Pteropus samoensis samoensis is currently found on the Samoan islands of Upolu, Savai'i, Tutuila, Ta'u, 'Ofu and 'Olosega (Wilson and Engbring 1993). A record in Flannery (1995) of Swains Island is most likely a mistake as there is no forest on Swains to support bats and no other records from Swains exist.

The Fijian subspecies, *P. samoensis nawaiensis*, is different in coloration from the Samoan subspecies. The entire head is yellow or white with the pale color extends below the shoulders to the mid-back and across the chest. *Pteropus samoensis nawaiensis* has been reported from the islands of Nayau, Ovalau, Taveuni, Vanua Levu, Viti Levu (Pierson et al. 1992a) and Loma Loma in the Lau islands (Brooke 1997). There is no published information on abundance in Fiji. Because this sub-species does not soar, possibly as response to predation by peregrine falcons, they are difficult to find during the day (White et al. 1988; Wilson and Engbring 1992; Pierson et al. 1992a)

Pteropus samoensis was present in Tonga prior to the arrival of Polynesians but is believed extinct (Koopman and Steadman 1995). Little research has been done in Tonga and it is possible that *P. samoensis nawaiensis* is still extant, roosting within or adjacent to the large *P. tonganus* colonies.

Recent population and hurricane impacts

The first published information of *P. samoensis* was Cox's (1983) observations of extremely low numbers of bats. No *P. samoensis* were seen on Savai'i and only 50 individuals were estimated still being present on 'Upolu. Cox observed one breeding pair on Tutuila and a single individual on Ta'u. In 1986, Cox and Tuttle estimated that 300 *P. samoensis* remained on Tutuila based on bats seen at the Mt Pioa pass (Cox and Tuttle 1986). Cox petitioned the USFWS to list *P. samoensis* as an endangered species in 1984. In response to the request, Wilson and Engbring (1993) conducted a single 30 minute survey at 29 sites in American Samoa and 21 sites in Western Samoa in 1986. They observed *P. samoensis* at 89% of the survey sites on all the major

islands of Samoa, with an average of 4.4 individuals per survey. Craig (et al. 1994) expanded Wilson and Engbrings data by multiplying the number of bats observed per hectare by the total forested area of Tutuila and arrived at an estimated population of 1,500 for 1986-87. When Wilson and Engbring repeated the surveys in 1989, they found evidence for a continuing decline in populations on all islands. However, the large between-year variation indicated that the number of bats observed was not critically low and they concluded that the number of bats remained roughly the same during 1986-1989 (Wilson and Engbring 1993).

Prior to Hurricane Ofa in January 1990, Pierson et al. (1992) believed the *P. samoensis* population on Tutuila to be less than 700 animals and possibly as low as a few hundred individuals. A month after Hurricane Val, in January 1992, they conducted surveys in the Afono and Amalau valleys. When the data was with surveys done at the same sites in 1988, 50% less bats were observed in Afono and 41% less bats were seen in Amalau. Because these valleys were some of the least damaged areas following Hurricane Val, they speculated that the valleys were refuges and that bats moved into the area. The data suggested that the *P. samoensis* population declined significantly although not as dramatically as the *P. tonganus* population. An estimate of 200-400 individuals was reached from DMWR surveys conducted monthly at 12 sites in 1992 (Craig et al. 1994). A third rapid survey by (Wilson and Engbring 1993) in 1993 suggested an overall 67% decline in the population between 1986 and 1993. Population estimates were not made from any of the survey data (Wilson and Engbring 1993).

Little work has been done on the Manu'a islands to document the *P. samoensis* populations. Annual surveys have been conducted since 1986 by Wilson and Engbring (1992) and DMWR. Methodology varied between 20 and 30 minute counts, each site was visited only once, either at dawn or dusk, and only three sites were surveyed on Ta'u. Surveys done this infrequently are not a reliable indication of population size. They reported a declining population, the "standard mean" of 3.8 bats/count in 1986, and 2.9 in 1989. The number of bats/count for Manu'a was similar in number to the Tutuila counts for 1986.

In Western Samoa, the number of bats observed on 'Upolu declined from 2.1 bats/²km in 1986 (Wilson and Engbring 1993) to 0.21 bats/²km in 1995 (Brooke 1997). Recent surveys on Savai'i, suggest that the population has increased to near the prehurricane levels, from 1.5 bats/²km in 1986 to 1.1 bats/²km in 1995. Unfortunately, these figures were derived from a very small survey sample and may be inaccurate. Wilson and Engbring (1993) only surveyed four sites, three of the four were in the Asau forestry area at the western end of the island. Brooke (1997) surveyed seven sites in 1995 but a thorough survey of Savai'i has not been done. Using the Department of Agriculture, Forests, and Fisheries (1992) assessment of the amount of remaining native forest ('Upolu = 253 ²km, Savai'i = 780 ²km) the 1995 *P. samoensis* population in Western Samoa was estimated to be less than 1,000 animals.

Current population estimates

Six sites on Tutuila were monitored monthly by DMWR in 1995-1996. The number of *P. samoensis* observed at each of the sites is quite different (Fig. 4). The greatest density of *P. samoensis* as well as the greatest month to month variation was seen in the Amalau valley, a site

that is used heavily for foraging, home ranges, and as a corridor. Maloata and Leone were also corridors where bats move through the area. This was particularly evident in Leone where most observations were of bats moving from south to north along the western ridge. The number of bats using these sites as home ranges may be much less than the number of bats observed during morning surveys.

A population estimate for Tutuila was made by expanding the means of the survey results to 69.9 ²km of upland forest habitat (Cole et al. 1988). These two years of data have a similar number of bats: 924 in 1995, 854 in 1996 (Brooke 1997). Surveys from Manu'a indicate that around 100 *P. samoensis* are present on the three islands (Brooke 1997). The estimated population for all of American Samoa is approximately 1,000 individuals.

Monitoring

How to monitor the *P. samoensis* population has been an ongoing challenge since 1986. Differences in the survey techniques make direct comparisons between years impossible. Initially, surveys were intended to provide a relative index of the population rather than a population estimate.

The current DMWR methodology described below has evolved from the work of numerous people. The original method used by Wilson and Engbring (1993) was to count all the bats flying within a valley or forested area during a single 30 minute period. As *P. samoensis* was believed to be primarily diurnal, observations were made throughout the day. Several problems with this simple method of surveying have become apparent.

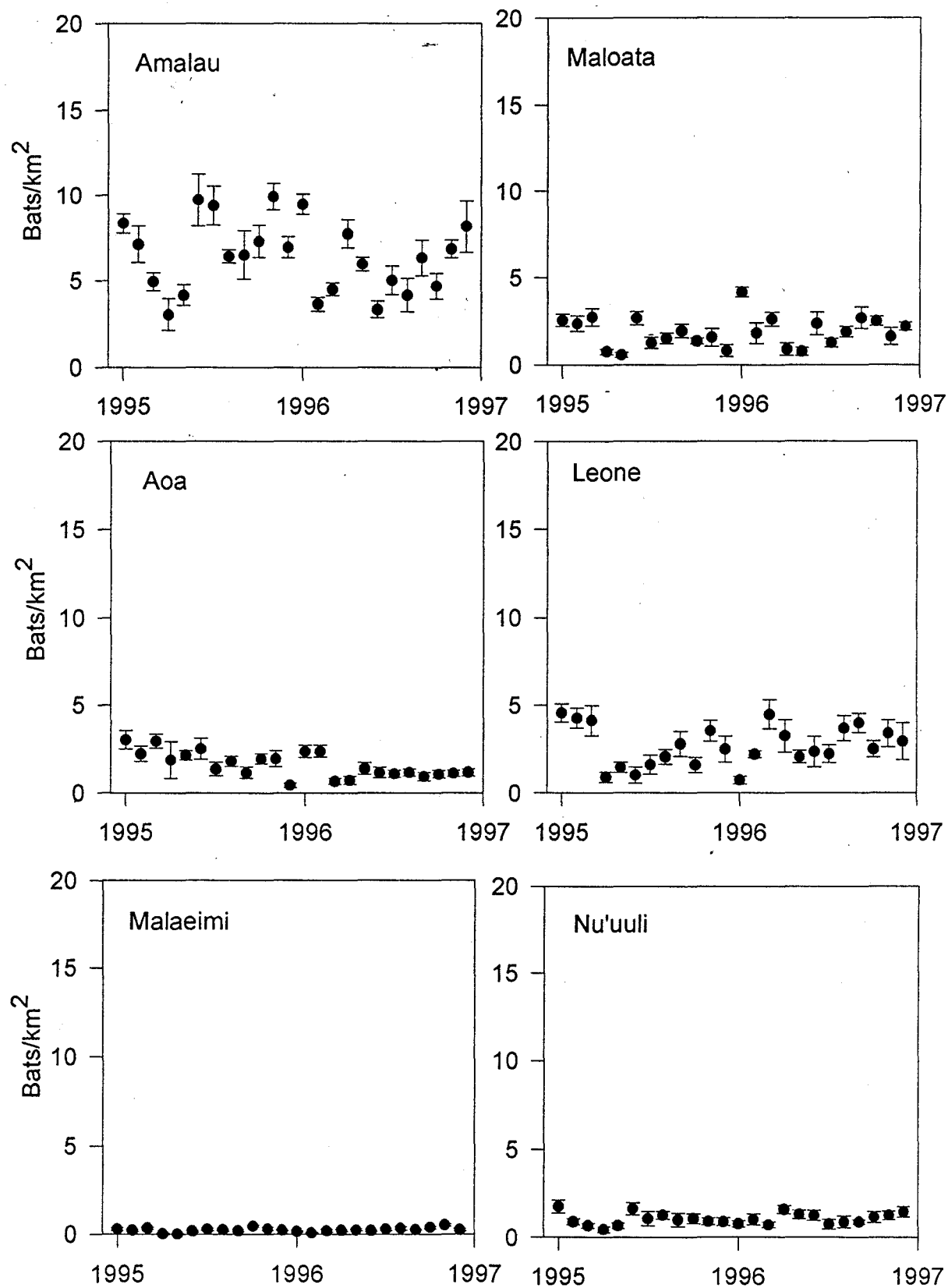
The survey counts in 1986-1989 were done only once or twice a year and observations were made throughout the day. The amount of diurnal activity of *P. samoensis* varies throughout the day depending on the time of year (Thomson et al. in press). In December and January, the number of *P. samoensis* seen in valleys where *S. inophylloides* was plentiful was greater than at other times of the year. Some survey areas show a drop in activity in April and May, the time when young are born. Radio tracking and repeated observations of known individuals have shown many bats return to their home territories near dawn. Surveys that start at first light count these returning individuals. This gives a better estimate of the number of bats using an area than surveys done later in the day when the number of foraging bats changes with abundance of fruiting or flowering trees

Confusion between the two species has consistently been a problem and even experienced observers have difficulty in some situations. Inexperienced or unmotivated observers get drastically different results from experienced observers (Craig 1992). By limiting the survey counts to one or two observers, variation in number of bats seen can be decreased enormously.

The number and location of survey sites on Tutuila has changed during the past ten years. The original 17 sites were expanded to 29 by DMWR in 1988 (Wilson and Engbring 1993). After the hurricanes, some of the sites were no longer appropriate and the number of sites was reduced to

Figure 4 DMWR *Pteropus samoensis* survey results, Tutuila, 1995-1996

Mean and standard error from monthly counts.



12. In 1995 sites were eliminated that faced east (where the rising sun blinded the observer) or were close to other sites (so that the same individuals would not be counted repeatedly). The remaining six sites were distributed the length of Tutuila. In a 1995 paper, Morrell and Craig attempted to clarify survey techniques. They compared weather conditions, time of day, and the number of counts needed to standardize data for diurnally active *P. samoensis* and *P. tongamus*. Field work for this paper was undertaken during the 3-8 months following Hurricane Ofa in 1991 and the rapidly declining population and hurricane induced behavioral changes were not considered (Grant et al. 1997).

The DMWR surveys for 1995-1996 were conducted at six sites on Tutuila each month. Surveys began at first light and continued for the next two hours. Data were collected during eight ten-minute sample periods, separated by five minute breaks, for a total of eight samples at each site per month. Zeiss 10x40 and 10x50 binoculars are used to distinguish between *P. samoensis* and *P. tongamus*. All survey areas were of valleys with an unimpeded forest view. Surveys were conducted only when there was little or no rain and wind. A map was drawn of each site dividing the valley into sections that followed the topography. Whenever a bat was observed in flight it was followed until it roosted, was lost within the vegetation, or flew out of the area. The valley section where each bat was lost from view was noted. Within each ten minute count, multiple individuals were recorded from a section only if more than one bat was seen simultaneously or bats were observed in widely different parts of the same section. Discriminating between individuals is the most difficult part of the surveys. Counts give a conservative estimate of the number of individuals at a site. The area of each site was determined from a USGS survey map and the mean number of *P. samoensis* observed per hectare was calculated. An estimate of the population on Tutuila island was obtained by expanding the combined means from all survey sites to the forested habitat of the island.

Annual surveys of the Manu'a islands continue to rely on the methods and sites initially used in 1986 (Wilson and Engbring 1993). Surveys are done in four 20 minute count periods with a 10 minute break between counts (Brooke 1997). Observations begin either at first light or approximately 3 hours before dark. This methodology is still used because of the small number of bats and difficulty in getting to Manu'a more frequently than once a year.

Twenty or thirty minute counts are useful for monitoring low numbers of bats, as on Manu'a. However, the ten minute counts currently used on Tutuila may be too long an observation period for high densities of bats. For example, in the Amalau valley it is not unusual to see 15 or more individuals in flight at one time. It is impossible to follow the flight path of all these bats without confusing individuals. New methods for monitoring higher densities will need to be investigated as the density of bats on Tutuila increases.

Roosts

Most observations of *P. samoensis* are of single individuals (Brooke in preparation) although aggregations of 4-11 bats are seen sporadically (Pierson et al. 1992a; Wilson and Engbring 1993; Banack 1996; Brooke 1997). A temporary aggregation of ca 60 *P. samoensis* with ca 80 *P. tongamus* roosting in adjacent trees was seen in the Amalau valley in 1996 (Brooke 1997). The

presence of both species suggests a local abundance of a food resource. No territorial behaviors have been seen among roosting *P. samoensis*. Brooke observed only one instance where a bat acted aggressively and prevented another individual from landing in the same tree in 288 h of observations. There appears to be little defense of roost sites.

Characteristics of roosts

Pierson (1993) and Banack (1996) reported that *P. samoensis* roosts were found primarily along ridge tops and crater rims. Banack suggested that roost trees may be limited as bats require a vertical drop to take off. Brooke (et al. manuscript) found bats to roost as frequently within the canopy of mature forest trees as on dead branches at the top of hurricane damaged trees. Although bats were most easily seen on ridges where they were silhouetted against the sky, *P. samoensis* roosts were also located in the bottom of valleys and along the shoreline in relatively flat areas.

Brooke (et al. manuscript) described the repeated use of specific roost branches by *P. samoensis*. The greatest number of roosts were in *Syzygium inophylloides*, a particularly hard species that withstood the hurricanes. Roosts were found from sea level to the top of Alava ridge at 488 m elevation. The mean slope of *P. samoensis* roosts was 51°, (range 10-68°, se=2.5), the height of roosts above the ground ranged from 4.6-18m, (mean =9m, se=0.6m), and the mean distance to the nearest house was 647 m, (range 250m-1,125m, se=2.0). Roosts were most numerous in valleys that have the greatest number of canopy trees that are used as foods (Table 5).

Table 5. Mean *Pteropus samoensis* per ²km from 1995-1996 DMWR surveys.

Secondary forest species: *Rhus taitensis*, *Hibiscus tiliaceus*, *Macaranga harveyana*, *Pipterus argenteus*.

Site	Mean (se) bats ² km	% tree spp bats eat	% secondary forest trees
Amalau	6.04 (0.8)	52.15	20.44
Leone	2.68 (0.58)	24.97	47.97
Maloata	1.85 (0.36)	59.1	6.25
Aoa	1.60 (0.34)	27.27	44.89
Nu'uuli	1.04 (0.25)	34.2	28.77
Malaeimi	0.25 (0.06)	35.6	34.25

Diet

The types of fruit eaten by *P. samoensis* were similar to those eaten by *P. tonganus* (Appendix 1). Although *P. samoensis* forages on breadfruit, papaya, and mango, they eat these agricultural fruits only when they are near the forest edge. Apparently, *P. samoensis* is more reliant on native fruits than *P. tonganus* but conclusive evidence that distinguish between the two species is lacking (Banack 1996). See the Diet section for *P. tonganus* for a review.

Surprisingly, there are no records of *P. samoensis* eating nectar of banana flowers (*Musa* spp), a frequent food of *P. tonganus*. A listing of fruits, flower and leaves eaten by both bat species in Samoa is given in Appendix 1. These records list 14 plant species observed eaten only by *P. samoensis*, ten species seen eaten only by *P. tonganus* and 19 species that both bats eat. Banack (1996) included another 13 plant species found in Samoa that *P. tonganus* has been reported to eat on other islands. A listing of fruits eaten by *P. samoensis* in Wilson and Engbring (1993) compiled by DMWR technicians contains several plant species that have not been confirmed by observations.

The importance of agricultural fruits and flowers in the diet can only be inferred from observations. *Pteropus samoensis* is frequently seen eating ripe breadfruit but there are a few observations of bats eating papaya. It is common to see *P. samoensis* in coconut trees but its unknown if bats are eating pollen or perhaps drinking water from small reservoirs in the leaves. Kapoc has a limited flowering season in July and may be a valuable food resource during that time.

Foraging behavior

During the day *P. samoensis* can be seen flying low over the forest apparently searching for fruiting or flowering trees (Grant et al. 1997). Although *P. samoensis* eats agricultural crops, such as papaya and breadfruit, bats are not seen flying in the more populated areas of Tutuila or any distance from the edge of native forest.

Radio tracking studies of *P. samoensis* from the Amalau valley area showed that bats roost and forage within the same forest and habitat. The foraging and core ranges of two males radio tracked for 62 h nocturnally and 70 h diurnally from November 1995-February 1996 are given in Fig. 5. Telemetry locations were analyzed by adaptive kernel method setting 100% of locations as the foraging area and the core area at 50% (Calhome Home Range Analysis Program).

The foraging areas for the two animals differed in size considerably. Bat #348 foraged within the Vatia valley and was followed, once, over Alava ridge where it remained for spent several hours on the cliff face above Pago Pago. Two other times the bat flew out of telemetry range over Siuono ridge, north-west of Vatia. The core area for both animals was between 0.18-0.24 ²km.

Pteropus samoensis actively defend feeding sites from other bats. Bats defended entire fruiting or flowering trees by chasing another bat that landed in the tree or flew close to it. Nearly 1/3 of all chases ended when the defending bat bit or attempted to bite the interloper (Brooke in preparation). When roosting in the tree, bats clap their wings together at an approaching animal and/or flick their wings rapidly in a shrugging motion (Brooke in preparation). Chases seen by Wilson and Engbring (1992) were thought to be courtship behavior.

Figure 5. Foraging and core areas for two *P. samoensis*. Map includes the north coast of Tutuila from Agapie cove to Matape point. Foraging area depicted by 100% isopleth, core area by 50% isopleth. Axis coordinates from USGS survey map of Tutuila.

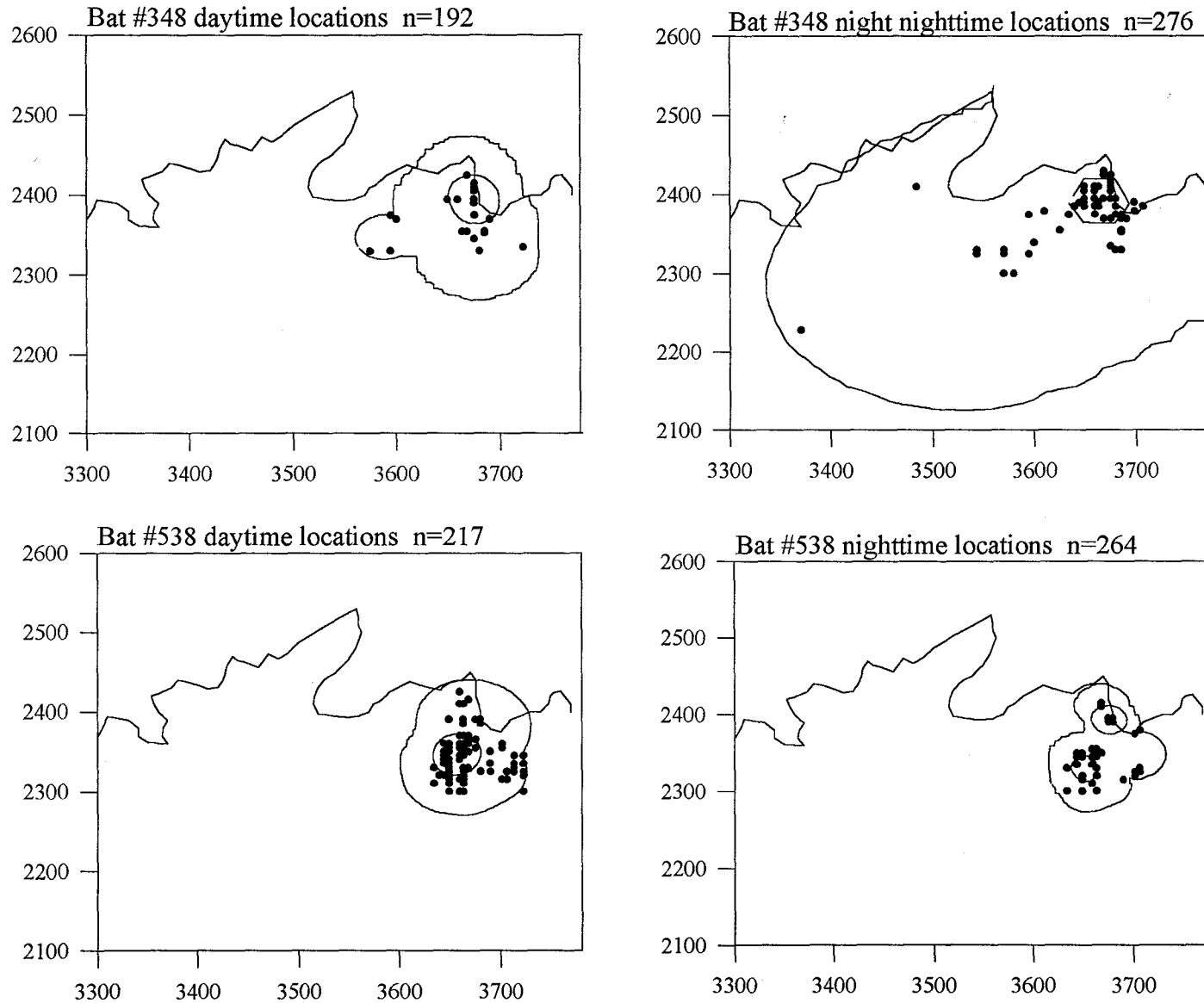


Table 6. Foraging and core ranges of radio tracked *Pteropus samoensis*.

Bat #	Daytime locations		Nighttime locations	
	Foraging distances	Core range	Foraging distances	Core range
348	2.412 ² km	0.237 ² km	8.110 ² km	0.238 ² km
538	1.234 ² km	0.185 ² km	1.747 ² km	0.191 ² km

Foraging habitat

Coxs' early observations (1983) of *P. samoensis* foraging in native forest have been substantiated by all later research (Pierson et al. 1992; Pierson et al. 1992a; Pierson 1993; Wilson and Engbring 1993; Banack 1996). *Pteropus samoensis* seeks out fruiting or flowering plants throughout the forest. Species composition of the forest is important in determining abundance of bats in an area. DMWR surveyed the relative abundance of canopy tree species at each of the six survey sites. The percentage of tree species that are eaten by bats and secondary growth trees (Appendix 1). The relative abundance of canopy tree species at the six DMWR *P. samoensis* survey sites was determined by calculating the percentage of coverage of trees within the field of view of a Nikon spotting scope, ca 3 m². Between 18-42 plots were observed at each site. Fifty trees species were identified in the survey areas and the percentage of 33 trees known food sources for *P. samoensis* was calculated for each site. Table 5 summarizes the results of the vegetation surveys and population density at the six survey sites. Appendix 2 lists the percentage of each tree species by site.

The two sites with the highest percentage of fruiting tree, Amalau and Maloata, had the least amount of secondary growth. Leone, the second in number of bat sightings, had more secondary growth than usable forest species although immediately west and north of the site is good forest. Most of the bats observed in Leone are moving along the ridge to the north and do not remain within the survey area. The Aoa site is the fourth in bat sightings but has more secondary growth and less edible plants than the two least populated sites. Aoa is the one site with a downward trend in the number of bat sightings during 1995-1996. Malaeimi and Nu'uuli, the two least populated sites, have nearly equal amounts of secondary growth species, unusable, and usable forest species.

Factors influencing population trends

The territorial behaviors and solitary social organization of *P. samoensis* have been thought to limit the population size (Cox 1984a). Banack (1996) credited territorial behavior as the basis for habitat division among widely spaced, small family groups and suggested that this contributed to low population densities. Brooke (in preparation) found extensive defense of food resources, both within the home range and outside of it, but little defense of roost sites or home ranges.

Pierson et al (1996) found that hurricanes were be less devastating to the *P. samoensis* than to *P. tonganus*. Because *P. samoensis* avoids villages and areas away from native forest, they did not sustain the enormous losses of *P. tonganus* after hurricane Ofa. At the present, habitat loss and illegal hunting are the greatest risks for the population. The lack of fear for humans and diurnal activity of *P. samoensis* make them an easy target for hunters.

Sensitivity to people

Roosting *P. samoensis* will let people approach closely before taking flight. Pierson described this as a lack of flight response to a threatening situation (personal communication). Bats also fly close to people, putting them at risk from hunters with slingshots or guns.

There are several *P. samoensis* roosts along the Vatia road, past Amalau valley. One *Ficus obliqua* that overhangs the road is within the home range of several *P. samoensis* and one adult female was frequently observed during 1995-1996 on a branch high above the road edge (Brooke in preparation). Bats roosting in the *Ficus* were not apparently affected by vehicle traffic, periodic roadside clearing by the village, or foot traffic. Few people realized there were bats concealed in the foliage.

Impacts of proposed park development

Trails in the forest within the National Park will undoubtedly run through the home ranges of *P. samoensis*. A limited amount of traffic should have little impact on bats who will be hidden in the foliage, well above people. The bats roosting above the Vatia road suggest that individuals will tolerate noise as long as they are not directly disturbed. Large groups of people and/or a constant flow of visitors may cause bats roosting close to trails to abandon those locations.

A greater concern is the use of trails by local residents for hunting. Trails through the forest may encourage hunting for bats, pacific pigeons, and fruit doves. Particularly when a hunting season is opened by DMWR, trails through the National Park are likely to be used by hunters who will shoot bats opportunistically.

Facilities that may be constructed at the cable-car and television antennae on Mt. Alava have slightly different considerations. Territorial roost sites are present along the road and the forest surrounding the building. Currently, most vehicle traffic is maintenance personnel for the radio and television antennas and locals using camping sites and plantations along the road. Pacific pigeons and flying foxes are easily visible along the Mt. Alava road. Several of the landowners of land adjacent to the National Park have said they use their camping sites for hunting. Local people use the road to hunt in spite of the protection offered as a National Park (Brooke personal observation). While any improvement in the Mt. Alava road is likely to increase hunting, an increased presence by the National Park staff and visitors to Mt. Alava may act as a deterrent.

Habitat

Recent changes in forest cover

While baseline data on quantity of habitat are unknown, 19th century and early 20th century accounts (e.g. Coulter 1941) suggest that most of American Samoa is in native forest. Aerial photos of American Samoa taken in the 1940's by the War Department show that most of Tutuila's 142 ²km were forested. Villages consisted of few fales, with very little cleared area surrounding them. Since World War II, however, the Tafuna Plain and most of the flat areas on Tutuila have been cleared. A 1984 overflight by NOAA showed that the native forest cover on Tutuila had been reduced to ca. 70.5 ²km of upland and coastal forest, with a commensurate increase in agricultural plantations to 49 ²km (Cole et al. 1988).

In Western Samoa a similar pattern of decline in the native forest has occurred since the 1950s (Taule'alo 1993). The islands of 'Upolu and Savai'i in Western Samoa have a greater area in native forest although damage from hurricanes Ofa and Val was extensive (Elmqvist et al. 1994). On 'Upolu the forested areas are fragmented and of the islands 1,132 ²km, 21% of the total land area (245 ²km) remains forested in non-merchantable trees (Taule'alo 1993). The 789 ha of merchantable forest is being cut at about 50 ha annually (Taule'alo 1993). The larger and less developed island of Savai'i has an area of 1,696 ²km, of this 47% of the total land area (780 ²km) remains forested (Taule'alo 1993). An estimated 151 ²km of merchantable forest is being cut at an annual rate of about 1,000 ha (Taule'alo 1993).

Protected areas

The National Park of American Samoa is important regionally as a refuge for bats and other wildlife. The National Park on Tutuila is comprised of 10 ²km of upland forest (Anon 1996). Within the Park there are also small areas of coastal forest, dwarf forest, scrub, and agricultural forest (Table 7 and Fig. 6). Much of the 21.4 ²km of the National Park is dwarf and moss forest, upland and coastal forest cover the lau bench and eastern escarpment with only a small section of scrub growth at Tufu point (Table 7 and Fig. 7).

In Western Samoa the O Le Pupu-pu'e National Park encompasses 2,850 ha of land on the from the insular divide of Mt. Le Pu'e to the southern coast of 'Upolu. Smaller forest reserves are present in Savaii at Falealupo and Tafua tai.

Value of different plant communities

Tutuila

Both *P. samoensis* and *P. tonganus* preferentially roost in mature forest (Brooke et al. manuscript). After the two recent hurricanes, *P. tonganus* colonies were found in secondary growth and agricultural plantations but these roosts were used temporarily.

Table 6. Types and amounts of forest cover in the Samoan archipelago. Present day area measures are given in acres. Numbers in () beneath the NPAS area measures give the percentage of that forest type for all of American Samoa. Additional loss of forest habitat has occurred since these measurements were taken.

Forest type acres	All Samoan Islands	Western Samoa ^A	Savai'i ^A	'Upolu ^A	American Samoa ^B	Tutuila ^B	Ofu Olosega ^B	Ta'u ^B	NPAS Samoa ^C	NPSA- Tutuila ^C	NPSA- Ta'u ^C
Total area					48,011				7,660	2,500	5,400
Upland/ lowland					22,763	17,186	996	4597	1,189	1,199	690
Coastal or littoral					2085	462	439	789	862	374	488
Mangrove					128	121	-	-		-	-
Dwarf					677	20	205	442	2,032	172	1,860
Moss					3042	-	94	2952			
Total native forest		103,319 (36%)	78,008 (47%)	25,31 (23%)	28,686	17,789	1906	8957		4,245	1,580
Secondary					608	576	-	25		398	
Agroforest		2,283 (1%)	1,689	594	15,510	12,327	1036	1915			

^A from Taule'alo 1993, unknown if data were collected prior to hurricane Ofa and Val or more recently.

^B 1984 data from Cole et al. 1988

^C National Park of American Samoa Management Plan 1996

Figure 6. Forest types within the National Park of American Samoa, Tutuila

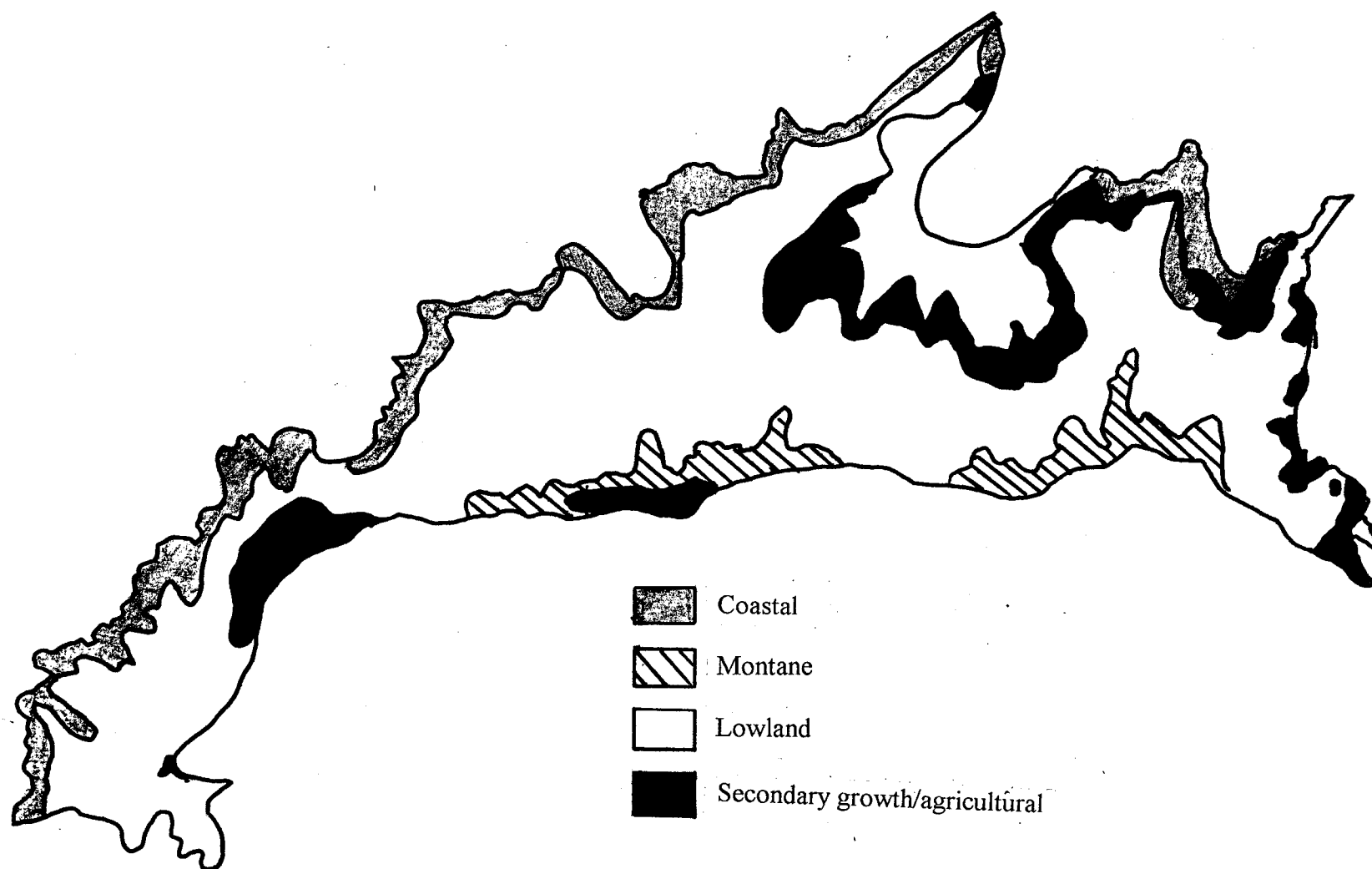
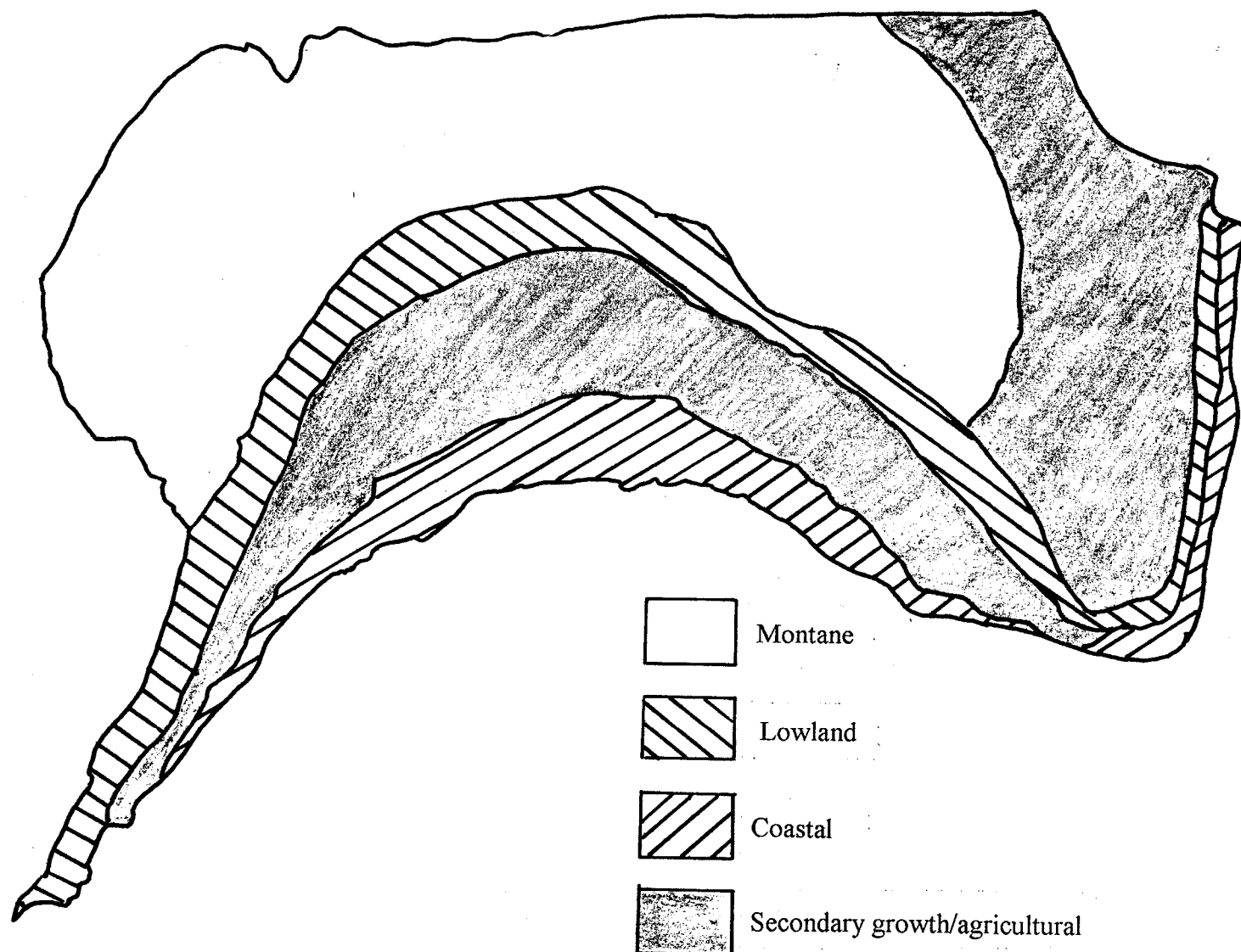


Figure 7 Forest types within the National Park of American Samoa, Ta'u



Both bat species find food plants in all habitats on Tutuila with the probable exceptions of mangrove and grassland areas. Within the National Park on Tutuila, plants that bats utilize as a food resource are plentiful in coastal, lowland, montane, secondary growth, and scrub forests. It is difficult to assign value to plant communities since the amount and frequency of fruits, flowers and leaves consumed by bats is unknown. The list of 50 forest species that bats have been observed to eat includes plants that were eaten frequently as well as those that were observed only once. Banack (1996) found that three of the six forest tree species she studied were preferred by bats foraging in the Amalau valley. An abundance of *Planchonella samoensis*, *P. garberi*, *Termanalia catappa*, or *Syzygium inophylloides* indicate valuable bat foraging habitat.

Coastal or littoral forest is a small component of the National Park, approximately 862 acres (Table 7). The dominant tree species of coastal forest areas within the park are *Barringtonia asiatica*, *Termanalia catappa*, *Calophyllum inophyllum*, *Diospyros samoensis*, *Garauga floribunda*, *Planchonella grayana*, *Guettarda speciosa* (Whistler 1992). With the exception of *Garauga*, all are eaten by bats (Appendix 1).

Most of the forest within the National Park on Tutuila is lowland forest (Table 7). The upland forest category of Cole et al. (1988) was divided by Whistler (1994) into lowland coastal, valley, ridge, and interior ridge forest. The dominant species of lowland valley forest, *Dysoxylum*, *Planchonella samoensis*, and *Inocarpus fagifer* are eaten by bats. *Barringtonia samoensis*, also a prevalent species, is thought to be a food.

Lowland ridge forest is not dominated by any one species (Whistler 1992). Three of the four characteristic canopy tree species are eaten by bats: *Syzygium inophylloides*, *Calophyllum neobudicum*, *Canarium vitiense*. *Buchanania merrillii* is not a known food. One of three characteristic sub-canopy species, *Diospyros samoensis*, is eaten by bats but there is no record that either *Myristica fatua* or *Canarium harvey* are eaten.

The most dominant tree in the interior ridges of the National Park on Tutuila, *Syzygium inophylloides*, is an important food source for both bat species. *Syzygium inophylloides* flowers from November-March and fruits are ripe March-October, almost a year-round resource. Banack (1996) found *S. inophylloides* to be one of the ten most frequently eaten fruits in the Amalau valley.

Above 350 m elevation, montane forest is dominated by *Dysoxylum samoense*, *Syzygium samoense*, *Crossostylis biflora*, *Palaquium stehlinii*, *Hedycarya denticulata*. Of these, *D. samoense* and *P. stehlinii* are known to be eaten by bats. *Faradaya amicorum*, a vine, and *Freycinetia reineckeii* are both common at higher altitudes and are food sources.

Ta'u

Few of the species found in Whistler's vegetation plots on Ta'u are known to be eaten by *P. samoensis* or *P. tonganus* (Whistler 1992). Bats eat the flowers and the seeds of the dominant tree in the littoral forest at Saua, *Barringtonia asiatica*. Two uncommon species in the littoral forest are eaten by bats, the fruits and flowers of *Guettarda speciosa* are eaten by *P. tonganus* but only a single record of bat use exists for *Diospyros samoensis* (Banack 1996). In the two

Dysoxylum lowland forest plots, the flowers of *Neonauclea forsteri*, a relatively common species is eaten but the only fruiting trees, *Ficus scabra* and *F. tinctoria* and *Planchonella garberi*, were uncommon. The montane forest west of Lata contains the greatest amount of an edible fruiting species. *Syzygium samoense* made up nearly a third of the forest species but only token amounts of *Fagraea berteriana* and *Ficus* spp. were present. *Freycinetia rickettii* grows at higher elevations in montane, scrub, and dwarf forest where fewer fruiting trees are found. This paucity of tree that are utilized by bats is reflected in the low number of *P. samoensis* recorded in the DMWR annual surveys.

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Appendix 1. Trees species eaten by *Pteropus tonganus* and *Pteropus samoensis* in Samoa.

Taken from Banack (1996) with new DMWR additions. Percentage nitrogen, fat and calories from Nelson (1997). Part eaten Fr = fruits, Fl = flowers, L = leaves. Bat species P.t. = *P. tonganus*, P.s. = *P. samoensis*. The first recorded observation of a bat eating species is given. Agricultural crops in bold.

Family	Genus and species	%N	%Fat	% kcal/g	Bat spp	Part eaten	Reference
Anacardiaceae	<i>Magifera indica</i>				P.t.	Fr	Cox 1983b
	<i>Spondias dulcis</i>				?	Fr	Whitmee 1874
Annonaceae	<i>Cananga odorata</i>	1.38	4.88	4.67	P.t.	Fl	Wilson 1993
					P.s.	Fr Fl	Trail 1994 Cox et al. 1992
Apocynaceae	<i>Alyxia odorata</i>				P.t.	L	Pierson et al. 1992
Araceae	<i>Epipremnum pinnatun</i>				P.s.	Fl	C. Solek DMWR
Araliaceae	<i>Polyscias samoensis</i>				?	Fl	Banack 1996
Asclepiadaceae	<i>Hoya australis</i>				?	L	Banack 1996
Barringtonaceae	<i>Barringtonia samoensis</i>	2.05	6.27	4.2			sniffing only at fruit Trail 1994
	<i>Barringtonia asiatica</i>				P.t.	Fl	Cox et al. 1992
					?	Fr	Brooke DWMR
					P.s.	Fl	Cox et al. 1992
Bombicaceae	<i>Ceiba pentandra</i>				P.t.	Fl	Cox 1983b Wilson & Engbring 1993
					P.s.	Fl	Wilson & Engbring 1993
Burseraceae	<i>Carnarium vitense</i>				?	Fr	Rainey et al. 1995
	<i>Garuga floribunda</i>				?	Fr	Rainey et al. 1995
Caricaeae	<i>Carica papaya</i>	0.85	3.88	4.02	P.t.	Fr	Whitmee 1887
					P.s.	Fr	Brooke DMWR
Combretaceae	<i>Terminalia catappa</i>	0.73	3.11	4.02	P.t.	Fr	Trail 1994
					P.s.	Fr	Banack 1996
	<i>Terminalia richii</i>				?	Fr	I. Gurr pers com
Ebenaceae	<i>Diospyrus elliptica</i>				?	Fr	Rainey et al. 1995
	<i>Diospyrus samoensis</i>				P.s.	Fr	Freifeld DMWR
Elaeocarpaceae	<i>Elaeocarpus ulianus</i>	0.96	2.29	4.4	P.t.	Fl	Banack 1996
					P.s.	Fr Fl	Trail 1994
Gesneriaceae	<i>Cyrtandra samoensis</i>				P.s.	Fr	Trail 1994

Family	Genus and species	%N	%Fat	% kcal/g	Bat spp	Part eaten	Reference
Guttiferae	<i>Calophyllum neo-butica</i>				?	Fr	Rainey et al.1995
	<i>Calophyllum inophyllum</i>	0.76	4.19	4.49	P.t.	Fr	Wilson & Engbring 1993
					P.s.	Fr	Trail 1994
	<i>Mammea glauca</i>				?	Fr	Rainey et al. 1995
Leguminosae	<i>Albizia saman</i>				P.t.	Fl	Banack 1996
	<i>Erythrina variegata</i>				P.t. P.s.	Fl	Trail 1994
					?	L	Banack 1996
	<i>Inocarpus fagifer</i>	1.83	4.71	4.41	P.t. P.s.	Fr L	Trail 1994
					?		Banack 1996
Liliaceae	<i>Collospermu samoense</i>				P.s.	Fr	Cox 1984
Loganiaceae	<i>Fagraea berteroaana</i>	0.78	13.2	5.44	P.t. P.s.	Fr	Cox et al. 1992
Meliaceae	<i>Aglaia samoensis</i>				?	Fr	Rainey et al. 1995
	<i>Dysoxylum maota</i>				P.s.	Fr	Cox 1983b
	<i>Dysoxylum samoense</i>				P.s.	Fr	Cox 1984
Moraceae	<i>Artocarpus altilus</i>	0.97	3.71	4.46	P.t. P.s.	Fr	Wilson & Engbring 1993
					P.t.	L	Craig DMWR
					P.s.	L	Pierson et al. 1992
	<i>Ficus obliqua</i>	1.18	4.65	4.91	P.t. P.s.	Fr	Trail 1994
	<i>Ficus prolixa</i>				P.s.	Fr	Trail 1994
					P.t.		Banack 1996
	<i>Ficus scabra</i>	1.72	6.66	4.33	P.s.	Fr	Trail 1994
						L	Brooke DMWR
	<i>Ficus tinctora</i>	1.57	8.96	4.27	P.s.	Fr	Trail 1994
						L	Banack 1996
	<i>Ficus uniaurculata</i>	1.86	5.67	4.22	P.s.	Fr	Banack 1996
Musaceae	<i>Musa spp;</i> <i>Musa paradisca</i>	0.72	2.81	4.15	P.t.	Fl	Pierson 1992
Myristicaceae	<i>Myristica hypargyrea</i>				P.t.	Fr	J. Richmond in Banack 1996
Myrtaceae	<i>Syzygium dealatum</i>				P.t.	Fr Fl	Banack 1996
	<i>Syzygium inophylloides</i>	0.45	1.39	4.65	P.t. P.s.	Fr Fl	Pierson et al. 1992

Family	Genus and species	%N	%Fat	% kcal/g	Bat spp	Part eaten	Reference
Myrtaceae	<i>Syzygium jambos</i>				P.t.	Fr	Cox 1983b
Orchidaceae	<i>Eria robusta</i>				P.s.	L	Pierson 1993
Palmae	<i>Cocos nucifera</i>				P.t.	Fl	Pierson et al. 1992
					P.s.		Banack 1996
Pandanaceae	<i>Freycinetia reineckei</i>				P.s.	L	Cox 1983b
					P.t.		Brooke DMWR
	<i>Pandanus tinctorius</i>				P.t.	Fr	Wilson & Engbring 1993
Piperaceae	<i>Piper gradfferi</i>				P.s.	Fr	Banack 1996
Rhamnaceae	<i>Alphitonia zizyphoides</i>				P.s.	Fl	Trail 1994
Rubiaceae	<i>Guettarda speciosa</i>				P.t.	Fr Fl	Banack 1996
	<i>Gynochthodes epiphytica</i>				?	Fr	Banack 1996
	<i>Neonauclea forsteri</i>				P.s.	Fl	Banack 1996
Rutaceae	<i>Citrus sinensis</i>				P.t.	Fr	Whitmee 1874
Sapindaceae	<i>Cupaniopsis samoense</i>				P.s.	Fr	Cox 1983b
Sapotaceae	<i>Palaquium stehlinii</i>	0.93	14.3	5.07	P.t. P.s.	Fr Fr	Banack 1996
							Trail 1994
	<i>Planchonella garberi</i>	1.74	2.74	4.68	P.t. P.s.	Fr Fl	Banack 1996
					P.s.	Fr	Trail 1994
	<i>Planchonella grayana</i>				P.t. P.s.	Fr	Trail 1994
	<i>Planchonella samoensis</i>	1.96	10.86	4.51	P.t.	Fr	Trail 1994
					P.s.	Fl	
Verbenaceae	<i>Faradaya amicornum</i>	1.15	6.38	4.8	?	Fr	Trail 1994

Appendix 2. Percentage of tree species in six valleys surveyed for *Pteropus samoensis*

Tree species	% observed per valley					
	Amalau	Aoa	Malaeimi	Leone	Nu'uuli	Maloata
<i>Pipturus argenteus</i>	2.7		0.3		0.1	1.3
<i>Buchanania merrillii</i>	2.9		3.4	1.1	2.5	
<i>Inocarpus fagifer</i>	2.7	2.5		0.6	0.7	0.8
<i>Ficus uniauriculata</i>	0.7					
<i>Ficus obliqua</i>	3.8	2.7				1.3
<i>Ficus prolixa</i>	2.5	4.2				1.0
<i>Ficus sp.</i>	1.6		0.1			
<i>Hibiscus tiliaceus</i>	4.1	25.3	12.8	1.4	8.3	3.8
<i>Syzygium inophylloides</i>	2.8	1.5	5.1	10.0	9.0	5.1
<i>Barringtonia samoensis</i>	0.4		0.3		1.7	0.5
<i>Dysoxylum sp.</i>	11.6	11.4	11.6	5.0	12.4	11.9
<i>Dysoxylum maota</i>	3.4					
<i>Fragraea berteriana</i>	3.0	0.3			1.2	2.0
<i>Bischofia javanica</i>	3.9		2.9	0.3	0.1	4.3
<i>Rhus taitensis</i>	11.8	19.2	20.1	42.8	18.0	0.3
<i>Alphitonia zizyphoides</i>	3.8	5.5	2.5	5.6	7.9	1.3
<i>Canarium vitiensis</i>	18.0	2.3	3.3	9.2	5.0	34.6
<i>Planchonella samoensis</i>	6.3		13.4		7.4	12.1
<i>Cananga odorata</i>	4.5	1.1	6.4	1.4	0.7	5.0
<i>Barringtonia asiatica</i>	0.4	2.3			1.0	
<i>Kleinhovia hospita</i>	0.8	1.3				
<i>Elattostachys falcata</i>	0.2					
<i>Neonauclea forsteri</i>	6.4	0.4	2.8	3.9	6.3	10.0
<i>Macaranga stipulosa</i>	0.9		0.8		1.7	
<i>Macaranga harveyana</i>	1.1	0.4	0.4	6.7	0.7	1.0
<i>Myristica fatua</i>		2.7	1.9	5.3	2.9	2.8
<i>Cocos nucifera</i>		8.6			0.4	
<i>Sterculia fanaiho</i>		0.0	1.3			
<i>Artocarpus altilis</i>		0.3				
<i>Adenanthera pavonina</i>		1.3		5.8		
<i>Elaeocarpus ulianus</i>		0.3	3.0		3.9	
<i>Terminalia catappa</i>		2.0				
<i>Thespesia populnea</i>		0.2				
<i>Citrus sp.</i>		0.2				
<i>Cerbera manghas</i>		0.6				
<i>Glochidion ramiflorum</i>		0.2				
<i>Mangifera sp.</i>		0.4				

Tree species	% observed per valley					
<i>Diospyros sp.</i>		2.3	2.1		1.9	0.1
<i>Crossostylis biflora</i>		0.0				
<i>Callophyllum neoebudicum</i>		0.3			1.9	
<i>Palaquium stehlinii</i>			4.5		0.7	
<i>Samanea saman</i>			0.8			0.6
<i>Olmolanthus nutans</i>					0.4	
<i>Planchonella grayana</i>					0.6	
<i>Ficus tinctoria</i>					0.1	
<i>Castilla elastica</i>						0.5
<i>Leucosyke corymbulosa</i>			0.5			
<i>Myristica hypargyrea</i>			0.3			
<i>Paraserianthes falcataria</i>					1.8	
<i>Cinamonum verum</i>				1.1		
<i>unidentified</i>					0.8	