

Population status and behaviours of the Samoan flying fox (*Pteropus samoensis*) on Tutuila Island, American Samoa

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Abstract

The small population and limited range of the Samoan flying fox *Pteropus samoensis* has generated concern regarding the survival of this large, diurnally active bat. During 1995–96, surveys were conducted monthly in six study valleys on Tutuila Island, American Samoa, to assess population size. The amount of diurnal and nocturnal activity was investigated to gauge the accuracy of diurnal surveys, and territorial behaviours were observed to determine how they influenced local dispersion. Individuals showed long-term fidelity to a series of roosts and small core areas that were used both nocturnally and diurnally. Territorial defence was observed only of temporary feeding territories in fruiting or flowering trees. Bats defended food resources by aerial patrols and extended aerial chases in which intruders were frequently bitten. Foraging movements changed seasonally, with up to 80% of individuals observed bypassing study valleys. The mean density of bats observed within the study valleys was 6.1 bats/km² (range = 0.9–18.5 bats/km²). *Pteropus samoensis* were active both nocturnally and diurnally with greatest activity in late afternoon and evening, 16:00–22:00. Because bats were most active at night, it is probable that daytime surveys of flying bats undercount the number of individuals present. Greatest densities were found in valleys that were contiguous with large tracts of forest inaccessible to people. Most observations of roosting bats were of solitary males on dead branches that jutted above the forest canopy, while females and dependant young roosted below the canopy, hidden within vegetation. Adult male–female pairs were rarely seen together other than during the mating period in August–January. The population has increased following a ban on hunting, but reliance on mature forest makes long-term species survival dependant, on protection of the limited mature forest remaining and continued hunting restrictions.

Key words: population, behaviours, *Pteropus samoensis*, Samoa

INTRODUCTION

Large flying fox fruit bats of the genus *Pteropus* (Chiroptera: Pteropodidae) are indigenous to the islands of the Pacific and Indian Oceans, Australia and South-east Asia (Rainey & Pierson, 1992). Particularly on small isolated islands with low biodiversity, flying foxes play an important role in maintaining forests by enabling seed and pollen dispersal (Fujita & Tuttle, 1991). Loss of viable flying fox populations may have a cascading effect on native forest ecosystems (Cox *et al.*, 1991; Rainey *et al.*, 1995).

The Samoan flying fox *Pteropus samoensis* is endemic to the Samoan and Fijian archipelagos (Pierson *et al.*, 1992). The Samoan population was believed to be near extinction as a result of habitat loss and extensive

commercial hunting in the 1980s and was classified as endangered by the International Union for Conservation of Nature and Natural Resources (Cox, 1983; Pierson *et al.*, 1992; Pierson *et al.*, 1996). Surveys of the Samoan Islands in 1989 found the largest population on Tutuila Island, American Samoa, but following hurricanes in 1990 and 1992 this population declined by 80% from hunting to c. 1.6 bats/km² (Wilson & Engbring, 1992; Craig, Trail & Morrell, 1994). Concern for the remaining population in American Samoa led to a hunting ban and the instigation of a population monitoring programme.

Pteropus samoensis differs from other flying fox species in several respects that complicate standard census count procedures. It is one of only a few bat species that is commonly active during the day and can be observed regularly soaring above the forest like a large hawk (reviewed in Thomson, Brooke & Speakman, 1998). It has been assumed that *P. samoensis*

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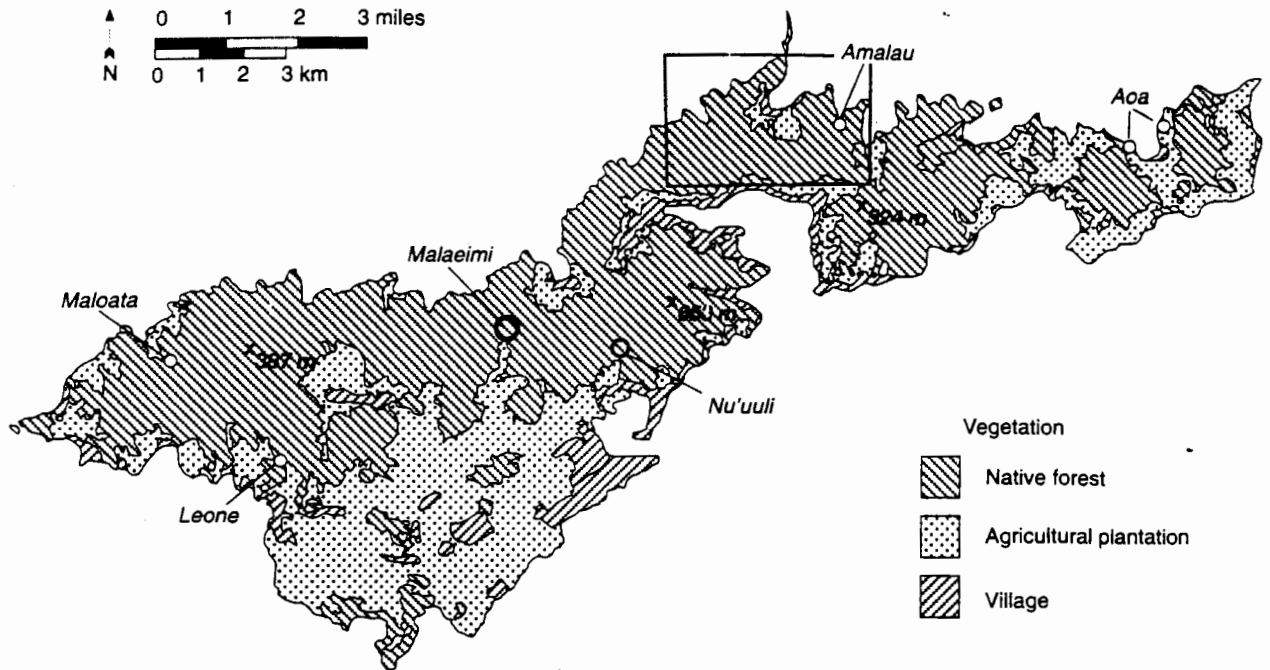


Fig. 1. Map of the Island of Tutuila showing location of six study valleys. Outlined area is enlarged in Fig. 4.

is primarily diurnal but how activity is apportioned throughout a 24-h period is unknown (Cox, 1983; Morrell & Craig, 1995; Pierson *et al.*, 1996; Grant, Craig & Trail, 1997). As diurnal flight is uncommon in bats, and flying foxes that are regularly active during the day are found only on isolated islands without diurnal predators, it seems probable that *P. samoensis* is also active nocturnally (Thomson *et al.*, 1998). If a significant part of the population is primarily active at night, daytime census counts may underestimate the population size.

Unlike most flying foxes that roost in large colonies, *P. samoensis* roosts solitarily or in pairs that are widely dispersed throughout the native forest (Pierson *et al.*, 1992; Wilson & Engbring, 1992). The repeated use of roost sites by pairs has been interpreted as a monogamous social organization, rarely found in bats (Cox, 1983; McCracken & Wilkinson, 2000). Dramatic aerial fights have been considered territorial disputes, mating behaviour and territorial defence of home ranges or roost sites (Cox, 1983; Pierson *et al.*, 1992; Wilson & Engbring, 1992). It is unclear what is being defended (mates, food resources, or territories) and unknown whether these behaviours influence the dispersion of individuals on these small islands.

The objectives of this study were to assess the population size and to describe the social organization of *P. samoensis* on Tutuila Island, as it may affect population distribution. The diurnal and nocturnal activity patterns were investigated to determine whether daytime observations are an accurate method of counting this species and territorial behaviours were observed to determine whether they influenced local dispersion.

METHODS

This study was conducted in the United States Territory of American Samoa (14°S, 170°W), c. 8000 km south of Hawaii in the southern Pacific Ocean. Tutuila, the largest island of American Samoa, is a long narrow island with an area of 142 km² (Fig. 1). Mature native forest covers about half of the island, 69.9 km² (Cole *et al.*, 1988). The climate is maritime and tropical, and the mean temperature was 26 ± 8.4°C (±SD) throughout the year (Cole *et al.*, 1988). Relative humidity was consistently high, between 82% and 86% at 17:00 all year, and annual rainfall at Pago Pago harbour was c. 3175 mm (Cole *et al.*, 1988). The topography is extremely rugged: the highest peak at 653 m, is within 1.7 km of the ocean. Numerous knife-edge ridges and cliffs characterize the eroded volcanic mountains and half the land area has a slope exceeding 70% (Nakamura, 1984). Villages and agricultural development are restricted to roughly one-fifth of the islands' land area and most of the islands' 45 000 inhabitants live along the southern coast (Anon, 1990).

Pteropus samoensis

Pteropus samoensis is a medium-sized flying fox, with an adult weight of c. 400–500 g and a forearm length of c. 130–155 mm (Brooke, 1997). Body and wings are dark brown, but the fur on the face, neck and shoulders varies considerably among individuals from a small patch of blonde fur on top of the head to grizzled grey fur covering the head, face and neck. The shoulders, neck and head of adult males can be orange to dark

russet, possibly an age-related colour variation. In several study animals, the terminal phalanx of the third metacarpal had been broken so that one wingtip was permanently upturned. Individual bats were identified using a combination of these characteristics.

The second bat species present on the island, *Pteropus tonganus*, is similar in size but in flight seems to have narrower wings and a heavier body (Craig, 1992; Wilson & Engbring, 1992; Norberg, Brooke & Trehwella, 2000). The 2 species differ in habitat use: *P. samoensis* roosts and forages within or adjacent to native forest while *P. tonganus* also forages in agricultural plantations, villages and urban areas away from continuous forest (Craig *et al.*, 1994; Pierson *et al.*, 1996; pers. obs.). Unlike *P. samoensis*, *P. tonganus* were most active nocturnally, emerging at dusk and returning at first light to colonial roosts. During 1995–96, c. 5000 *P. tonganus* were found in 10–15 colonies (Brooke, Solek & Tualaulelei, 2000).

Surveys

Surveys that monitored dispersion and foraging patterns were conducted monthly on Tutuila during 1995–96 in 6 valleys that had an unimpeded view of the forest (Fig. 1). The Amalau valley (within the U.S. National Park of American Samoa), the Maloata valley, and surrounding areas are part of the least disturbed mature native forest in the Samoan archipelago (Whistler, 1994). More than half of the canopy cover in these 2 valleys consists of tree species that *P. samoensis* use for food (Brooke *et al.*, 2000). The Aoa valley study site consisted of the hillsides surrounding Aoa village. The Leone, Nu'uuli and Malaeimi study sites were located at the northern end of each valley. To the south of the survey sites, the land was agricultural plantation, secondary growth and residential areas (Fig. 1). Forty per cent or less of the canopy cover in these 4 valleys contained fruit-producing trees used as food sources (Brooke *et al.*, 2000). Vegetation of the study areas was classified as 'upland forest' and was characterized by high species diversity and dense canopy cover (Cole *et al.*, 1988). Varying amounts of agricultural plantation, including banana *Musa* spp., coconut *Cocos nucifera*, breadfruit *Artocarpus altilis* and papaya *Carica papaya*, or young secondary growth including *Rhus taitensis* and *Alphitonia zizyphoides*, were present at lower elevations of each site (Table 1).

Each survey began at first light and continued for 2 h. The number of different individual *P. samoensis* seen in flight was recorded during 8 10-min sample periods, separated by 5-min breaks, for a total of 8 samples (80 min) at each valley per month. Zeiss 10 × 40 and 10 × 50 binoculars were used to distinguish between *P. samoensis* and the occasional *P. tonganus* using characteristics of body and wing shape and the frequency and depth of wingbeats (Craig, 1992; Wilson & Engbring, 1992). A Questar spotting scope was also used for behavioural

observations. To minimize observer differences in species identification only 2 observers conducted surveys. Surveys were conducted only when there was little or no rain and wind.

A map was drawn depicting each study valley as seen from the survey observation point. During surveys, each bat was observed in flight until it roosted, was lost within the vegetation, or flew out of the valley. The location where the bat was lost from view and trees where bats were observed roosting were recorded on the map. The sex of bats was recorded when possible and also their proximity to other roosting individuals. If a bat emerged from the vegetation near where a bat had previously disappeared into the canopy, it was assumed to be the same individual and not recounted. Within each 10-min count, multiple individuals were recorded only if >1 bat was seen simultaneously or bats were observed in widely different parts of the valley. Consequently, the number of bats recorded in each count was a conservative estimate of the number of individuals present.

In addition to bats that were seen foraging, roosting, or entering the valleys to roost, the steep ridges that formed the valley boundaries were used as flyways. Bats flew above the forest canopy following the ridgeline from the first point where the ridge could be observed and continued until they flew from sight without entering the valleys. During the 1996 surveys, the number of bats by-passing valleys and their flight direction were recorded.

Survey data were log transformed, $\log(x + 1)$, and a model 1 orthogonal 2 factor ANOVA run on the effects of site, month and site-by-month on the mean number of bats observed in each study valley. The area of each valley was determined from a United States Geological Survey map and the mean number of *P. samoensis* observed/ha was calculated.

The number of females observed with young clinging to the ventral side during surveys was recorded. Focal animal behavioural observations of courtship, mother–young interactions and feeding were made throughout the day at various island locations during August 1994–April 1997.

Whenever an aerial chase was observed during surveys, notes were made of where the chase started, outcome (attempted and actual bites, locking feet, or abandonment of the chase before contact was made) and where each bat flew afterwards. Only encounters that were observed from start to finish were recorded. I also compared the number of chases that were observed during 20 days of dawn-to-dusk observations in the Amalau valley (5 days each in January, March, July and October 1995; Thomson *et al.*, 1998). These counts were conducted from first light until dusk using the same protocol of the dawn surveys: 10-min observation periods with a 10-min break between each period. As the number of bats in flight increased in the late afternoon, it was not possible to follow the flight path of multiple individuals simultaneously later than 15:00 in June and 17:30 in October.

Table 1. Mean (\pm SD) of *Pteropus samoensis* observed within valleys, Tutuila Island, during monthly surveys, valley area and percentage in plantation and secondary growth. Number of chases and follows, 1995–96

Valley	Area km ² (% in plantation and secondary growth)	All bats/km ² observed 1995–96	Bats/km ² within valley 1996	Chases	Follows
Amalau	0.214 9	43.4 \pm 15.2	18.5 \pm 8.9	32	7
Maloata	0.34 6.7	10.35 \pm 3.9	7.05 \pm 4.73	10	4
Leone	0.204 12	11.1 \pm 9.6	5.52 \pm 0.21	18	0
Aoa	0.613 8.6	4.74 \pm 2.8	2.72 \pm 0.52	8	4
Nu'uuli	0.576 21	3.65 \pm 2	2.05 \pm 1.77	5	1
Malaeimi	0.939 7.5	2.08 \pm 1.3	0.94 \pm 0.92	5	5
Mean total		6.13 \pm 2.84	12.15 \pm 4.8		

Radio-telemetry

Two immature male *P. samoensis* were captured in the Amalau valley, 8 November 1995 at 20:30 in vertically strung mist nets hung c. 30 m above the ground in the canopy of a fruiting *Ficus prolixa* (Munn, 1991). Each bat was outfitted with a 7 g radio-collar (HoloHill Systems, Ltd, Canada) weighing <3% of the individual's mass. Although there have been no tests of how radio transmitters influence the behaviour of large pteropodid bats, the mass of these transmitters was well below the 5% threshold that can influence behaviour of aerially foraging insectivorous bats (Aldridge & Brigham, 1988). Cotton crochet string was threaded through the radio and through Tygon tubing (1/8 inch external diameter) that acted as a collar. In control tests, the string disintegrated after c. 60 days, releasing the transmitter.

Both individuals were followed concurrently for 62 h nocturnally and 70 h diurnally from 10 November 1995 to 23 January 1996). The bats were tracked for the maximum amount of time that was permitted by weather and personnel: 1 continuous 24-h period, 2 all-night sessions from 19:00–05:00, 2 dawn–dusk sessions and 14 diurnal or nocturnal sessions of 4–8 h.

Position fixes were obtained from the intersection from 2 or 3 bearings recorded at 15-min intervals and plotted on a 1:24 000 map. When both animals could be detected from 1 location, their positions were followed continuously. If only 1 animal was within receiver range, it was monitored for as long as possible before moving to 1 of 8 fixed base stations at c. 1-km intervals on the Vatia road where the second animal could be predictably located. These set locations were chosen for a clear view of the surrounding landscape. The rugged terrain limited the range of radio reception to c. 4.5 km rather than the size of the transmitters. The accuracy of resolution at 100 m was c. 20 m. Data obtained on the night bats were released were excluded from the analysis.

Small changes in signal location, e.g. when bats moved within the canopy of a tree, were not recorded as

position changes. Location changes were recorded when the animal's position had changed by at least 10 m. When the bats flew over ridges they were out of contact for up to 10 min, consequently the amount of time in flight could not be calculated and the number of moves per h has been used as an indication of activity. The number of moves was adjusted for different effort of telemetry hours throughout the day.

Telemetry locations were analysed by the adaptive kernel method (Calhoun Home Range Analysis Program, U.S. Forest Service Pacific Southwest Research Station and California Department of Fish and Game). By convention, the foraging area was set at 95% of position fixes and the core use area at 50%. Daytime was defined as being 06:00–18:00 and nighttime as 18:00–06:00, approximately following dawn and dusk in American Samoa in December. Diurnal and nocturnal activity was judged by the number of changes in position or flights/h.

RESULTS

Surveys

The number of bats counted in surveys varied between sites and throughout the year (Fig. 2, Table 1). The effect of both site and month on the number of bats observed were highly significant ($P < 0.0001$). No relationship was found between area of study valleys and number of bats observed (Pearson correlation, $P > 0.050$) (Table 1). The total number of bats observed did not differ significantly between the 2 years (Mann–Whitney rank sum test, $P = 0.9$).

Half of the bats counted during surveys by-passed the valleys either flying above ridges or at great height above valley floors. A mean of 6.13 bats/km² was observed foraging or roosting within the valleys (Fig. 2, Table 1). All surveys at two sites (Amalau and Maloata) had a significantly greater number of bats by-passing the valleys on ridge-flyways than remaining within the valleys (paired *t*-tests, d.f. = 7, $P < 0.01 - < 0.001$).

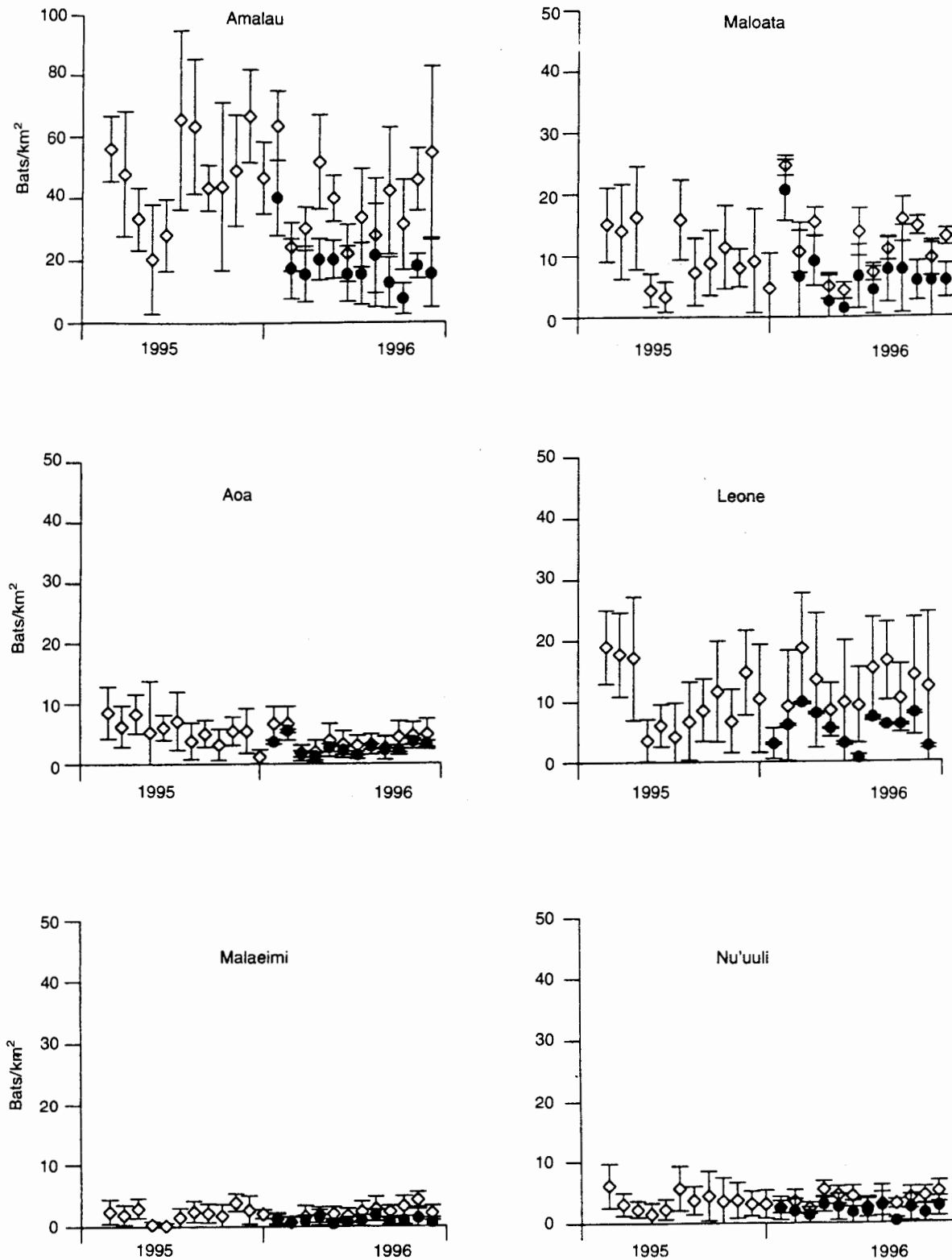


Fig. 2. Total *Pteropus samoensis* observed (mean \pm SD) during monthly dawn surveys at six study valleys on Tutuila Island, 1995–96 (open diamonds). Bats remaining within study valleys (mean \pm SD) 1995 (closed circles).

The seasonal use of flyways was most obvious at Leone where bats flew along the western ridge, from south of the valley toward the north and into the uninhabited forested interior of the island (Fig. 1). In July, 80% of bats observed by-passed this valley but the use of the

ridge-flyway declined to zero in November and December.

The number of bats seen in each of the eight daily sample periods differed significantly (one-way ANOVA, $P < 0.001$). The mean number of bats observed increased

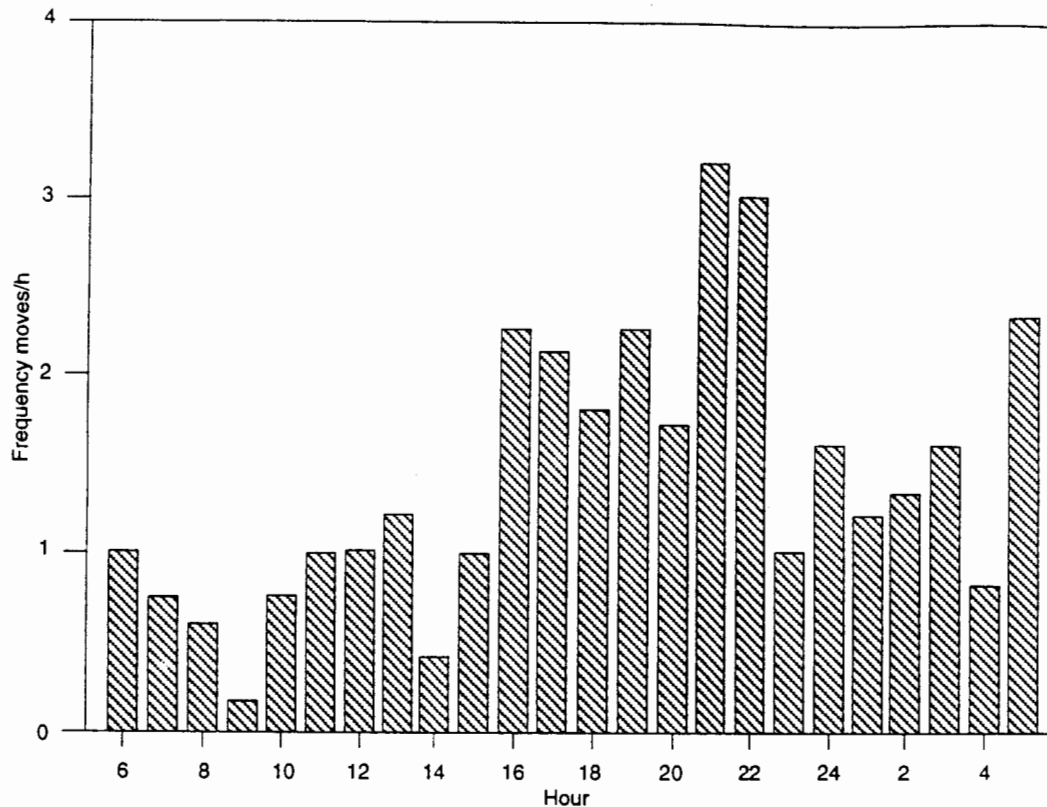


Fig. 3. Activity pattern of two radio-tracked *Pteropus samoensis* shown over 24 h. Frequency of movements has been adjusted for telemetry effort/h.

during the 40 min after first light, then declined in the following 75 min. In the first three 10-min sample periods, the number of bats observed increased from 4.36 to 4.78 bats/km² (all sites pooled), and in the following five count periods the mean number of bats declined to 2.51 bats/km² (SD = 2.19) in the last period.

Nocturnal activity

The radio-collared bats roosted and foraged in the mature upland forest of the Amalau and Vatia valleys and the surrounding ridges in the U.S. National Park. Both animals were active throughout the day and night but were least active after dawn when the number of moves/h reached a mean low of 0.17 at 09:00. (Fig. 3). Activity increased in the late afternoon and early evening between 16:00–22:00 (mean = 2.2 moves/h, SD = 0.7) and the bats were most active from 21:00 to 22:00 (mean = 3.1 moves/h, SD = 0.1). The frequency of movements was significantly greater between 21:00 and 22:00 than during the remainder of the night, from 23:00 to 05:00 (mean = 1.4/h, SD = 0.5) or during the day from 06:00 to 15:00 (mean = 0.7 moves/h, SD = 0.3) (Tukey pairwise multiple comparison tests, all pairs $P < 0.05$). Neither bat would have been counted during morning surveys as both returned to their core areas before dawn and remained stationary for several hours.

Foraging and core-use areas

The daytime foraging areas of both bats were contained within their nocturnal foraging areas (Fig. 4). The core areas used at night and during the day were similar in size for both animals and were used consistently by both individuals throughout the 74 days they were followed. Home ranges (core and foraging ranges) of both bats overlapped with each other and those of numerous other individuals observed daily. Although it was not possible to estimate the number of other individuals using the same foraging or core areas, an indication of the number of bats foraging in nearby Amalau valley can be estimated from morning surveys where the mean number observed in 1996 was 18.5/km² (SD = 8.9). The nocturnal foraging and core areas were also shared with numerous *P. tonganus*.

The foraging area of bat A (Fig. 4) represents a minimum size as it was not possible to follow it for several hours on two nights when it flew beyond receiver range over the inaccessible Siuono ridge, north-west of Vatia village. Although its foraging range encompassed Vatia village, the bat remained in upland forest above the village and did not approach the populated area.

Roosting bats

Thirteen roost sites that were used repeatedly by six individuals were identified in Amalau valley. Roosts

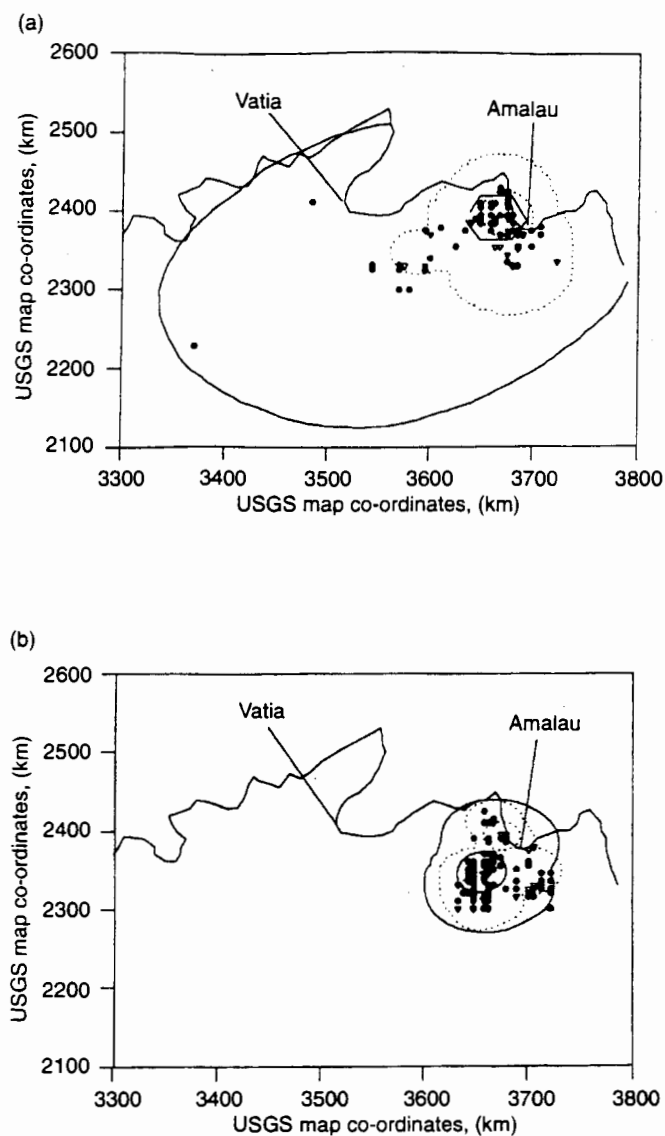


Fig. 4. Nocturnal and diurnal foraging and core ranges of two radio-tracked *Pteropus samoensis* on the north coast of Tutuila Island. Solid line, nocturnal foraging and core areas; closed circles, telemetry points; dotted line, diurnal foraging and core areas; open triangles, telemetry points. (a) Bat A nocturnal foraging area = 8.18 km², core area = 0.2 km²; diurnal foraging area = 2.3 km², core area 0.25 km². (b) Bat B nocturnal foraging area = 1.75 km², core area = 0.2 km²; diurnal foraging area = 1.2 km², core area = 0.2 km². Axis co-ordinates taken from the USGS topographic map of Tutuila Island.

were spaced c. 25–120 m apart within 12 ha, on dead branches or hidden within foliage. The mean distance between the roost trees used by one individual was 30.6 m, (SE = 7.8, range 10–50 m). These trees were not the only roost sites that were used by each bat, since all the individually identified bats were not re-sighted daily. The Amalau valley area was used by many bats and the six individuals followed were only a portion of the animals that were regularly sighted within this section of forest.

The majority of roosting bats observed during survey counts were single males without other bats in the same tree or in nearby trees, although several sightings were too distant to determine sex or to conclude that no other bats were nearby (Table 2). Single males were most frequently seen on prominent branches that emerged above the canopy, while females were most frequently observed hanging within the canopy. During 2 years of observations, some individuals were undoubtedly sighted more than once. Male–female pairs were observed only in August–March, while only females with non-volant young or juveniles were observed during April–July. Roost groups that were larger than a possible family, four to 11 bats, were seen infrequently but consistently (Table 2). An unusually large aggregation of c. 60 *P. samoensis* was present in the Amalau valley for 3 days in October 1996, roosting adjacent to an equally temporary colony of *P. tonganus*.

Roosting bats typically did not react or respond to other bats passing nearby. The use of highly visible roost sites by males suggests that they may be used to advertise the bats' presence, but there was little evidence that roosts were defended. Only once was an open-winged threat display (see below) directed toward an approaching bat.

Reproductive behaviour

Between August and January, the enlarged testes of adult males were clearly visible as they roosted. Males chattered frequently and followed females as they climbed among branches or flew short distances to an adjacent tree. Copulations were observed only in September–October ($n = 6$), including one male that copulated with two females within a 10-min period. In October 1996, pairs occupied five of the roost sites in the Amalau valley where only single males had previously been seen.

Both males ($n = 13$) and females ($n = 2$) scent-marked by rubbing their chin against small branches or epiphytes or by drawing the plants across the sebaceous glands on the back of the neck. Seasonal development of sebaceous neck glands in pteropodid bats has been linked with high plasma-testosterone levels and breeding activity (Martin *et al.*, 1995). Most observations (73%) were made between September and December suggesting that scent-marking plays a role in sexual communication, as a type of self-advertisement, delineating territories, or possibly to help synchronize seasonal breeding as has been suggested for tamarin monkeys (Epple, Golob & Smith, 1979).

Non-volant young were first observed carried by females in late March. Most observations were during June ($n = 24$, 71% total young carried) when the number of small (< one-quarter adult size), medium (c. one-quarter to half adult size) and large pups (c. half + adult size) carried by females were nearly equal. Births were less frequent after June, but young bats were occasionally seen until November. Large-sized juveniles were

Table 2. Roosting associations of *Pteropus samoensis*, 1994–97

No. bats	Males (on prominent branches/ within canopy)	Females (on prominent branches/ within canopy)	Male and female	Female and juvenile	Sex and age unknown
1	64 (51/13)	21 (4/17)			74
2			11	8	13
3					5
4–11					8
c. 60					1

Table 3. Courtship and mating behaviour, juvenile–adult interactions and food defence

Chases $n = 78$	Attacks $n = 12$	Follows $n = 21$	Patrolling $n = 17$
Bite	33% Male landed on female (September–December)	25% Juvenile behind adult	33% Occurred September–January
Attempted bite	31% Juvenile landed on adult	16% Male behind female	28% Chased other bats from fruiting trees
Chase aborted, no bite	27% Directed at bat landing in fruiting tree	25% Unknown	61% Patrolling bat landed in fruiting tree
Pursuing bat returned to where chase started	44%		5%

observed from September to March, roosting with an adult female. When observed for several hours, juveniles eventually climbed onto the female and were wrapped within her wings as they hung together ($n = 8$).

Interactions

Four types of behavioural interactions were classified into three general categories: courtship and mating behaviour; juvenile–adult interactions; food defence. Two types of aerial pursuits were observed: ‘follows’ were uncommon while ‘chases’ were observed frequently. A follow was identified as the slow flight of a juvenile or male following behind a female, in and out of the forest canopy and did not seem to be aggressive (Table 3). During August, the following individuals were markedly smaller in size than the leading bats, probably newly volant juveniles flying behind their mothers ($n = 7$, 33%). In October, six follows were observed where a male pursued another adult-sized bat, probably a female. One lengthy follow ended when both bats landed in a tree and mated (C. Solek, pers. comm.). ‘Chases’ were clearly aggressive and the pursuing bat frequently attempted to bite the intruder (Table 3). During a chase the bats flew away from the forest canopy and the bat being chased tried to avoid its pursuer by dodging and rapidly changing flight direction. Chases seem to be part of the defence of temporary foraging sites and did not correlate with the number of bats observed in census counts (Pearson correlation, $P > 0.05$: Amalau $r_s = 0.3$, Maloata $r_s = 0.2$, Leone $r_s = 0.2$, Aoa $r_s = 0.05$, Malaemi $r_s = 0.1$, Nu'uuli $r_s = 0.05$). During 20 days of dusk-to-dawn observations in Amalau valley, 109 chases were observed. A significantly greater number of chases were seen in January

($n = 73$) than during March, July and October (range = 9–13 per 5-day count) (Tukeys' test, $P < 0.05$). During January, bats were frequently seen feeding in 18 large flowering *Syzygium inophylloides* trees in the valley.

A few bats were observed ‘patrolling’ a section of forest by repeatedly flying back and forth for up to 30 min (Table 3). Patrolling seemed to be defence of fruiting or flowering trees since patrolling bats frequently chased bats that approached fruiting trees. All but one observation was made between September and January when the availability of preferred fruits peaked and *S. inophylloides* were in flower (Banack, 1998).

The most uncommon behaviour was an ‘attack’, where a bat landed directly on top of another dislodging it from its roost. Attacks were observed throughout the year and included courtship behaviour (male landing on a female), juveniles and adult interactions (juvenile landing on a female) and food defence (bat landing on another that had arrived at a fruiting tree) (Table 3).

Food defence

Defence of foods depended on the size and abundance of fruit or flowers. Both males and females actively defended entire trees or a specific large fruit they were unable to remove from the tree, such as breadfruit *Artocarpus altilis*. Medium-sized fruits, such as *Terminalia catappa*, *Palaquium stehlinii*, *Planchonella samoensis*, *S. inophylloides* and *Inocarpus fagifer*, were frequently carried by bats away from the tree to be eaten. Bats defended only the immediate area where they were foraging on abundant small fruits and flowers, such as *Ficus obliqua* or *F. prolixa* and flowering *S. inophylloides*. During the brief period when a large

Ficus obliqua teemed with fruit, up to 12 *P. samoensis* were seen foraging simultaneously during the day. In flowering *S. inophylloides* trees, most observations were of a single bat in a tree ($n = 13$) but I observed groups of four–eight *P. samoensis* feeding in trees with dense flowers (> 10000 flowers) ($n = 6$). Bats defended the fruit or flowers where they were feeding from others by striking at the other bat with a closed wing, biting and vocalizing, and threatened others by wing clapping: quickly bringing their wings together so that the forearms hit with a loud clap ($n = 7$). Open-wing threat displays, where a bat quickly flared both wings open perpendicular to its body, were observed among feeding bats when a bat was interrupted by another ($n = 4$) and has been described for other pteropodid bats defending foods (Lieuweiler, 1962; Gould, 1977; Richards, 1990; Wiles, Engbring & Falanruw, 1991).

Sunning behaviour

On calm sunny mornings, open-wing displays seem to be thermoregulatory in nature and not a threat display. Bats roosting on prominent and exposed branches opened one or both wings as sunlight first fell on them, faced into the sun and slowly rotated back and forth, their wings hanging loosely downward rather than perpendicular to the body as in threat displays ($n = 36$). Unlike threat displays, bats held their wings open for up to 31 min (mean = 11.7, $SD = 9.4$) when no other individuals were nearby. It was not possible to measure the temperature of bats in the sun, but when shade temperature increased to *c.* 30°C, bats folded their wings and moved into the shade. Sunning bats were seen in all months except January and March. Only once was a bat seen fanning its wings, behaviour common in other species to reduce heat load by increasing convective and evaporative cooling (Laburn & Mitchell, 1975).

DISCUSSION

The population of *P. samoensis* on Tutuila had increased to 6.13 bats/km² from the low 2–4 bats/km² observed after two severe hurricanes in 1991 and 1992 (Craig *et al.*, 1994). The current population is approaching the first estimates of 6.5–9.5 bats/km² made in 1986–90, when the population was already in decline from extensive hunting for export to Guam (Cox, 1984; Craig *et al.*, 1994). *Pteropus samoensis* were clearly active both diurnally and nocturnally; daytime activity that declined in the morning and increased in the afternoon has also been reported in other studies (Wilson & Engbring, 1992; Pierson *et al.*, 1996; Thomson *et al.*, 1998). This general pattern was confirmed again by the data from radio-telemetry that showed the greatest activity in the late afternoon and night. Since all surveys for *P. samoensis* have been conducted at a time when some animals were inactive, the number of bats has undoubtedly been underesti-

mated and densities should be considered minimal estimates. Craig *et al.* (1994) speculated that they had observed only one-third to half of the bats present and they adjusted their density estimate upwards accordingly. Mark–resight techniques could help determine the percentage of animals inactive during surveys and would provide statistical rigor that is currently lacking (White, 1996). So far, the difficulty of capturing a sufficient number of bats has prevented the use of this approach.

Bats did not exclude other individuals from foraging ranges or core-use areas but aggressively defended their immediate feeding sites, as is typical of other flying fox species (Nelson, 1965; Marshall, 1985; Richards, 1990, 1995; Wiles *et al.*, 1991). Aerial chases by bats defending food plants have also been reported from nectarivorous and frugivorous neotropical bats and are probably common behaviours of other pteropodid species (Sazima & Sazima, 1977; Lemke, 1984; Petryszyn, 1997). Most of the trees on which *P. samoensis* forages produce small amounts of fruits or flowers over extended periods (Whistler, 1980; Trail, 1994). Combined with the heterogeneous distribution of trees, defence of large areas by individual flying foxes is impractical. Variation in number of bats that by-passed study valleys reflect the changing availability of foods throughout the year, but the 2 years of the study were insufficient to attribute monthly fluctuations in bat numbers to specific food resources.

Bats roosting singly or females with dependant young were observed but adult pairs were only seen during the time when courtship behaviour was observed, in September–December. It is probable that some mating occurred over a longer period as some young were born over an extended period of 8 months. Speculation that *P. samoensis* form pair bonds and may have a monogamous social system originated from repeated sightings of two bats roosting together (Cox, 1983; Pierson *et al.*, 1992). If roosting bats were mated pairs, a volant juvenile should have also been present for 6 or more months making a family group of three. Groups of bats that could have been families were rarely observed and no observations were made of male parental care as would be expected in a monogamous social organization (McCracken & Wilkinson, 2000). I was unable to determine if bats mated with the same partners for > 1 year, in part because I did not find pairs associated throughout the year. It seems unlikely that *P. samoensis* forms long-standing pairs, and they may have a type of polygynous mating system.

While most flying fox taxa (genus *Pteropus*) roost in groups that may contain thousands of individuals, coloniality is flexible in several species. For example, on Guam, colonies of *P. mariannus mariannus* range in size from 20 to 1000, but on the island of Palau most *P. mariannus pelewensis* roost solitarily or in small groups of < 200 (Wiles, 1987; Wiles, Engbring & Otobed, 1997). There are also differences in individual behaviour as with colonial *P. tonganus* in American Samoa, where single bats may remain during the day near fruiting trees

that they actively defend at night (pers. obs.). As all flying foxes aggregate at food sources, a possible reason for temporary groups of *P. samoensis* is to be close to ephemeral food abundance.

Flexible activity and roosting patterns give *P. samoensis* a survival advantage in the Samoan islands where there is little predation pressure and frequent hurricanes cause severe environmental changes. Daytime activity allows greater foraging time and access to different foods, such as the increased nectar flow and higher concentration of sugars during the day in *Syzygium inophylloides* flowers (pers. obs.). Thomson *et al.* (1998) found both the greatest numbers of diurnally active bats and the most consistent activity throughout the day during January when bats were observed foraging in the flowering trees. Diurnal foraging also reduces direct competition for foods with *P. tonganus* and limits exposure to occasional predation by barn owls *Tyto alba* (Grant & Banack, 1995). This strategy is less advantageous in the Fijian islands where flying foxes are a major component in the diet of peregrine falcons (White, Brimm & Clunie, 1988). Consequently, *P. samoensis* does not soar above the forest canopy and, because they are not easily observed, there is no information on the size of the Fijian population (Wilson & Engbring, 1992).

The distribution of *P. samoensis* on Tutuila continues to be influenced by hunting. A hunting ban, begun in 1992, has helped the population to increase following the two hurricanes but a few hunters continued to regularly take flying foxes. The extremely small number of bats observed during surveys in the Malaeimi valley was the result of hunting (Brooke *et al.*, 2000). In this study and others, the greatest number of *P. samoensis* were observed in valleys with high forest diversity that were adjacent to undisturbed, inaccessible tracts of upland forest, the Amalau and Maloata valleys (Cole *et al.*, 1988; Whistler, 1994; Brooke *et al.*, 2000). Like *P. samoensis*, several other pteropodid taxa with low population sizes are characterized by a reliance on native forest for roosting and foraging habitat, i.e. *Acerodon jubatus* in the Philippines and *P. livingstonii* in the Comoro Islands (Heideman & Heaney, 1992; Reason & Trehwella, 1994). In contrast, species that coexist with rare taxa but continue to have large populations in spite of hunting and declining habitat area, are species that move between forest fragments or away from forest to forage in agricultural areas, i.e. *P. tonganus* and *P. vampyrus* (Rainey & Pierson, 1992). The long-term survival of *P. samoensis* in American Samoa will depend on the preservation of continuous, relatively undisturbed forest tracts and limited hunting.

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