

# SPATIAL AND TEMPORAL MOVEMENT PATTERNS OF THE FLYING FOX, *PTEROPUS TONGANUS*, IN AMERICAN SAMOA

SANDRA ANNE BANACK,<sup>1,2</sup> Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA  
GILBERT S. GRANT,<sup>3</sup> Department of Marine and Wildlife Resources, Pago Pago, AS 96799

**Abstract:** The flying fox (*Pteropus tonganus*) is 1 of the most widely distributed *Pteropus* species but is restricted to island habitats. Flying foxes experienced a precipitous population decline on American Samoa during the early 1990s due to the impact of hurricanes and overhunting. At that time, little was known about its breeding biology, resource needs, activity patterns, and spatial requirements. To make wise conservation decisions to facilitate population recovery, we used radiotracking and observational techniques to determine space use and activity patterns of *P. tonganus*. Juvenile males were netted with greater frequency (50%,  $n = 14$ ) than other age and sex classes. Radiocollars were placed on 18 animals. Daytime activity included grooming and intraspecific interactions at the colonial roost. Collared animals departed from day roosts to forage in the early evening an average of 17 ( $\pm 4$  SE) min after sunset. Movement patterns and roost locations of *P. tonganus* divided the island into 2 groups, 1 east and 1 west of Pago Pago. Individuals with roosts on the west side of the island flew farther—22.8 ( $\pm 8.3$  SE) km—in a single night than individuals from the east side—4.8 ( $\pm 0.6$  SE) km. Roost shifts were occasionally documented in both collared and non-collared animals. Foraging was noted in both agroforest and primary forest spanning the entire island. Shifts in foraging sites were common. These results suggest that the population of *P. tonganus* on Tutuila, American Samoa, should be managed as a cohesive group and that primary forest should be protected to provide adequate roosting and foraging habitat for this species.

JOURNAL OF WILDLIFE MANAGEMENT 66(4):1154–1163

**Key words:** activity, flying fox, island, movement, *Pteropus tonganus*, Samoa, Tutuila.

Bats are the only naturally occurring mammals in the Samoan archipelago. Two species of flying fox, *Pteropus samoensis* and *P. tonganus* (Chiroptera: Pteropodidae), coexist on 4 islands of American Samoa including Tutuila. *Pteropus tonganus* has a broad distribution and is found exclusively on islands from the Schouten Islands of Papua New Guinea in the west through the Cook Islands in the east (Mickleburgh et al. 1992, Rainey and Pierson 1992, Miller and Wilson 1997). Censuses conducted by the Department of Marine and Wildlife Resources (unpublished data) revealed only about 2,000 *P. tonganus* on Tutuila at the beginning of this study, representing an 80% to 90% population decline as a result of 2 recent hurricanes (Feb 1990 and Dec 1991) and subsequent human predation (Daschbach 1990, Craig et al. 1994, Grant et al. 1997). To enhance population recovery efforts, several studies were initiated. Studies of its reproductive biology revealed that *P. tonganus* roosts in large colonies in secluded areas, maintains a harem social structure, and

breeds year-round on Tutuila (Grant and Banack 1999). Foraging ecology studies documented that *P. tonganus* is a keystone species in this area because of its role in seed dispersal and pollination (Banack 1998).

Little is known about the movement patterns or spatial use of resources of flying foxes on oceanic islands. Understanding movement within an island provides important information for understanding spatial and temporal patterns of habitat use and gene flow to enhance conservation efforts. We report on radiotracking studies to document spatial and temporal patterns of habitat use and infer gene flow on Tutuila. Our research efforts provided useful data that can be used to develop a population recovery plan for *P. tonganus*.

## STUDY AREA

Our investigation was conducted primarily on the island of Tutuila, American Samoa (14°S, 170°W), in the South Pacific (Fig. 1). Results from animals captured in Savai'i, Western Samoa, also were included. The natural vegetation of Samoa is tropical rainforest with tremendous biodiversity. Common canopy-forming plants in the inland primary forest include *Syzygium* spp., *Inocarpus jagifer*, *Planchonella* spp., *Dysoxylum* spp., *Canarium vitiense*, and *Ficus* spp. A few of the plants common in the coastal forests are *Scaevola taccada*.

<sup>1</sup> Present address: Department of Biological Science, California State University, Fullerton, CA 92834, USA.

<sup>2</sup> E-mail: sbanack@fullerton.edu

<sup>3</sup> Present address: Department of Math and Sciences, Coastal Carolina Community College, Jacksonville, NC 28546, USA.

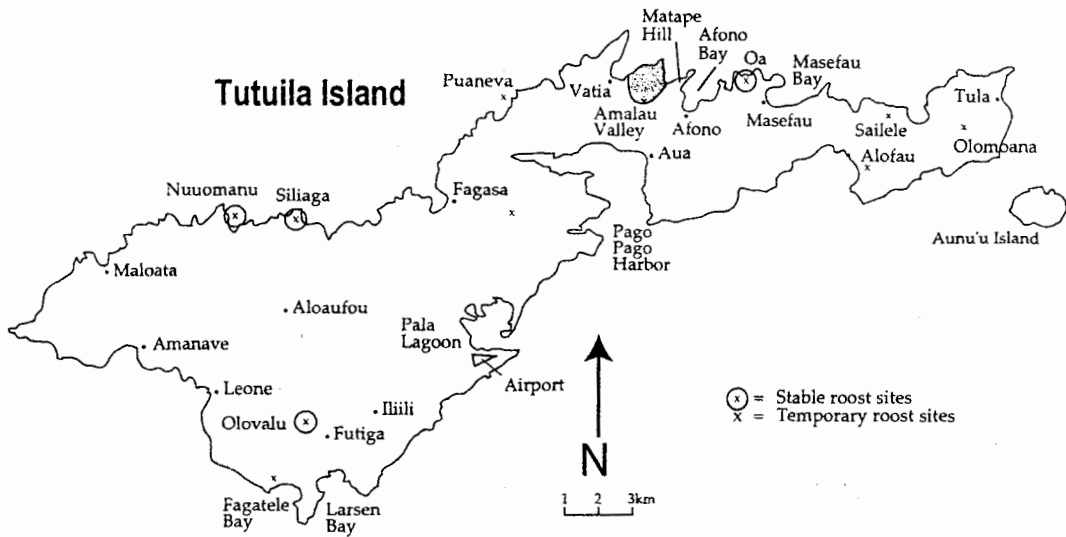


Fig. 1. Roost sites of *Pteropus tonganus* in Tutuila Island, American Samoa, 1992–1994. Data were collected in monthly roost surveys as part of regular monitoring by the Department of Marine and Wildlife Resources.

*Cocos nucifera*, *Hernandia nymphaeifolia*, *Erythrina variegata*, *Tournefortia argentea*, *Pandanus tectorius*, *Hibiscus tiliaceus*, *Barringtonia asiatica*, *Neisosperma oppositifolia*, *Pisonia grandis*, and *Terminalia catappa*. Virtually all of the lowland rainforest on Tutuila has been destroyed or altered by human activities. As a result, intact primary forest on Tutuila is almost exclusively in rugged and remote areas.

## METHODS

Flying foxes were netted from December 1992 until October 1994 using 4-in. mesh mist nets set at flyways and feeding sites throughout the island. Nets were strung on ropes hung 6 to 10 m in the air from trees or surveying poles using a pulley system. Basic information was recorded from all netted animals: date caught, sex, age, reproductive condition, forearm length, and mass (Table 1). In addition, we placed a numbered stainless-steel thumb band on most animals before fitting selected animals with radiocollars under the direction and guidelines of the Department of Marine and Wildlife Resources.

We collared animals with 1 of 2 models of Telonics (Mesa, Arizona, USA) radiotransmitters weighing 21.5 g (model 070) or 30.0 g (model 075). One model (075) was equipped with an activity sensor set at either 10-min or 1-min intervals. Transmitters were fitted around the necks of the animals using 4 methods: 9 were attached with leather cat collars, 5 were attached with wire

bands coated with sheepskin, 3 were attached with wire bands coated with rubber tubing, and 1 was attached with a wire coated with both rubber tubing and sheepskin. All collars had a weak link designed to wear off, releasing the transmitter in 3 to 6 months. Batteries had an anticipated life of 4 to 6 months.

All animals were released at the capture site. Collared animals were then monitored for longer movements to and from roosting and foraging sites, micro-movements within a foraging site, and activity (time spent active vs. inactive). Data collected before the second day following an animal's release were not included in this analysis to allow each animal adequate time to adjust to the collar. The sampling regime for each animal varied depending on the time of year, the location, and the number of simultaneously collared animals; however, both day and night hours were included in the samples.

Activity sensors were triggered with head movements in excess of a 45° angle. A yawn was sufficient in 1 instance to change the sensor from inactive to active mode (pulse frequency >60/min). The 1- and 10-min sensors required the collar to be motionless for a full 1 min and 10 min, respectively, before returning to an inactive mode (pulse frequency <60/min). The delay period was subtracted from active values to produce final calculations of time active and inactive. A reduction in power surplus was calculated following

Table 1. *Pteropus tonganus* netted in mist nets on Tutuila, American Samoa, 1992–1994. Two individuals brought into Department of Marine and Wildlife Resources for rehabilitation (\*) also are included.

Sex <sup>a</sup>	Age class <sup>b</sup>	Forearm length (mm)	Mass (g)	Date of capture	Date of last signal	No. roosts used
M	ad	144	390	21 Nov 1992	29 Nov 1992	1
M	ad	142	485	01 Dec 1992	15 Mar 1993	1
M	ad	134	314	10 Dec 1992	11 Mar 1993	1
M	ad	147	385	11 Dec 1992		
M	juv	117	230	24 Feb 1993	01 Jul 1993	1
M	ad	147	500	26 May 1993	18 Jun 1993	1
M	ad	144	495	26 May 1993		
M	ad	142	515	03 Nov 1993	16 Nov 1993	1
M	juv	108	185	03 Nov 1993	22 Dec 1993	1
M	ad	134	590	09 Nov 1993	30 Nov 1993	1
M	juv	122	214	17 Nov 1993		
M	ad	147	515	29 Nov 1993	07 Feb 1994	5
M	ad	140	459	29 Nov 1993		
M	juv	128	259	29 Nov 1993		
F	juv	109	149	14 Dec 1993	17 Dec 1993	1
F	juv	115	210	14 Dec 1993	18 Jan 1994	3
M	juv	130	285	14 Dec 1993		
M	juv	129	398	28 Feb 1994	14 Apr 1994	9
M	ad	152	500	09 Mar 1994		
M	juv	132	300	26 Apr 1994	21 Jun 1994	2
F	ad	144	415	03 May 1994	29 Jul 1994	3
M	juv	130	267	01 Jun 1994	08 Jul 1994	3
M	juv	127	271	24 Jun 1994	30 Jun 1994	1
M	juv	—	385	28 Jun 1994	25 Jul 1994	1
M	juv	119	235	29 Jun 1994		
M	juv	130	330	21 Jul 1994		
M	juv	125	265	25 Jul 1994		
M	juv	124	235	11 Aug 1994		
M	juv	125	237	02 Sep 1993*	04 Sep 1993	—
M	ad	145	450	24 Mar 1993*		

<sup>a</sup> F = female, M = male.<sup>b</sup> ad = adult, juv = juvenile.

Caccamise and Hedin (1985). A chi-square goodness-of-fit test was calculated to determine significance on day and night active intervals. Daylight hours were considered between 0500 and 1800. Two-sample *t*-tests were conducted using Minitab version 13. Flight distances were calculated based on the longest flight noted for each individual relative to its habitat on either the west or east side of the island.

A stepwise regression procedure (SAS 6.09) examined the determinants of distance traveled (km) by collared flying foxes. Four variables were entered: east or west (indicating what part of the island the animal was from), sex (male or female), forearm length (mm), and transmitter mass as a fraction of body mass used to examine the effect of the transmitter package. A linear regression was calculated to examine the effect of the transmitter on both the number of days of information gathered and on the number of roost shifts per animal corrected for the number of days that they were followed.

## RESULTS

We netted 26 *P. tonganus* in Tutuila and 2 *P. tonganus* in Savai'i, Western Samoa. Among the *P. tonganus* netted, 57% were juveniles ( $n = 16$ ; 14 juvenile males and 2 juvenile females), only 1 was an adult female (3%), and 39% were adult males ( $n = 11$ ; Table 1). Also included in our data set were 2 animals (1 adult male and 1 juvenile male) rehabilitated by the Department of Marine and Wildlife Resources. Body mass ranged from 149 g to 590 g (adult = 463 [ $\pm 20$  SE] g; juvenile = 262 [ $\pm 16$  SE] g). Mean forearm length for adults was 143 ( $\pm 1.4$  SE) mm and 123 ( $\pm 1.8$  SE) mm for juveniles. Radiocollars resulting in a mean reduction in power surplus of 9.8% ( $\pm 0.3\%$  SE) were placed on 16 netted *P. tonganus* and 2 animals rehabilitated by the Department of Marine and Wildlife Resources all on Tutuila. We put forth considerable effort to determine the fate of every animal we collared. One flying fox removed its collar within the first 2 days of placement, and the collar was recovered. Of the remaining 17 col-

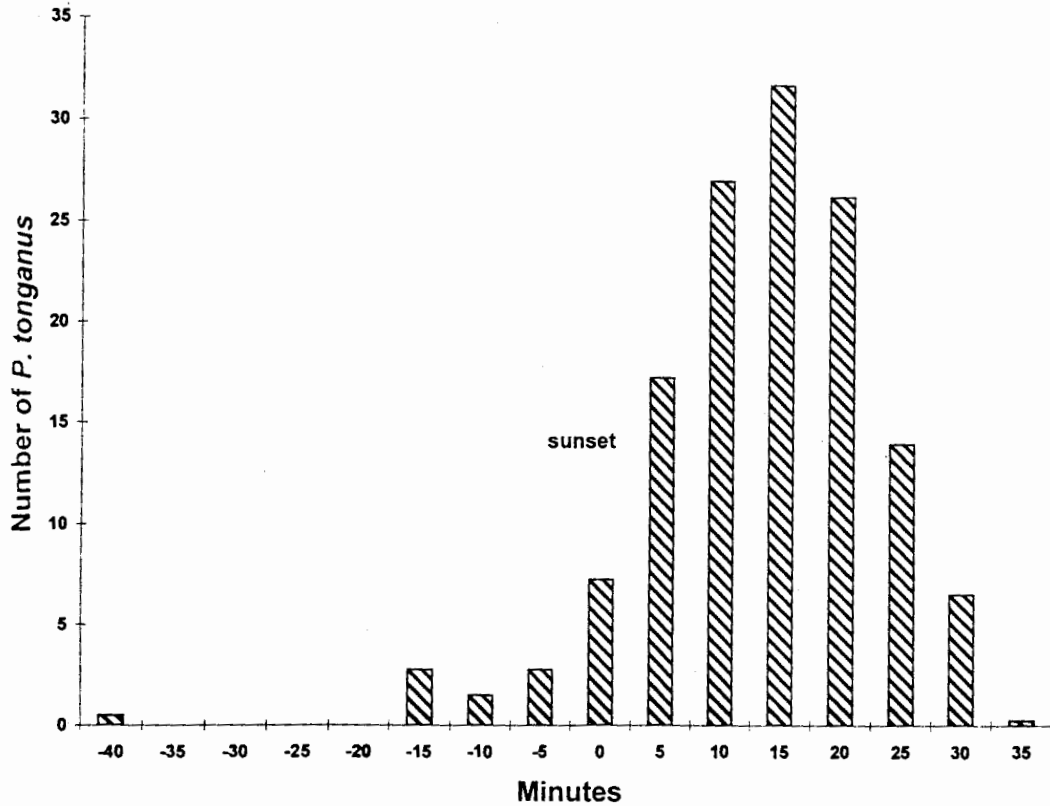


Fig. 2. Mean roost departure times measured in minutes from sunset for *Pteropus tonganus* colony at Oa, American Samoa. Only those individuals traveling west to southwest are presented. Roost counts were conducted from Matape Hill 6 Dec 1993, 15 Dec 1993, 27 Jan 1994, and 12 Feb 1994.

bars, 9 were recovered (6, 8, 13, 23, 45, 56, 70, 91, and 104 days after placement), 3 batteries or transmitters quit functioning (27, 37, and 127 days after placement), and 5 fell in inaccessible places and were thus lost (3, 21, 35, 49, and 87 days after placement). Visual observations were made of collared animals whenever possible, and all observations revealed healthy animals with no apparent stress due to collaring.

### Activity Patterns

Collared *P. tonganus* departed from day roosts in the early evening an average of 17 ( $\pm 4$  SE) min after sunset (range 69 min before sunset to 107 min after sunset;  $n = 42$ ) and returned in the early morning an average of 125 ( $\pm 25$  SE) min before sunrise (range 22 to 436 min;  $n = 21$ ). Colony departure times of uncollared flying foxes were similar to departure times of individual collared animals. Most animals within any roost left between 10 and 20 min after sun-

set (Fig. 2). In Tutuila, sunset times vary less than 1 hour throughout the year (1803 on 21 Jun, summer solstice; and 1851 on 22 Dec, winter solstice). Flying foxes departed early on cloudy, dark evenings, and after periods of persistent wet weather during normal foraging hours. Flying foxes delayed departure when it rained at dusk.

Our observations at a roost site indicated that adult harem-holding males were the first to return to the roost. Following their arrival, they engaged in scent marking, vocalizations, and wing displays as territorial advertisements. Non-harem males roosted in peripheral trees adjacent to the most concentrated part of the colony. As a result, they were more difficult to see under the low light conditions of early morning. We do not know whether adult males we collared held harems or not.

The activity sensors on the collared animals indicated that the flying foxes were significantly more active at night than during the day (1-min

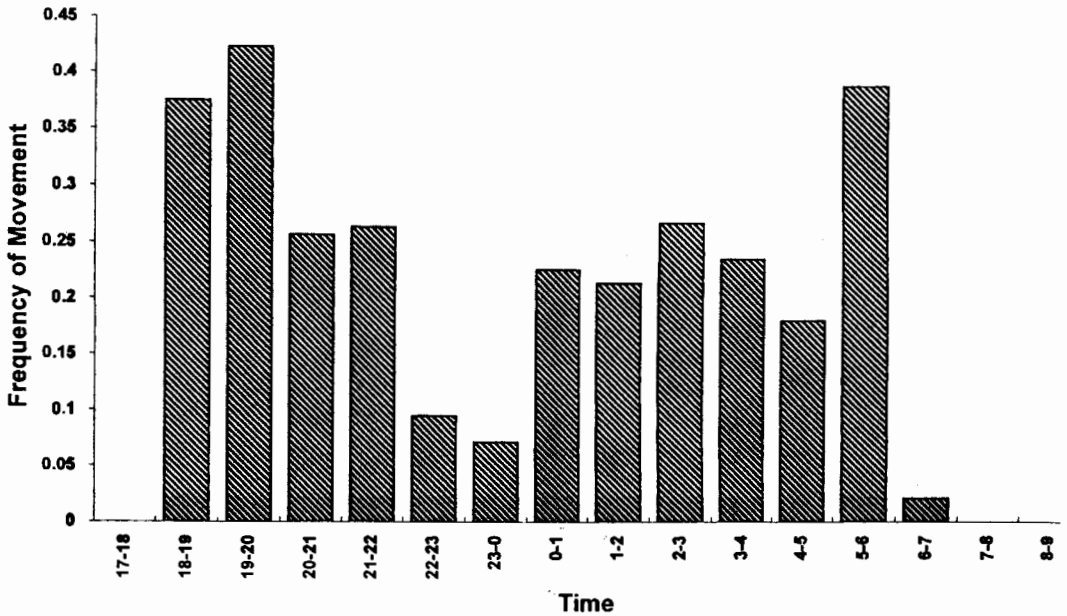


Fig. 3. Micro-movement patterns observed for 3 radiocollared adult male *Pteropus tonganus* within a plantation where they were foraging in Amalau Valley, American Samoa, 1992–1994. The flying foxes arrived between 1800 and 1900 and left by 0700. Data represent 8 nights of observations.

sensor:  $\chi^2 = 9.2$ ,  $df = 3$ ,  $P = 0.03$ ; 10-min sensor:  $\chi^2 = 12.1$ ,  $df = 2$ ,  $P = 0.002$ ). Visual observations confirm daytime activity as being predominantly movement at a roost site including maintenance behavior and intraspecific interactions. Periods of continuous activity averaged  $15 (\pm 3 \text{ SE})$  min during the day ( $n = 61$ ) and  $150 (\pm 23 \text{ SE})$  min at night ( $n = 46$ ) for males collared with the 10-min-delay sensor.

A typical evening following collared animals revealed a pattern of foraging on nectar from banana flowers (*Musa* spp.) within nearby plantations shortly after leaving the roost, followed by an extended flight to forage elsewhere. These same plantations often were visited before returning to the roost site the following morning. All animals exhibited a decrease in activity during the middle of the day and during the middle of the night (Figs. 3, 4). The exact timing of the night rest varied between individuals. Activity patterns also varied slightly with weather conditions.

### Space Use

Movement patterns divided the island flying foxes into 2 groups, 1 east and 1 west of Pago Pago harbor (Figs. 1, 5). Only 1 individual was observed moving between groups and then only on 1 night out of 13 all-night tracking episodes. Ani-

mals on the west side of the island flew significantly greater distances than animals on the east side of the island (west  $\bar{x} = 22.8 [\pm 8.3 \text{ SE}]$  km; east  $\bar{x} = 4.8 [\pm 0.6 \text{ SE}]$  km,  $t = 3.92$ ,  $df = 14$ ,  $P = 0.002$ ). Juvenile males displayed what appeared to be "exploratory flight," traveling long distances (maximum recorded 46.7 km) within a single night (Fig. 5). Of the 4 variables examined as determinants of distance traveled, only the membership in east or west groups was significant (Table 2). The west group of bats traveled an estimated 7.85 km more per night. Percentage transmitter mass had a positive coefficient in relation to the distance traveled but was not significant. Finally, age and sex were not significant ( $P > 0.15$ ) and were thus removed from the model.

Collared and non-collared flying foxes occasionally switched roost sites. Island-wide roost surveys conducted quarterly in conjunction with the Department of Marine and Wildlife Resources in American Samoa indicated regular fluctuations in the number of individual flying foxes at each roost. Temporary relocations of small groups of *P. tonganus* to previously abandoned roost sites were documented on at least 4 occasions. One of these roost shifts occurred at the time a large number of *Palaquium stehlinii* flowers opened in the surrounding primary forest. One juvenile male fly-

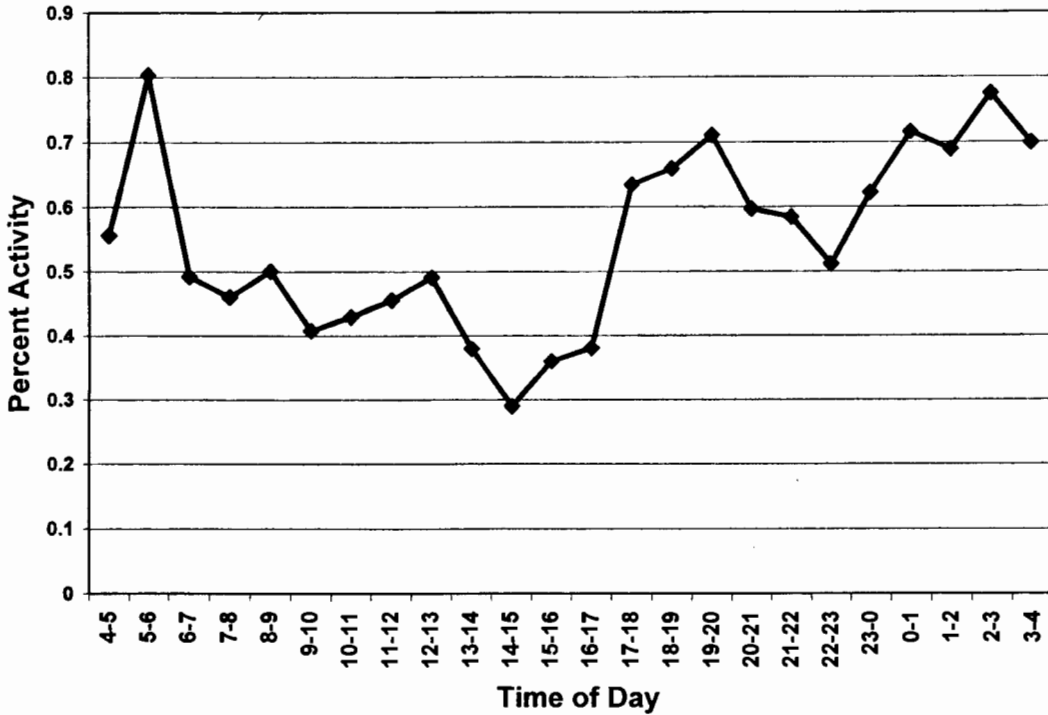


Fig. 4. Average activity patterns of all *Pteropus tonganus* collared with activity radiocollar sensors ( $n = 10$ ), American Samoa, 1992–1994. Percent activity represents the ratio of time recorded as active over the total time recorded during each hour of the day.

ing fox equipped with a radiotransmitter changed day roosts 8 times and moved between 4 different foraging sites in 45 days. This animal moved initially with the entire colony (1,200 animals) in response to a construction explosion near the roost site. Subsequent movements of this collared animal were in association with a small number of other flying foxes but not necessarily the same individuals. Five other collared animals moved roosts an average of once every 25 ( $\pm 0.004$  SE) days. Other radiotracked flying foxes remained at the same day roost during the time we were able to follow them (Table 1). Roost shifts of radiocollared *P. tonganus* were often documented to be in association with small aggregations of non-collared animals. A comparison of the number of roost changes with the relative transmitter package mass revealed no correlation ( $R^2 = 0.009$ ). Likewise, a comparison of the transmitter weight as a fraction of body weight on the number of days of information obtained from collared animals showed no correlation ( $R^2 = 0.01$ ).

All flying foxes monitored for more than 7 days foraged at more than a single site. Foraging was

noted within agroforest plantations 57 times and within primary forest 21 times. However, it is much easier to locate and monitor animals foraging within plantations, which occur along roadways. The importance of finding animals foraging within primary forest should not be overlooked. Additionally, plantations and forests are frequently contiguous and we observed *P. tonganus* foraging mostly within a plantation but also taking fruit from surrounding forest trees when available. Nine collars were dropped within plantations, 5 within undisturbed primary forest, and 1 under a roost tree.

Micro-movements within a foraging site showed frequent movements during the early evening and early morning and a rest between 2200 and midnight (Fig. 3). On a single evening we followed an adult female within a banana-coconut plantation from 1921 (shortly after her arrival) until 2207 (166 min). During this time she traveled in a zigzag fashion starting at a compass bearing of  $300^\circ$  relative to our position and traveling as far as  $60^\circ$  before returning. She stopped along the way during this progression, remaining an average of 7.6 min per location.

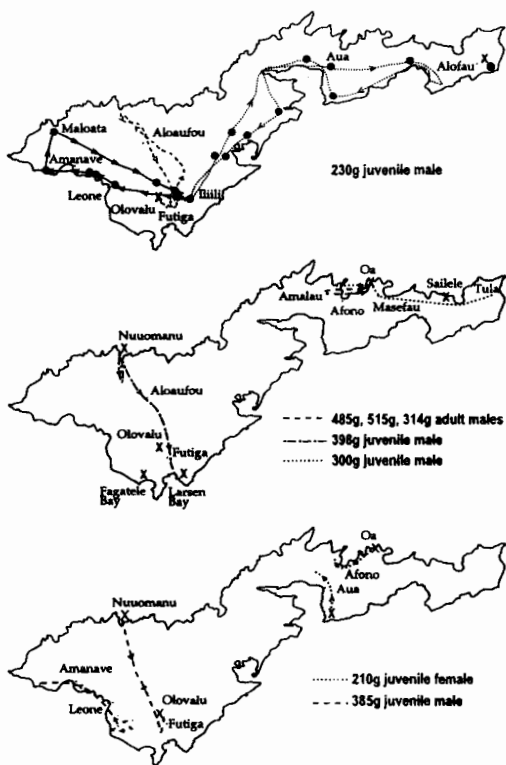


Fig. 5. Selected single evening movement patterns of radiocollared *Pteropus tonganus* on Tutuila, American Samoa, 1992–1994. Arrows show direction of movement. Abbreviations: \* = stopping points through night; x = roost sites. All lines of 230-g juvenile male are the same animal on different nights.

## DISCUSSION

Although the radiocollared flying foxes we studied tended to move either on the west or the east half of the island, this does not mean that they are reproductively isolated since overlap in foraging areas did occur. In addition, flying foxes are strong fliers and capable of traveling long distances (Ratcliffe 1931, 1932; Nelson 1965; Roberts 1977; Eby 1991; Spencer et al. 1991). The wing morphology of *P. tonganus* is designed for long, fast flights (Richmond et al. 1998). Our sample contained animals from only 3 of 4 primary roosts. The 2 large and inaccessible colonies on the northwest side of the island, 11 km and 6 km west of Pago Pago, were underrepresented in this study. Flying foxes from these colonies probably forage along the rugged terrain on the north shore of the island in areas difficult to both net and monitor. Movements along this area likely bridge populations between the east and west

sides of Pago Pago harbor. During this study, an abundance of foraging habitat (primary and agroforest) existed on the west side of the island making long trips eastward nutritionally unnecessary; however, flying foxes may be traveling for non-nutritional purposes such as dispersal.

We observed roost shifts and foraging shifts among both collared and non-collared flying foxes. Roost shifts were not unique to any particular age or sex group within the small sample of the animals we radiocollared. Harem-holding males would be expected to shift roosts less frequently, however, than other members of a roost. Eby (1991) reported radiocollared *P. poliocephalus* moving individually between large roost aggregations in response to food availability. Our study animals behaved in a similar fashion but on a smaller scale. Because breeding in *P. tonganus* occurred year-round during our study (Grant and Banack 1999), partial colony shifts may facilitate gene flow between the more western and eastern roosts.

The harem breeding structure of *P. tonganus* restricts the number of males contributing to the next generation, so the effective population size ( $N_e$ ) is less than the census population size. Nevertheless, consistent gene flow between the east and west sides of Tutuila Island would facilitate the spread of alleles. Thus, without additional data on gene flow, the animals should be managed as a single breeding population.

Another consideration of the effective population size is inter-island dispersal. A colony of *tonganus* periodically appears on Aunu'u (G. Grant, unpublished data) but this is undoubtedly part of the Tutuila population. Nevertheless infrequent dispersal from the Manu'a Island group and potentially from Western Samoa is likely, particularly during heavy storms or hurricanes. When disturbed, *P. tonganus* tends to high, circling the roost. This behavior during storm would allow animals to be blown to other islands in the Samoan archipelago. These infrequent events would also increase the effective population size.

Current population patterns do not necessarily reflect historic patterns. The relatively recent human population explosion on Tutuila and flying fox population decline due to the recent hurricanes probably has greatly influenced observed movement patterns. Human disturbance has altered roosting sites, and habitat destruction has altered foraging sites. In addition, many roosts have faced repeated human

Table 2. Stepwise regression procedure (SAS program) examined the determinants of distance traveled (km) by radiocollared *Pteropus tonganus* in Tutuila, American Samoa, 1992–1994. East–west indicates from what part of the island the animal was captured. Weight fraction measures the effect of the transmitter package as a fraction of the animal body weight. Sex (male and female) and forearm length (mm) were also entered in the analysis but excluded due to a low predictive value.

Variable	Parameter estimate	SE	Partial $R^2$	F	P
Step 1 East–west	8.7	1.7	0.30	27.2	0.001
Step 2 East–west	7.4	1.8	0.30	27.2	0.001
Weight fraction	30.0	20.1	0.02	2.2	0.14

turbance, largely due to flying fox hunting, and *P. tonganus* often was wary of human activity. The current distribution of roosts located in inaccessible places likely is an artifact of such disturbance. In contrast, the *P. tonganus* colony on Tongatapu, Tonga, where flying foxes are protected by mandate of the king, is in the middle of an area with heavy human disturbance. Additionally, the abundance of resources present during our study and the small numbers of flying foxes also influenced movement patterns. As the population of *P. tonganus* recovers to its pre-hurricane levels, greater movement would be expected as flying foxes are forced to search further to obtain sufficient resources.

Flying fox foraging activity occurs both in the primary forest and agroforest. Although we were able to track *P. tonganus* to agroforest areas more frequently than to primary forest, this is an artifact of the difficulty of accurately locating animals in rugged terrain during the night and is not a reflection of the actual time spent foraging in each habitat. On extended flights the animals stopped at both forested and agroforested areas along the way. Although it was difficult to determine the activity of the animal during these rests, it is likely that some foraging did occur. This evidence in conjunction with foraging studies (Banack 1998) suggests that *P. tonganus* probably spent more time within the forest than we were able to document.

The observed micro-movements of animals within a foraging site is consistent with observations of *Pteropus giganteus* (McCann 1934:144–145). McWilliam (1985–86) reported smaller, less dominant flying foxes traveling more in a single night than larger, dominant animals. This is consistent with our observations of the exploratory flights of juveniles.

The additional weight carried by collared animals may have an effect on overall activity budgets, flight speed, or metabolism of flying animals (Gessaman and Nagy 1988, Rayner et al. 1989); however, several factors suggest the activity patterns reported in this study were representative of normal behavior for flying foxes. First, flying foxes reduce the energy required for flight by soaring and gliding. Soaring and gliding behavior allow flying foxes to fly with less energy than those that flap their wings continuously (Norberg 1990). Therefore, one would predict that they may be capable of carrying heavier loads. Second, flying foxes feed predominantly on fruit and flower resources which do not require highly maneuverable flight as would be expected for insectivorous microchiropterans (Aldridge and Brigham 1988). Third, behavior patterns are consistent with other species in the genus *Pteropus*. Fourth, as noted above, behavior patterns observed in collared bats (distance traveled, departure times, and roost shifts) were not noticeably different from non-collared animals. Finally, visual observations of collared animals showed no apparent stress.

In hindsight, we would not have placed the collars we had on the smallest animals in this study. However, there is no evidence to suggest that this led to unusual behavior or the mortality of these animals. We recommend that studies be conducted to directly examine the load-carrying ability of megachiropterans. Our data suggest that members of the genus *Pteropus* are capable of carrying transmitter packages affecting approximately 10% of their power surplus. Nevertheless, further studies should be conducted to determine the impact of carrying additional weight on the behavior of pteropodid bats.

Since few studies have radiotracked members of the family Pteropodidae (Jacobsen et al. 1986, Eby 1991, Spencer et al. 1991, Augee et al. 1995), we relied heavily on natural history characteristics and visual observations of collared animals to evaluate how flying foxes reacted to the transmitters and collars. All observations showed “normal” behavior in comparison with non-collared animals. During this study, we regularly saw flying foxes carrying *ifi* fruit (*Imocarpus fagifer*), weighing an average of 126.6 g (range 39–269 g;  $n = 53$ ) and representing approximately 36% of an animal’s mean body mass over distances exceeding 4 km. In addition, females of both *Pteropus* spp. in Samoa regularly carried juveniles that were approximately half their own body weight and

occasionally carried juveniles approaching two-thirds their own body weight (Banack 1996). Carrying juveniles of considerable size is not unusual in megachiropterans. Nelson (1965) found females carrying juveniles 57% of the female's body weight. Ratcliffe (1932) reported female *Pteropus poliocephalus* (adult body weight 600–1,000 g; Hall and Richards 2000) carrying large juveniles (approx. 300–500 g) almost the size of adult *Pteropus scapulatus*. Ansell (1986) summarized records of pteropodid females carrying juveniles ranging from 19% to 95% of the mother's weight, the latter being a set of twins. Tuttle (1986) reported *Epomophorus gambianus* females carrying juveniles two-thirds the weight of their mothers. Similarly, pregnant females of both megachiropteran and microchiropterans have been reported to carry full-term fetuses commonly weighing 20% to 30% of the females' normal body mass (range 12–50%) (Marshall 1947, Myers 1978, Kurta and Kunz 1987, Falanruw 1988, Hughes and Rayner 1991). Although the ability to carry large juveniles and heavy fetuses does not by itself indicate that transmitter loads had no effect, they do suggest that carrying heavy loads is not unusual. Our observations and statistical regression analyses indicated no correlation between the transmitter weight and either the number of days the collared animal was active or the number of roost shifts. This suggests that these animals were capable of carrying the transmitters without undue stress for the short period of time before the collar fell off.

## MANAGEMENT IMPLICATIONS

We recommend treating the entire population of *P. tonganus* on Tutuila, American Samoa, as 1 breeding population. We also recommend a genetic analysis of the local population structure within Tutuila that would provide valuable information on past population structure, gene flow, and related genetic diversity. Use of satellite transmitters could provide additional valuable spatial and activity data, especially in remote rugged landscapes. We hypothesize low genetic variability due to the harem structure and bottleneck this population has periodically experienced. Spatial patterns indicate broad and comprehensive use of island resources spanning primary forest and secondary forest. Because of the importance of this species as a keystone species and its noted use of primary forest, we strongly support protecting primary forest habitat in management plans. In addition, restricted

access to traditional roost sites on currently remote parts of the island will maintain roost stability and minimize stress.

## ACKNOWLEDGMENTS

We are grateful to J. Richmond, S. Vignieri, D. Meek, and P. Meek for field assistance. We are indebted to L. Vernon for invaluable data entry. Artwork was provided by M. Sullivan, A. Stout, and B. Allen. W. Lidicker, D. McCullough, C. D'Antonio, P. Cox, and D. Wilson provided valuable criticisms of earlier drafts of this paper. We thank E. Pierson, A. Brooke, and W. Rainey for advice on and critiques of radiotracking methodology, and M. B. Fenton and an anonymous reviewer for helpful reviews of this paper. This work was supported by equipment purchased by the Department of Marine and Wildlife Resources in American Samoa, and by grants from the National Park Service and the National Geographic Society. This research was included in a dissertation submitted by SAB in partial fulfillment of the requirements for a Ph.D. at the University of California, Berkeley.

## LITERATURE CITED

- ALDRIDGE, H. D. J. N., AND R. M. BRIGHAM. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. *Journal of Mammalogy* 69:379–382.
- ANSSELL, W. F. H. 1986. Records of bats in Zambia carrying non-volant young in flight. *Arnoldia Zimbabwe* 9:315–318.
- AUGEE, M. L., D. FORD, AND M. TREADWELL. 1995. Short-term fate of radio-tracked, juvenile, grey-headed flying foxes *Pteropus poliocephalus* released at a colony site in Sydney Australia. *Bat Research News* 36:16–17.
- BANACK, S. A. 1996. Flying foxes, genus *Pteropus*, in the Samoan archipelago: interactions with forest communities. Dissertation, University of California, Berkeley, USA.
- . 1998. Diet selection and resource use by flying foxes (genus *Pteropus*). *Ecology* 79:1949–1967.
- CACCAMISE, D. F., AND R. S. HEDIN. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin* 97:306–318.
- CRAIG, P., P. TRAIL, AND T. E. MORRELL. 1994. The decline of fruit bats in American Samoa due to hurricanes and overhunting. *Biological Conservation* 69:261–266.
- DASCHBACH, N. 1990. After the hurricane. *Bats* 8:14–15.
- EBY, P. 1991. Seasonal movements of grey-headed flying foxes, *Pteropus poliocephalus* (Chiroptera: Pteropodidae), from two maternity camps in northern New South Wales. *Wildlife Research* 18:547–559.
- FALANRUW, M. V. C. 1988. On the status, reproductive biology and management of fruit bats of Yap. *Micronesica* 21:39–51.
- GESSAMAN, J. A., AND K. A. NAGY. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. *Condor* 90:662–668.

- GRANT, G. S., AND S. A. BANACK. 1999. Harem structure and reproductive behaviour of *Pteropus tonganus* in American Samoa. *Australian Mammalogy* 21:111–120.
- , P. CRAIG, AND P. TRAIL. 1997. Cyclone-induced shift in foraging behavior in flying foxes in American Samoa. *Biotropica* 29:224–228.
- HALL, L., AND G. RICHARDS. 2000. Flying foxes, fruit and blossom bats of Australia. University of New South Wales Press, Sydney, Australia.
- HUGHES, P. M., AND J. M. V. RAYNER. 1991. Addition of artificial loads to long-eared bats *Plecotus auritus*: handicapping flight performance. *Journal of Experimental Biology* 161:285–298.
- JACOBSEN, N. H. G., P. C. VILJOEN, AND W. FERGUSON. 1986. Radio-tracking of problem fruit bats (*Rousettus aegyptiacus*) in the Transvaal with notes on flight and energetics. *Zeitschrift für Säugetierkunde* 51:205–208.
- KURTA, A., AND T. H. KUNZ. 1987. Size of bats at birth and maternal investment during pregnancy. *Symposia of the Zoological Society of London* 57:79–106.
- MARSHALL, A. J. 1947. The breeding cycle of an equatorial bat (*Pteropus giganteus* of Ceylon). *Proceedings of the Linnean Society of London* 159:103–111.
- MCCANN, C. 1934. Notes on the flying-fox (*Pteropus giganteus*, Brunn.). *Journal of the Bombay Natural History Society* 37:142–149.
- MCWILLIAM, A. N. 1985–86. The feeding ecology of *Pteropus* in north-eastern New South Wales, Australia. *Myotis* 23–24:201–208.
- MICKLEBURGH, S. P., A. M. HUSTON, AND P. A. RACEY. 1992. Old World fruit bats: an action plan for their conservation. Chiroptera Specialist Group, International Union for Conservation of Nature and Natural Resources (IUCN/SSC), Gland, Switzerland.
- MILLER, C. A., AND D. E. WILSON. 1997. *Pteropus tonganus*. *Mammalian Species* 552.
- MYERS, P. 1978. Sexual dimorphism in size of vespertilionid bats. *American Naturalist* 112:701–711.
- NELSON, J. E. 1965. Behaviour of Australian Pteropodidae (Megachiroptera). *Animal Behaviour* 13:544–557.
- NORBERG, U. M. 1990. *Vertebrate flight*. Springer-Verlag, Berlin, Germany.
- RAINEY, W. E., AND E. D. PIERSON. 1992. Distribution of Pacific island flying foxes. Pages 111–122 in D. E. Wilson and G. L. Graham, editors. *Pacific island flying foxes: proceedings of an international conservation conference*. U.S. Fish and Wildlife Service Biological Report 90(23), Washington, D.C., USA.
- RATCLIFFE, F. N. 1931. The flying fox (*Pteropus*) in Australia. Council for Scientific and Industrial Research Bulletin 53, Melbourne, Australia.
- . 1932. Notes on the fruit bats (*Pteropus* spp.) of Australia. *Journal of Animal Ecology* 1:32–57.
- RAYNER, J. M. V., G. JONES, AND P. M. HUGHES. 1989. Load carrying by flying bats. Pages 235–245 in V. Hanák, I. Horáček, and J. Gaisler, editors. *European Bat Research 1987*. Charles University Press, Prague, Czechoslovakia.
- RICHMOND, J. Q., S. A. BANACK, AND G. S. GRANT. 1998. Comparative analysis of wing morphology, flight behaviour, and habitat use in flying foxes (Genus: *Pteropus*). *Australian Journal of Zoology* 46:283–289.
- ROBERTS, T. J. 1977. *The mammals of Pakistan*. Ernest Benn, London, United Kingdom.
- SPENCER, H. J., C. PALMER, AND K. PARRY-JONES. 1991. Movements of fruit-bats in Eastern Australia, determined by using radio-tracking. *Wildlife Research* 18:463–468.
- TUTTLE, M. D. 1986. Gentle fliers of the African night. *National Geographic* 169:540–558.

Received 11 September 2001.

Accepted 19 May 2002.

Associate Editor: Russell.