BIOTROPICA 29(2): 224–228 1997

Cyclone-induced Shift in Foraging Behavior in Flying Foxes in American Samoa[1]

Gilbert S. Grant[2], **Peter Craig**, and **Pepper Trail**

Department of Marine and Wildlife Resources, P.O. Box 3730, Pago Pago, American Samoa 96799, U.S.A.

ABSTRACT

Tropical cyclones pass over or near American Samoa on average about once every 3 years. Because many trees may be stripped of leaves, flowers, and fruit, cyclones exert a major impact on the feeding ecology of nectivorous and frugivorous flying foxes. We examined search time and in-tree time immediately postcyclone (3–6 weeks) and during a recovery period (15–16 months after the last cyclone). Both *Pteropus tonganus* and *P. samoensis* increased search time and decreased tree time (an indication of less food available per tree) immediately after the passage of cyclone Ofa.

Key words: *cyclones; Samoa; flying foxes; feeding ecology;* Pteropus.

TWO SPECIES OF FLYING FOXES OCCUR in American Samoa. The less common Samoan flying fox (*Pteropus samoensis*) is primarily diurnal in its activity patterns while the similar white-necked flying fox (*P. tonganus*) is primarily nocturnal (Cox 1983, Wilson & Engbring 1992, Craig *et al.* 1994, Morrell & Craig 1995).

Three major tropical storms passed over or near the Samoan archipelago between January 1987 and December 1991: Tusi in January 1987, Ofa in February 1990, and Val in December 1991. Flying fox populations in American Samoa declined 80–90 percent as a result of these cyclones and of the subsequent overhunting of the remaining animals (Craig *et al.* 1994). However, flying foxes may exhibit behavioral plasticity in foraging behavior or reproductive strategies that facilitate population recovery from the impacts of such severe storms.

In this paper we present data demonstrating a shift in foraging behavior by *P. tonganus* and *P. samoensis* immediately after passage of Cyclone Ofa on 3 February 1990. High winds knocked down many trees and stripped many remaining trees of leaves, flowers, and fruits (Elmqvist *et al.* 1994, Pierson *et al.*, in press). Food for the frugivorous and nectivorous flying foxes was scarce and patchy in distribution. Because of this, we predicted that individual bats would increase search time and decrease time feeding and resting in individual trees.

[1] Received *12 September 1994*; revision accepted *6 November 1995.*

[2] Department of Biological Sciences, University of North Carolina, Wilmington, North Carolina 28403.

METHODS

Data from three census methods utilized on Tutuila, American Samoa, are presented in this paper: search time/tree time activity data for both bat species during postcyclone and recovery periods, island-wide (12 sites) repetitive counts beginning at dawn of individual bats of both species, and island-wide counts of all *P. tonganus* in daytime roosts.

We monitored the daytime activity patterns of flying foxes near Mt. Pioa (Rainmaker Mountain), Tutuila Island. This site offered a clear view of a forest with known bat activity. Both native montane rainforest and agroforest vegetation were present. Postcyclone observations were made from 14 February to 15 March 1990 (3–6 wk after passage of Ofa). Few flowers and fruit were available in the study area immediately after the cyclone.

The following (November 1990–April 1991) cyclone season passed without significant storms, allowing the forest to begin the process of recovery. However, during the next year, an extremely severe cyclone, Val, struck in December 1991. There were no significant storms in the 1992–1993 season again allowing vegetation recovery. Our "recovery period" observations were made from 4 March to 30 April 1993. Thus, the 1993 observations were made 15–16 mo after the passage of the last storm (Cyclone Val). Most vegetation, with the exception of downed and dead trees, had recovered. Fruit, flower, and leaf production had apparently returned to precyclone conditions. To minimize seasonal changes in foraging behavior due to nectar and fruiting cycles of favored plants, we made both postcyclone and recovery period observations during the same time of year.

The bats were observed during all daylight hours from 0600 to 1900. Observations for each daytime hour averaged 5.4 hr in postcyclone conditions for a total of 70 observation hours. Observations for each daytime hour averaged 4.3 hr in recovery period conditions for a total of 55.8 hr. Total numbers of bats observed in 1993 were corrected by multiplying 70/55.8 times the recovery period numbers. Observations were made during favorable weather/viewing conditions in both samples (*i.e.*, not during rain, fog, or low light level conditions).

All bats observed were selected arbitrarily, excluding only bats that could not be identified to species. For a discussion of the species identification problem on American Samoa see Craig (1992). Trained observers began recording the activity of an individual bat when it was first seen (frequently when it flew out of a tree or first entered the viewing area) and followed it until it left the study area or became lost from view within the study area. In general, the activity of only one bat was followed at a time. Activities recorded included bat species, time it flew into the area, flying-over time, cruising (search) time, landing in trees, emerging from trees, flying out of area, or when lost from view. Time in trees consisted of feeding, sleeping (hanging relatively motionless), climbing, and other maintenance behaviors. Because of the observation distance and the visual barriers caused by vegetation, observers could not always clearly differentiate activities while the bats were in the trees, and data presented here are simply time spent by the bats in the trees. The distinction between flying over and searching (cruising) was fairly clear. Bats flying over were generally soaring high above the forest canopy and appeared to be traversing the study area or using thermals above the ridge tops rather than cruising close to the canopy with frequent direction changes.

Numbers of bats observed represent a subset of the total of bats present in the area and therefore should not be taken as an estimate of the population in the area. Because only one bat could be followed at a time, many bats using the area were not followed.

The second census method was employed to further document the temporal shift in foraging activity. We sampled 12 sites on Tutuila Island (on a monthly basis). At each site, five 20-min counts (alternated with 10-min rest intervals) of all individual bats were made, beginning at first light (just before sunrise) and terminating about 2.5 hr later.

Quarterly censuses were made at all known daytime roosts of *P. tonganus* to determine its island-wide population. Since this species is primarily nocturnal, morning censuses (method #2) did not provide an accurate estimate of its population.

RESULTS

The activity patterns of 93 individual *P. tonganus* were observed in the postcyclone study. Of these, 30 bats flew over the study area (non-searching behavior) and an additional 16 bats were lost from view. Forty-seven bats (51%) exhibited searching behavior—cruising low over vegetation—and 42 (89%) of the searching bats landed in trees. The activity patterns of only 24 *P. tonganus* were observed during the recovery period study. Six bats (25%) were classed as flyovers, and four bats were lost from view. Fourteen bats (58%) exhibited searching behavior, and eight (57%) of the searching bats landed in trees.

The activity patterns of 246 individual *P. samoensis* were observed in the postcyclone study. Of these, 73 bats flew over the study area and an additional 37 bats were lost from view. Searching behavior was exhibited by 136 (55%) bats and, of these, 117 (86%) landed in trees. The activity patterns of only 82 *P. samoensis* were quantified during the recovery period study. Ten were flyovers and 15 were lost from view. Searching behavior was exhibited by 57 (70%) bats and, of these, 46 (81%) landed in trees.

Daytime search time by *P. tonganus* increased slightly (but not significantly), and time in trees (feeding, roosting, maintenance behaviors) decreased slightly (but not significantly) immediately following the cyclone (Table 1). Significant increases in search time and decreases in tree time occurred for *P. samoensis* immediately after the cyclone (Table 1).

Postcyclone tree time between species did not differ significantly, while recovery period tree times between species did (Table 2). However, *P. tonganus* did not roost within the study area and some *P. samoensis* probably did roost here. In the highly colonial diurnal roosts of *P. tonganus*, the entire day is typically spent hanging in trees. A significant difference in recovery period search time but not postcyclone search time occurred between the *P. samoensis* and *P. tonganus* species (Table 2).

Both species decreased tree time and increased search time immediately after the cyclone, but the ratio of search time/tree time was more pronounced for *P. samoensis* (Table 3).

Early morning censuses (Fig. 1) conducted at

TABLE 1. *Postcyclone and recovery period searching and in-tree time activity patterns of flying foxes in American Samoa. Data are presented as mean ± standard deviation (sample size). Probability is based on Mann-Whitney test.*

Activity	1990 Post-cyclone	1993 Recovery period	*P*
Pteropus tonganus			
Search time	3.9 ± 2.5 (47)	2.9 ± 2.4 (14)	0.167
Tree time	10.2 ± 9.0 (42)	14.0 ± 24.0 (8)	0.560
Pteropus samoensis			
Search time	4.5 ± 3.3 (136)	1.4 ± 1.3 (57)	0.000[a]
Tree time	9.3 ± 16.3 (117)	87.3 ± 76.8 (46)	0.000

[a] Significant.

12 sites on Tutuila between February 1992 (two months after Cyclone Val) and March 1994 illustrate decreased diurnal activity over time by *P. tonganus* during a period when the island's population was known to be increasing significantly. Roost counts of *P. tonganus* progressively increased from a low of about 800 bats in 1990 to 3600 bats in February 1994. Increased numbers of *P. samoensis* during this period reflects population increases by this species (Fig. 1) and perhaps a return to its preferred diurnal foraging time.

DISCUSSION

Flying foxes are strong interactors in South Pacific islands where they serve as the principal pollinators and seed dispersers of highly endemic island floras (Cox *et al.* 1991). Extinction of flying foxes may ultimately lead to loss of plant diversity on these islands. Populations of both *P. samoensis* and *P. tonganus* declined dramatically (80–90%) in American Samoa from 1987 to early 1992 due to three cyclones and the subsequent overhunting of the remaining animals (Craig *et al.* 1994). The cyclones destroyed numerous trees and stripped flowers, fruit, and leaves from many surviving trees. Many flying foxes starved, some entered coastal villages to feed on downed fruit, and many were taken by dogs, cats, pigs, and humans during the few months after the cyclones (Daschbach 1990, Craig *et al.* 1994, Pierson *et al.*, in press).

Both *P. samoensis* (Pierson *et al.*, in press) and *P. tonganus* (P. Craig, pers. comm.; T. Leary, pers. comm.) consumed leaves and relocated to refugia—feeding and roosting areas that escaped the major impact of the cyclones (Trail & Grant 1994, Pierson *et al.*, in press).

Precyclone studies indicated that *P. samoensis* was primarily diurnal and that *P. tonganus* was primarily crepuscular-nocturnal (Cox 1983, Craig & Syron 1992, Wilson and Engbring 1992). The rapid increase in numbers of *P. samoensis* (Fig. 1) cannot be due entirely to reproduction. *Pteropus samoensis* is a seasonal breeder, producing at most one young a year (Banack and Grant, unpubl. data). Recent radiotelemetry studies and other observations on American Samoa have shown that on occasion some *P. samoensis* are active after dark (Banack and Grant, unpubl. data). We suspect a portion of this increase in diurnal activity is due to a gradual shift back to daytime activity by those *P. samoensis* that foraged at night during the lean, postcyclone period. Banack and Grant (unpubl. data) have observed some *P. tonganus* foraging during the morning hours on flowers that produce nectar after sunrise. Thus, both species exhibit some plasticity in activity patterns.

In spite of the fact that we observed an increased percentage of bats of both species exhibiting searching behavior during the recovery period, the amount of time each bat spent searching was

TABLE 2. *Activity differences between* samoensis *and* tonganus *in postcyclone and recovery conditions on American Samoa.*

Activity	*P*
Recovery period search time	0.0129[a]
Post-cyclone search time	0.9911
Recovery period tree time	0.0011[a]
Post-cyclone tree time	0.2520

[a] Significant.

TABLE 3. *Ratio of search time to tree time for two species of flying foxes on American Samoa.*

Species	Recovery period	Post-cyclone
samoensis	0.02	0.48
tonganus	0.21	0.38

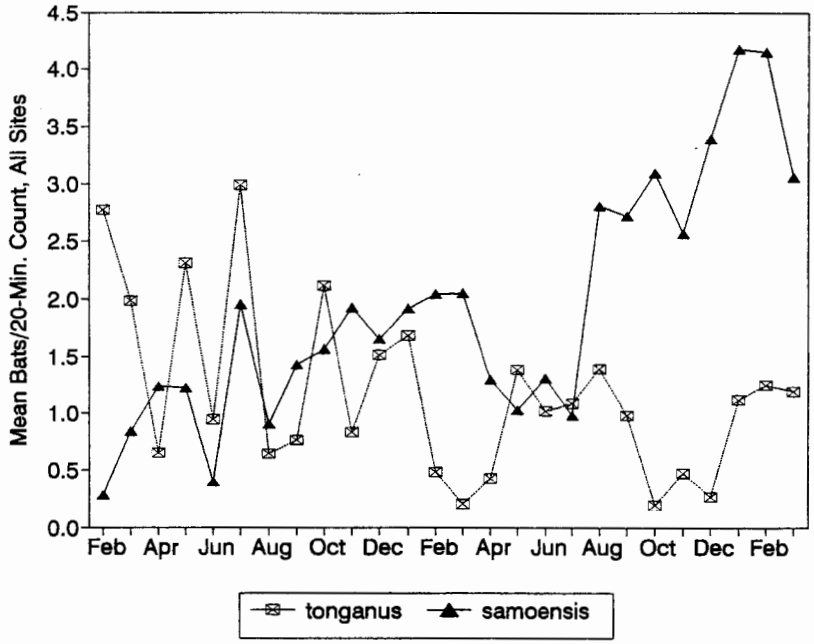

FIGURE 1. Monthly dawn counts of *Pteropus tonganus* and *P. samoensis* at twelve sites on Tutuila, American Samoa, 1992–1994.

greater immediately after passage of the cyclone. It is not surprising that both *P. samoensis* and *P. tonganus* altered foraging behavior during the stressful period after a cyclone. *Pteropus tonganus* foraged throughout the day, spent more time searching for food, and spent relatively less time in trees within a foraging area (an indication of reduced food availability per tree). After the cyclone, *P. samoensis* foraged throughout the day, probably foraged at night, and also spent more time searching and less time in trees within the foraging area.

Our recovery period data were obtained in 1993, 15–16 mo after the passage of the last cyclone (Val, 6–8 December 1991), and probably represent the more typical activity patterns of both species when food resources are not limited, as reported by Craig and Syron (1992), Wilson and Engbring (1992), Craig *et al.* (1994), Elmqvist *et al.* (1994), and Pierson *et al.* (in press). A gradual return to normal activity patterns (increase in diurnal activity by *P. samoensis* and a decrease in diurnal activity by *P. tonganus*) was seen in the months following cyclone Ofa (Morrell & Craig 1995) and cyclone Val (Fig. 1). *Pteropus tonganus* is primarily a nocturnal and crepuscular feeder while *P. samoensis* feeds primarily during daylight. Both species overlap in the few hours near dawn and dusk and expand their feeding niches in times of food stress. Both can consume leaves when necessary, shift foraging times, and relocate to refugia, but only *P. tonganus* appears to reproduce throughout the year (Grant 1994, Grant and Banack, unpubl. ms.). Young of *P. tonganus* attain independence throughout the year. In contrast, most *P. samoensis* young attain independence during the cyclone season. This nonseasonal reproductive strategy of *P. tonganus* facilitates more rapid recovery from depressed population levels.

ACKNOWLEDGMENTS

We thank Aso Mase, Wayne Syron, Edwin Seui, Kiso So'oto, and Ailao Tualaulelei for aid in data gathering and Sandra Banack and Gary Wiles for suggestions improving this manuscript. This study was funded by the Federal Aid in Wildlife Restoration Act administered by the U.S. Fish and Wildlife Service.

LITERATURE CITED

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

———, T. Elmqvist, E. D. Pierson, and W. E. Rainey. 1991. Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. Conservation Biology 5: 448–454.

Craig, P. 1992. Species identification problems during fruit bat surveys in American Samoa. Dept. Marine and Wildlife Resources (American Samoa), Biol. Rept. Ser. No. 25. 19p.

———, and W. Syron. 1992. Fruit bats in American Samoa: their status and future. *In* D. E. Wilson and G. L. Graham (Eds.). Pacific Island Flying Foxes: Proceedings of an International Conservation Conference. Pp. 145–149. USF&WS Biological Report 90(23). U.S. Fish and Wildlife Service, Washington, D.C.

———, P. W. 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(3): 14–15.

Elmqvist, T., W. E. Rainey, E. D. Pierson, and P. A. Cox. 1994. Effects of tropical cyclones Ofa and Val on the structure of a Samoan lowland rain forest. Biotropica 26: 384–391.

Grant, G. S. 1994. Harem structure and reproductive behavior of *Pteropus tonganus* in American Samoa. Abstract. Sixth Australasian Bat Conference, Southern Cross University, Lismore, Australia.

Morrell, T. E., and P. Craig. 1995. Temporal variation in fruit bats observed during daytime surveys in American Samoa. Wildlife Society Bulletin 23: 36–40.

Pierson, E. D., T. Elmqvist, W. E. Rainey, and P. A. Cox. In press. Effects of tropical cyclonic storms on flying fox populations on the South Pacific islands of Samoa. Biotropica.

Trail, P. W., and G. S. Grant. 1994. Cyclone effects on flying-fox populations in American Samoa: Patterns of decline and recovery. Abstract. Sixth Australasian Bat Conference, Southern Cross University, Lismore, Australia.

Wilson, D. E., and J. Engbring. 1992. The flying fox *Pteropus samoensis* and *Pteropus tonganus*: Status in Fiji and Samoa. *In* D. E. Wilson and G. L. Graham (Eds.). Pacific Island Flying Foxes: Proceedings of an International Conservation Conference. Pp 74–101. USF&WS Biological Report 90(23). U.S. Fish and Wildlife Service, Washington, D.C.