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Effects of Tropical Cyclonic Storms on Flying Fox Populations on the South Pacific Islands of Samoa

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Abstract: *The South Pacific islands of Samoa have two extant flying fox species,* Pteropus samoensis *and* P. tonganus. *Following two severe cyclonic storms, we examined their differential behavioral responses and evaluated the effectiveness of recently established reserves in providing refugia. Although the cyclones disrupted activity patterns and foraging behavior for both species, comparisons with pre-storm data suggested that the more common, widely distributed* P. tonganus *experienced more severe population declines than the endemic* P. samoensis. *This differential mortality could be explained by a combination of ecological and behavioral factors.* P. tonganus *had a greater tendency to enter villages to feed on fallen cultivated fruits, making it more vulnerable to human hunting and predation by domestic animals. In addition,* P. samoensis *appeared to use survival strategies not observed in* P. tonganus. *Leaves, which were far more available than flowers or fruits in the immediate post-storm period, comprised a major part of the post-storm diet of* P. samoensis. *This species also fed on the fleshy bracts of a storm-resistant native liana, (*Freycinetia reineckei*). In contrast, a seasonally important food of* P. tonganus *is nectar from the delicate flowers of* Syzygium inophylloides *(asi), a canopy tree that is very vulnerable to wind damage and has become increasing scarce with the clearing of lowland forest. Rainforest reserves, established prior to the storms, served as adequate refugia for local* P. samoensis *populations, which appeared to feed relatively close to their roosts, primarily in native forest, but did not protect* P. tonganus *populations, which traveled outside reserves to forage in areas lacking hunting bans. Although wind damage was patchy and not consistent between storms, areas of high topographic complexity (e.g., volcanic cones and deep valleys) were the most likely to retain areas with some foliage and should be given priority in the design of future reserves.*

El efecto de las tormentas ciclónicas tropicales sobre las poblaciones de zorros voladores en las islas del Pacífico Sur de Samoa.

Resumen: *Las islas del Pacífico Sur de Samoa tienen dos especies existentes de zorros voladores,* Pteropus samoensis *y* P. tonganus. *Luego de dos severas tormentas ciclónicas, examinamos sus diferentes respuestas de comportamiento y evaluamos la efectividad de las reservas recientemente establecidas para proveer de refugio. Si bién los ciclones perturbaron los patrones de actividad y forrajeo en ambas especies, las comparaciones con datos previos a las tormentas sugieren que la especie mas común y ampliamente distribuída,* P. tonganus, *experimentó declinaciones poblacionales mas severas que la especie endémica* P. samoensis. *Esta mortalidad diferencial podría ser explicada por una combinación de factores ecológicos y de comportamiento.* P. tonganus *presentó una mayor tendencia a entrar en las aldeas para alimentarse de frutos cultivados caídos, haciendose mas vulnerable a la caza por humanos y a la de predación por parte de animales domésticos. Además,* P. samoensis *pareció usar estrategias de supervivencia no observadas en P. tonganus. Las hojas, que estuvieron mucho mas disponibles que las flores o frutos inmediatamente después de las tormentas, comprendieron la mayor parte de la dieta de* P. samoensis, *durante el período posterior a las tormentas. Por otra parte, esta especie se alimenta de las bracteas carnosas de una liana nativa resistente a las tor-*

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*mentas, (*Freycinetia reineckei*). En forma opuesta, un importante alimento estacional de* P. tonganus *es el nectar de las delicadas flores de* Syzygium inophylloides *(asi), un árbol del dosel que es muy vulnerable al daño causado por el viento y que además se ha hecho cada vez mas escaso debido a la tala de los bosques en las tierras bajas. Las reservas selváticas, establecidas antes de las tormentas sirvieron como refugios adecuados para las poblaciones locales de* P. samoensis*, las cuales parecieron alimentarse relativamente cerca de sus dormideros, principalmente en el bosque autóctono, pero no protegieron a las poblaciones de* P. tonganus*, las cuales se alejaron de las reservas para forrajear en áreas no protegidas de la caza. Si bien el daño causado por el viento fue irregular e inconsistente entre las tormentas, las áreas de una gran complejidad topográfica (por ej. conos volcánicos y valles profundos) fueron las mas probables de retener áreas con algo de follage y por lo tanto se les debe asignar prioridad en el diseño de futuras reservas.*

Introduction

Many species of larger flying foxes (Pteropodidae, Megachiroptera) are experiencing long-term population declines, particularly on small islands, from overhunting, deforestation, agricultural control measures, and introduced predators (Cheke & Dahl 1981; Wiles 1987; Mickleburgh et al. 1992; Pierson & Rainey 1992). Starting in the 1970s, a major increase in mortality among several Pacific island species arose from commercial hunting and export for a luxury food market in Guam and the adjacent Commonwealth of the Northern Marianas (Wiles & Payne 1986; Stinson et al. 1992; Wiles 1992). To counter the evident—if not well quantified—declines, several conservation measures, such as local hunting restrictions (Wiles 1987; Falanruw 1988; Craig et al. 1994), international trade limitation under the CITES treaty (Bräutigam & Elmqvist 1990), and protection of habitat (Cox & Elmqvist 1991), have been implemented on some of the affected islands.

Flying foxes play a significant role in the human economy of paleotropical regions (Chambers & Esrom 1988; Fujita & Tuttle 1991; Wiles & Fujita 1992). On oceanic islands they are often the only native terrestrial mammals and share the pivotal ecologic roles of pollinators and seed dispersers for canopy trees with a limited assemblage of primarily birds and invertebrates (Cox et al. 1991, 1992; Elmqvist et al. 1992; Rainey et al. 1995). Although conservation plans to maintain recently depleted flying fox populations and their habitats must consider demographic processes (such as changes in geographic distribution, reproductive output, and relative abundance), it is critical in the tropical mid-latitudes of the Pacific also to consider cyclonic storms. These storms can have major impacts on island biotas (Brokaw & Walker 1991; Waide 1991; Gannon & Willig 1994), presenting especially serious challenges to frugivorous and nectarivorous animals, such as bats. Population declines were documented for frugivorous and nectarivorous bats on Puerto Rico after Hurricane Hugo (Gannon & Willig 1994). In the paleotropics there are reports of substantial population reductions following cyclones for *Pteropus rodricensis* on Rodrigues Island (Carroll 1984), *Pteropus niger* on Mauritius (Cheke & Dahl 1981), *Pteropus mariannus* on Guam (Wiles 1987), and *Pteropus samoensis* and *Pteropus tonganus* on Samoa (Craig & Syron 1992; Craig et al. 1994).

On the South Pacific islands of Samoa, including both the independent nation of Western Samoa, and the U.S. Territory of American Samoa, flying fox populations were significantly depleted by commercial hunting during the 1980s, when up to 8000 individuals per year were reported as shipped to Guam (Cox 1984*b*; Bräutigam & Elmqvist 1990; Wiles 1992). Contemporaneous concerns about the consequences of forest habitat loss led to development or expansion of natural reserve systems in both jurisdictions. In 1988 legislation was passed by the U.S. Congress authorizing a national park for American Samoa. In 1989 and 1990 several indigenously controlled rainforest reserves were established on Savai'i, the largest island in Western Samoa, in part with the goal of maintaining populations and habitats of flying foxes (Cox & Elmqvist 1991).

While flying fox populations were still depressed by the hunting pressure of the early to mid 1980s, two severe cyclones struck Samoa. On 1–3 February 1990, Cyclone Ofa, the most severe storm in more than 160 years, hit the islands with winds up to 216 km/hour (Ulafala 1990) and caused severe forest damage (Fig. 1). A SPOT-SAT satellite false-color image, taken two weeks after the storm, showed that only small patches, comprising less than 1% of the primary forest, retained normal foliage on the eastern third of Savai'i. Twenty-two months later (6–8 December 1991) Val, a storm of comparable intensity, struck the islands (Pandaram 1992). Again forest damage was extensive, with more than 90% of the primary forest defoliated (Elmqvist et al. 1994). We were interested in the responses of two Samoan flying fox species, *Pteropus samoensis* and *Pteropus tonganus*, to the damage caused by the cyclones.

Although the two species are of similar size and show some overlap in activity patterns and diet, differences between the species are pronounced (Cox 1983; Pierson et al. 1992*a*, 1992*b*). The more common *P. tonga-*

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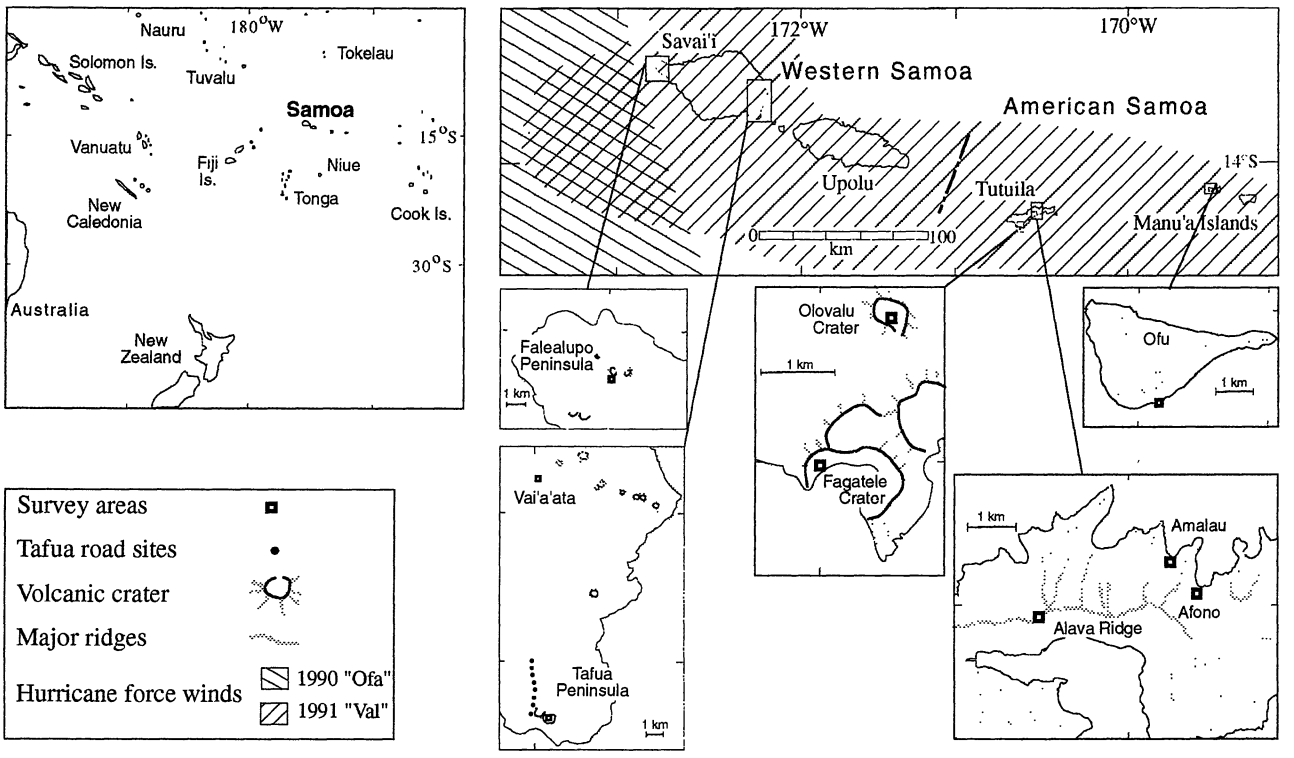


Figure 1. A map of the Samoan Islands showing the flying fox study sites.

nus (three recognized subspecies) is widely distributed throughout the southern Pacific, from Samoa to coastal islands north of Papua New Guinea and the Cook Islands (Mickleburgh et al. 1992; Rainey & Pierson 1992). It forms aggregated roosts (10^2–10^3), at least seasonally, in many localities and is primarily nocturnal (Elmqvist et al. 1992; Cox 1983). Although this species feeds on the fruits and flowers of native forest trees, it also frequents plantations and villages.

P. samoensis (two recognized subspecies) is less common and extant only in Samoa and Fiji (Wodzicki & Felten 1975; Mickleburgh et al. 1992). Archeological investigations on 'Eua, Tonga indicate the *P. samoensis* was extirpated there subsequent to Polynesian colonization (Koopman & Steadman 1995). It is most often found alone or in small family groups (male, female, and young). It is predominantly diurnal or crepuscular (Cox 1983), generally showing peaks of activity in early morning and late afternoon (Pierson et al. 1992*a*; Wilson & Engbring 1992). Although often found feeding in secondary or coastal forest or on the edge of agricultural areas, it is rarely found in plantations and seems to prefer native forest.

Because *P. tonganus* appeared to have a broader feeding niche than *P. samoensis*, exploiting relatively intact native forest, agroforest, and plantations, we predicted that it would be less affected by food scarcity following cyclones. Furthermore, from its greater initial abundance, we predicted *P. tonganus* would have a lower probability of local extinction as a result of the cyclones. Because *P. samoensis* has a much smaller total range (in latitude, land area, and number of islands), frequent stochastic extinctions, in concert with anthropogenic declines in forest cover, could pose a serious threat to the survival of the species. A critical issue is whether the newly established reserves include sufficient area and topographic complexity to prevent local extinctions of either of the two flying fox species. The specific goals of this study were (1) to examine the behavioral responses of two flying fox species to major cyclonic storms; (2) to evaluate whether storm or storm-related impacts differed for the two species within and outside the reserves; (3) to identify dominant mortality factors; and (4) to assess whether the reserves served as refugia.

Methods

Study Sites

Studies were conducted in the Samoan archipelago (13–14°S, 171–172°W) on the islands of Savai'i in Western Samoa and Tutuila and Ofu in American Samoa, primarily on sites for which data on pre-cyclone abundance of flying foxes were available (Fig. 1). Three study areas were selected on Savai'i, two within forest reserves (the Falealupo and Tafua Rain Forest Reserves), and one (Vai'a'ata) outside the reserves. In the Tafua Rain Forest Reserve

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(ca. 5000 ha) on the Tafua peninsula, Savai'i, the highest point on the peninsula is a small volcanic cone 108 m above sea level, whereas most of the area is a low-relief lava plain below 30 m. The Falealupo Rain Forest Reserve is a similar lowland forest of about 5000 ha. Vai'a'ata is located at about 600 m and constitutes a mix of plantations and native mid-altitude forest.

In American Samoa there were five study areas, one on the south side of Ofu and four on Tutuila: Afono and Amalau Valleys, Olovalu Crater, and Alava Ridge. The Ofu, Alva Ridge, Afono and Amalau Valley sites all have substantial tracts of native forest and all were at that time proposed for inclusion in the National Park of American Samoa. Privately owned Olovalu Crater is a de facto wildlife sanctuary. Hunting of birds and bats has been prohibited in the two Savai'i Reserves and in Olovalu Crater since before Cyclone Ofa. In 1992, the Governor of American Samoa declared a temporary largely unenforced moratorium on the hunting of bats and fruit pigeons.

Data were collected prior to the storms in July 1987, January 1988, June-July 1988, and January 1990 and after the storms in May-June 1990, October-November 1990, January 1991, August 1991, January 1992, September 1992, and January 1993.

Survey Techniques

Documenting roosting behavior and activity patterns of the two flying fox species required different survey methods. For *P. tonganus*, information on population status was gathered by monitoring evening emergence (Racey 1979) from known colony sites at Olovalu Crater, on Ofu, and at fixed stations along a known flyway on the Tafua Peninsula (Fig. 1). For *P. samoensis*, a number of roosting sites have been monitored on a regular basis since 1987 in Tutuila and since 1988 and 1990 in Savai'i. Additional information on activity patterns (no. of bats observed per unit time), and foraging behavior was obtained by observations from fixed stations in Afono and Amalau Valleys. All observations were made using 10 × 50 binoculars, a 20–60× spotting scope, or night-vision equipment.

Results

Emergence Counts of *P. tonganus*

P. tonganus populations showed severe declines following Cyclone Ofa, both inside and outside reserves. In January 1990, a few days prior to Cyclone Ofa, a colony of *P. tonganus* that roosted on the west coast of the Tafua Rainforest Reserve was monitored at six stations for five nights as it flew across the Tafua Road toward presumed foraging sites to the east (Fig. 1). These surveys yielded a maximum single night count of 5636 individuals (Table 1). These same stations were monitored four times over 2 years after Cyclone Ofa and three times in the year following Cyclone Val (Table 1). Although there were indications of an increasing trend in January and August 1991 (11–18 months after Ofa), counts dropped again after Val. Station counts in January 1993, 13 months after Val, were higher than counts in January and August 1992, yet they still suggest that there was a 90–99% decline in the Tafua Peninsula population of *P. tonganus*.

In the Falealupo Rainforest Reserve on Savai'i a colony of several hundred *P. tonganus* roosted in a small volcanic crater (Fig. 1). In June 1990, 4 months after Ofa, no more than 5 animals were seen at this site. In August 1991, when the crater emergence was monitored, there were 22 observations of *P. tonganus.* On 16 January 1993, 2 hours of observation (17:30–19:30) at two stations yielded only 2 possible sightings of *P. tonganus*.

Prior to the cyclones there were reports of significant numbers of *P. tonganus* roosting in Olovalu Crater (W. Knowles, personal communication; N. Daschbach, personal communication). Because this site was not consistently occupied, it was assumed to be an alternate roost for a colony generally located at Fagatele Bay less than 2 km away, which was estimated in June 1986 at about 5000 individuals (Wilson & Engbring 1992). After Cyclone Val the colony abandoned the heavily damaged roost trees at the exposed coastal Fagatele site, and an aggregation of about 1000 was counted in Olovalu Crater in January 1992. In January 1993, 653 *P. tonganus* were counted emerging there at dusk. Assuming roost fidelity and a stable colony structure, these data indicate an 80–87% decline for this colony. Speculations that the Fagatele Bay colony may have dispersed were not supported by observations elsewhere on the island. Other roost sites, known prior to the cyclones, were either abandoned or contained only a few animals in January 1992. There was no evidence of *P. tonganus* roosting individually or in small groups, except in the immediate post-storm period.

On Ofu, D. Wilson (personal communication) observed several hundred *P. tonganus* flying down from a presumed roost on the ridge behind Vaoto Lodge (Fig. 1) in August 1989. This site was not surveyed after Ofa, but a few weeks after Val, in January 1992, a dozen animals were roosting in a tree above the lodge. One year later, in January 1993, 104 *P. tonganus* emerged from a roost site along the ridge line, suggesting that the colony on this very small island was one-third its former size.

In July 1987 a colony of at least several hundred *P. tonganus* roosted intermittently on the ridge between Afono and Amalau Valleys on Tutuila. This roost site was abandoned after Ofa, and no animals were observed there until January 1993 when a colony was counted on emergence at 322. How this colony relates to the one observed there in 1987 is unknown.

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Table 1. Departure counts for *Pteropus tonganus* colony in Tafua Rain Forest Reserve before the first cyclone, after Cyclone Ofa (post-Ofa), and after Cyclone Val (post-Val).

	Station number								*Mean number/*	*Mean number/*
Date	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*station*	*station/observation period*
1990										
Pre-cyclone										
Jan. 25	218	1101	1479	—	—	—	—	—	933	
26	—	1619	2229	946	—	—	—	—	1598	
28	—	2233	2263	—	—	—	—	—	2248	
29	—	2654	2080	—	—	—	—	—	2367	
30	271	2198	1943	624	347	253	—	—	939	1403.6 (n = 16)
Post-Ofa										
May 30	—	1	9	—	—	—	—	—	5	
31	—	5	1	—	—	—	—	—	3	4.0 (n = 4)
Oct. 20	0	0	0	0	1	1	—	—	0	
22	—	22	8	—	—	—	—	—	15	
24	—	10	2	—	—	—	—	—	6	
28	—	8	—	—	—	—	—	—	8	4.7 (n = 11)
Nov. 1	—	7	3	7	—	—	—	—	6	
7	—	29	49	—	—	—	—	—	39	
8	—	43	13	—	—	—	—	—	28	21.6 (n = 7)
1991										
Jan. 1	—	—	16	—	—	—	—	—	16	16.0 (n = 1)
Aug. 2	—	200	—	—	—	—	—	—	200	
7	—	159	—	46	96	—	—	—	100	
8	64	116	109	—	—	—	—	—	96	
9	72	162	35	37	—	158	6	—	78	
12	—	80	—	43	—	405	—	—	176	111.8 (n = 16)
1992										
Post-Val										
Jan. 17	—	1	—	—	—	—	—	—	1	
18	1	0	—	5	—	4	9	9	4	4.1 (n = 7)
Aug. 20	0	0	0	—	—	—	—	—	0	
22	0	1	0	—	—	—	—	—	0	
23	0	0	0	—	—	—	—	—	0	0.1 (n = 9)
1993										
Jan. 13	—	—	15	13	53	—	—	—	27	
14	—	—	—	—	—	20	17	—	19	23.6 (n = 5)

Roost Surveys of *P. samoensis*

Table 2 indicates the number of known *P. samoensis* roosts within and outside reserves, before and after the cyclones. Overall the number of identified roosts increased inside reserves and decreased outside reserves after Cyclone Ofa (Fig. 2). Before cyclones we identified 13 *P. samoensis* roosts, each with 2–8 individuals. In addition, Vai'a'ata, Savai'i, was identified by Wilson and Engbring (1992) in 1989 as having an unusually large concentration of 41 *P. samoensis*. Additional *P. samoensis* roosts were located in Olovalu Crater following Cyclone Ofa and on Alava Ridge following Cyclone Val (Table 2). All monitored roost sites, except the one at Vai'a'ata, are located near or on the rims of small volcanic cones (Tafua, Falealupo, and Olovalu) or near ridge crests (Afono, Amalau, Alava).

Because of their relatively exposed locations, all *P. samoensis* roost areas experienced severe wind damage. In some cases regularly occupied roost trees fell, and in all cases the areas were completely defoliated after both Ofa and Val. Despite the remarkably rapid recovery of the forest (Elmqvist et al. 1994)—(most areas having 70–90% canopy cover one year after Val)—ridge vegetation remained the most visibly damaged (in some areas only 20–50% canopy cover), with many trees only partially refoliated by January 1993.

Despite serious damage, all pre-storm roost areas within the Savai'i reserves were occupied by *P. samoensis* on every subsequent visit after both storms (Table 2). The Tafua Crater, which had been somewhat sheltered from the storm, functioned as a refuge: 4 months after the storm the number of identified roosting areas increased from four before Ofa to five and four months later to nine. Eight roosts were located a few weeks after Val and 12 one year later.

In Falealupo the two roosts present before Ofa were still occupied after Ofa (June 1990 and August 1991) and after Val (January 1993) despite the loss of many canopy emergents on the cone after each storm.

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Table 2. Number of identified *Pteropus samoensis* roosts at selected sites in Samoa before the first cyclone, after Cyclone Ofa (post-Ofa), and after Cyclone Val (post-Val).

	Inside reserves			*Outside reserves*			
Date	*Falealupo*	*Tafua*	*Olovalu*	*Vai'a'ata*	*Afono*	*Amalau*	*Alava*
Pre-Cyclone							
July 1987	—	—	—	—	2	5	—
July 1988	2	—	—	—	—	5	—
July 1989	—	—	—	1[a]	—	—	—
January 1990	—	4	—	—	—	—	—
Post-Ofa							
June 1990	2	5	—	0	—	4	—
October 1990	—	9	3	0	2	5	—
August 1991	2	—	—	0	—	5	—
Post-Val							
January 1992	—	8	5	—	2	—	7
January 1993	2	12	7	0[b]	2	4	1

[a] *This site was unusual because it had over 40 animals (Wilson & Engbring 1992).*
[b] *Wilson & Engbring 1993.*

The first survey of Olovalu Crater, nine months after Cyclone Ofa in November 1990, identified three *P. samoensis* roosts. In January 1992, a few weeks after Cyclone Val, five *P. samoensis* roosts were found. Two additional roosts were located in January 1993. This site sustained less damage than many areas.

Three surveys at Vai'a'ata in the year and a half after Ofa indicated that the concentration of *P. samoensis* seen by Wilson and Engbring in 1989 was gone. Although a few animals were observed foraging in the area in late afternoon, none appeared to be roosting there. No *P. samoensis* were seen there by Wilson and Engbring (1993) one year after Val.

Prior to Cyclone Ofa, in July 1987, two *P. samoensis* roosts were identified in Afono Valley and five on the ridge above Amalau Valley. The number of roosts in Afono Valley has remained the same on all subsequent visits (November 1990, January 1992, and January 1993), although the number in Amalau Valley has fluctuated between four and five, and was at four in January 1993. In January 1992, a few weeks after Val, seven *P. samoensis* roosting sites (1–2 individuals each) were identified, associated with a series of defoliated small cones along the 5.5-km Alava Ridge road. This road experienced a substantial amount of recreational four-wheel drive traffic during 1992, and one of the roosting cones was partially cleared for a taro (*Colocasia esculenta*) plantation. In January 1993 only one roost, the one farthest from the main road), appeared occupied.

Pre- and Post-Cyclone Activity Patterns

Figure 3 illustrates the activity patterns for the two flying fox species prior to the cyclones. *P. samoensis* could be seen flying at any hour of the day, with peaks of activity associated with foraging in the early morning and late afternoon. The majority of *P. tonganus* foraged at night, and during *Mangifera indica* (mango; mago) or *Ceiba pentandra* (kapok; vavae) season could be heard all night long squabbling in feeding trees in villages. The foraging times of the two species, however, overlapped considerably. *P. tonganus* was sometimes active after dawn and frequently appeared in foraging trees well before dark. On a number of occasions *P. tonganus* were observed feeding simultaneously in the same trees with *P. samoensis*. Although *P. samoensis* showed a flexible foraging pattern, feeding alone on some resources (*F. reineckei* or *Artocarpus altilis* [breadfruit; 'ulu]) and in groups on others (*Planchonella torricellensis* [mama lava], *Cananga odorata* [moso'oi], or *Ficus obliqua* [banyan] [aoa]), *P. tonganus* typically was encountered in aggregations (Elmqvist at al. 1992).

Immediately following both Cyclones Ofa and Val, *P. tonganus* showed considerable disruption of its normal activity pattern. It disappeared from most known roost sites, became far more diurnal, and was generally observed feeding alone. It also showed an increased tendency to enter villages and seek fruit very close to human habitation. In contrast, *P. samoensis* remained in pre-cyclone roost sites and continued to forage diurnally, primarily within the forest. The only noticeable change was that, immediately after the storm, its activity appeared to be more evenly distributed throughout the day, and the late afternoon activity peak was not evident. Also, soaring behavior, characteristically observed near roost sites in late afternoon, was seen less often.

In January 1993, one year after Val, *P. samoensis* activity patterns were comparable to those displayed prior to the cyclone, with some activity in the early morning, a hiatus mid-day, and a peak in activity in the late afternoon (Fig. 4). *P. tonganus*, on the other hand, had become exclusively nocturnal. The pattern followed at the

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Olovalu Crater roost, where all the animals departed the roost within about a 30-minute period beginning just prior to sunset (Fig. 5), was repeated at three other *P. tonganus* roosts that were monitored (two on Tutuila and one on Ofu).

Post-storm Mortality

Following Ofa, dramatic declines (90–99%) were observed for known *P. tonganus* populations, and less severe but nevertheless significant declines in *P. samoensis* populations outside reserves (Wilson & Engbring 1993). Although villagers reported seeing dead birds after both storms, we received no accounts of direct storm mortality to flying foxes. One of us (Cox) was on Savai'i during and immediately following Ofa and saw no evidence of direct storm mortality.

About three weeks after Ofa, thin, stressed flying foxes (almost exclusively *P. tonganus*) began coming into villages to forage for fallen papaya and breadfruit and were described as crawling around on the ground in search of food. One observer (I. Gurr, personal communication) described seeing dead flying foxes hanging in a tree on Tutuila, suggesting death from starvation, but such reports were relatively rare. Reports of predation by domestic animals were extremely common, however. Many villagers emphasized the frequency with which the bats were killed by cats, dogs, and pigs. In one household

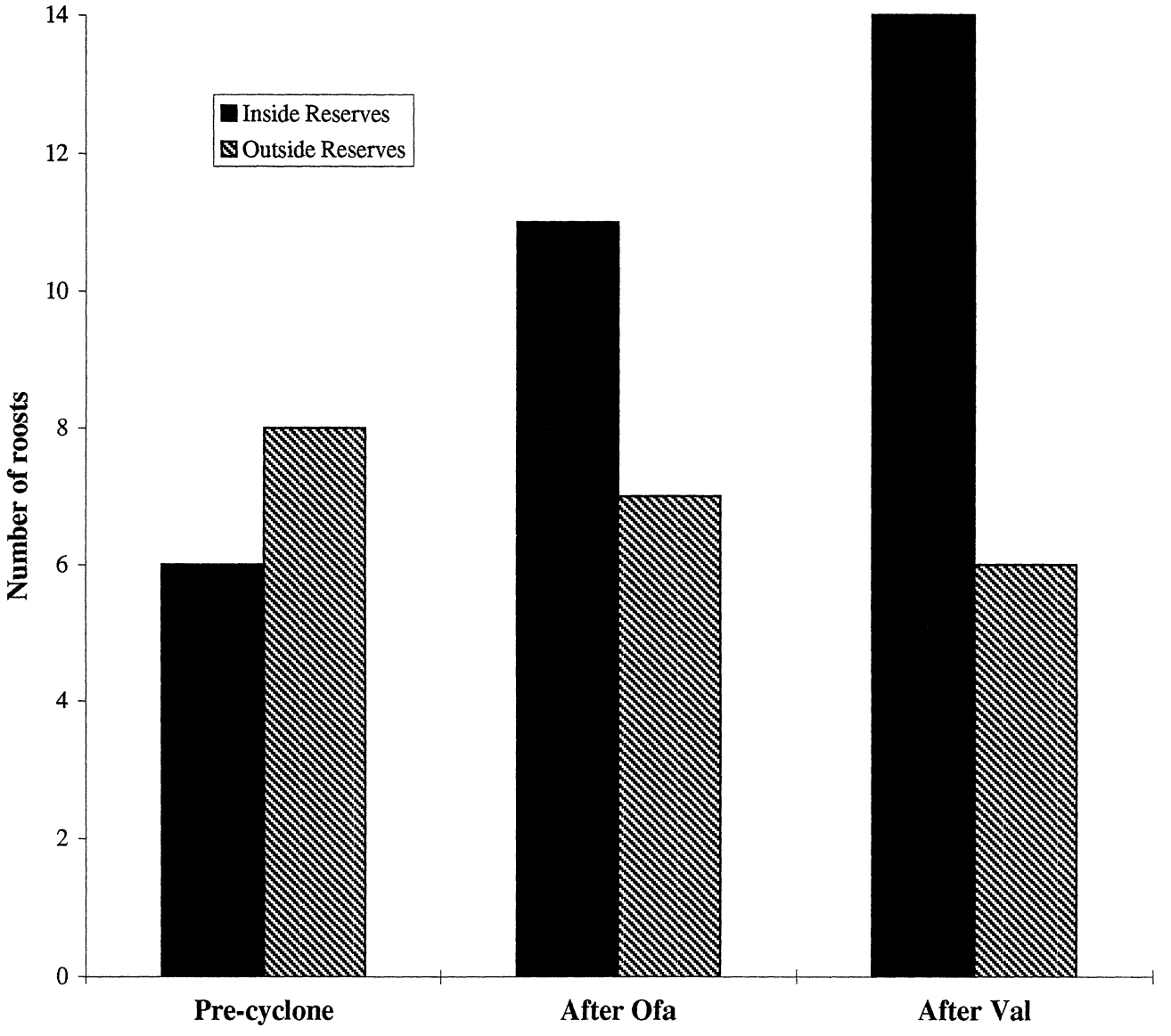


Figure 2. The maximum number of P. samoensis *roost sites inside and outside reserves before and after the two cyclones (Ofa and Val). Alava Ridge and Olovalu Crater are not included because there are no pre-cyclone data for these areas.*

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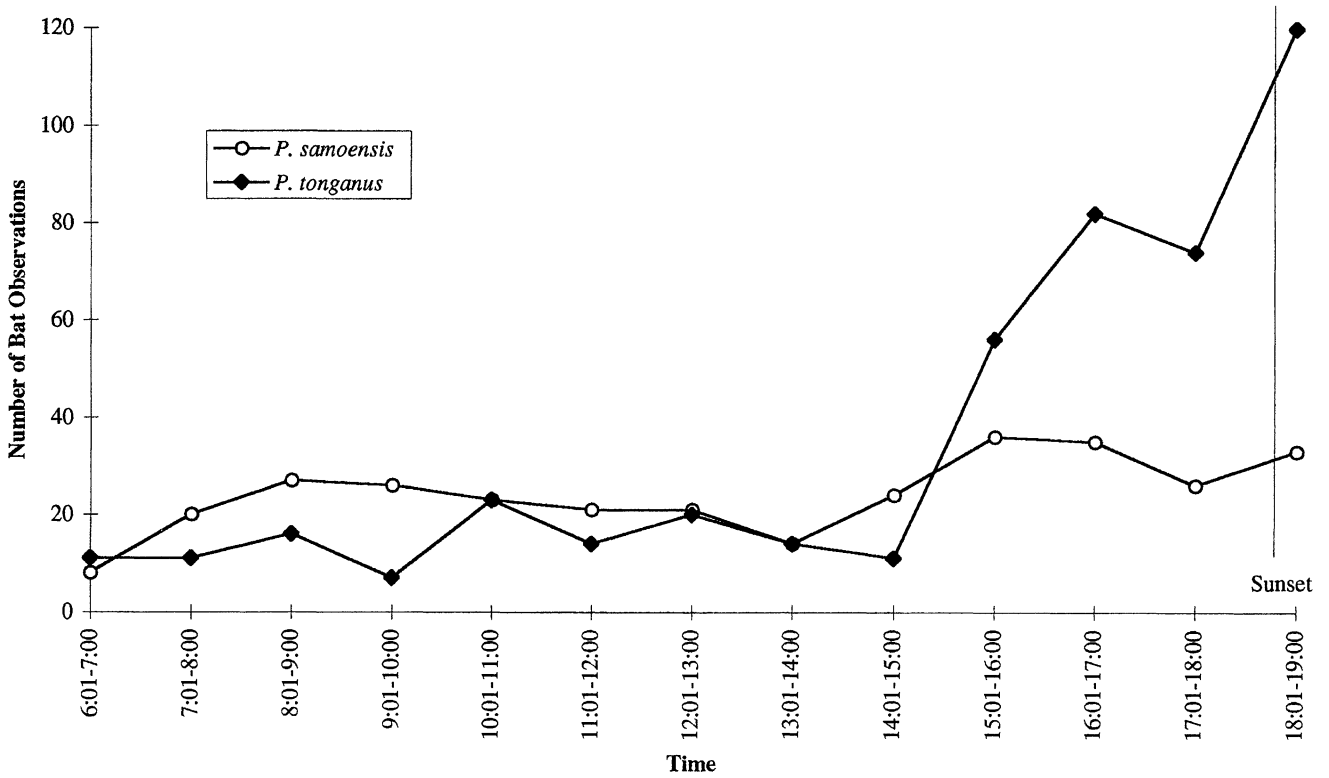


Figure 3. A comparison of diurnal activity patterns for P. tonganus *and* P. samoensis *in Afono Valley, January 1988, before the two cyclones.*

alone in Western Samoa, a family cat killed 15 *P. tonganus* (J. Lundgren, personal communication).

Likewise, reports of intensive post-storm hunting were prevalent. Because they had lost the protective cover of foliage, were weakened by lack of food, and in many cases were foraging on the ground inside villages, the animals were easy targets for adult hunters and rock-throwing children (Daschbach 1990). There were reports in American Samoa of animals being killed by the hundreds. Although in many cases they were killed for food, in one village so many were killed that the village could not consume them all, and carcasses were discarded in the sea. At the same time many people rescued and fed starving flying foxes. Nevertheless, it was only inside the reserves of Falealupo and Tafua or on extensive tracts of private land (e.g., Olovalu Crater) that animals were protected from hunting.

The situation after Val appeared different. Because *P. tonganus* populations had not recovered from the severe reduction after Ofa, this species did not face the same degree of resource shortage after Val. Although a number of nutritionally stressed *P. tonganus* were observed in January 1992 feeding close to villages, there were no reports comparable to those after Ofa of animals feeding on the ground. Presumably, levels of predation by domestic animals were consequently reduced. Also, extensive educational programs after Ofa, particularly in American Samoa (Daschbach 1990), had increased public awareness of the ecological importance of flying foxes and probably contributed to reduced hunting after Val.

Feeding Observations

Observations in January 1988 suggest that a primary food for *P. tonganus* in this season is *Syzygium inophylloides* (asi) nectar. On 4 January in Afono Valley, in eight feeding observations, *P. tonganus* was observed visiting *S. inophylloides* flowers. At the same site *P. samoensis* was observed feeding only on the fruits of *F. obliqua*. Also in January 1988, at other sites on Tutuila, *P. samoensis* was seen feeding on the fruits of *C. odorata* and both flying fox species were seen feeding on the fruits of the introduced rubber tree *Castilla elastica* (pulu). Reliable observers (S. Gurr & P. Gurr, personal communication) reported that flying foxes (species not identified) were feeding in December-January on the fruits of *Terminalia richii* (malili) and the flowers of *P. torricellensis*. The flowers and fleshy bracts of the native forest liana, *F. reineckei*, are also a seasonally important food for *P. samoensis* (Cox 1984*a*).

In the weeks following Ofa the food-stressed flying foxes feeding in villages ate remnants of tree crops: *Carica papaya* (papaya; esi), *Mus paradisiaca* (bananas; fa'i), and *A. altilis* (Daschbach 1990; J. Lundgren; personal

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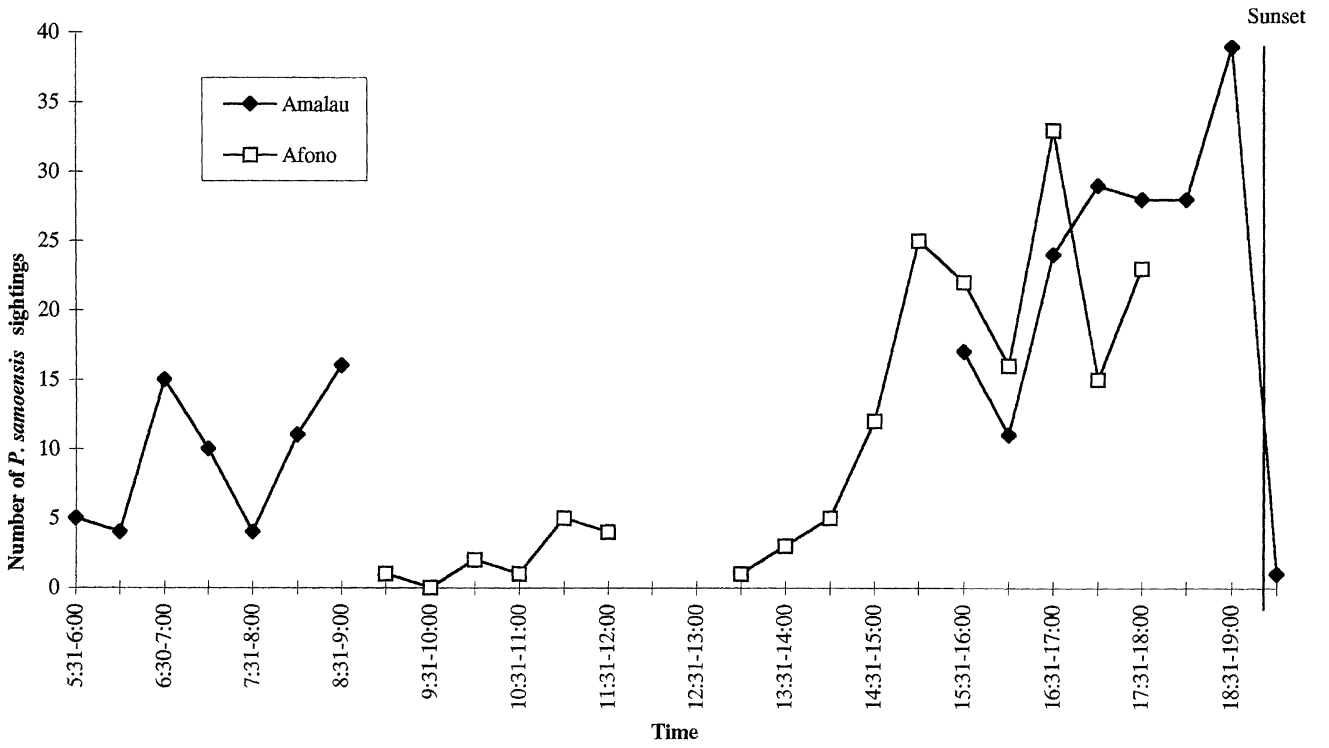


Figure 4. Diurnal activity patterns for P. samoensis *in Amalau and Afono Valleys in January 1993, 13 months after Cyclone Val.*

communication; I. Gurr, personal communication). The majority of these observations involved *P. tonganus* and—very rarely—*P. samoensis*. In June 1990, 4 months after Ofa, *P. samoensis* was observed feeding on the petioles of an unidentified vine that had proliferated on defoliated trees.

In January 1992, about 4 weeks after Cyclone Val, *P. tonganus* appeared to be foraging primarily on the nectar of *Cocos nucifera* (coconut; niu). Of 11 feeding observations, seven were on coconut, and all but one involved agricultural crops. Reliance on agricultural areas is also suggested by the observation that, during the evening exodus of the *P. tonganus* colony from Olovalu Crater toward foraging sites, 75% headed for the Tafuna Plain, the area with the highest concentration of food plantations on Tutuila, and only 12% departed in the direction of native forest. In contrast, all *P. samoensis* in Olovalu crater departed to the north or northwest, toward the inland forest. In January 1992 *P. samoensis* was observed feeding on the bracts of *F. reineckei*, which had survived the storm, and newly emergent *A. altilis* leaves.

In January 1993, one year after Val, food resources were extremely abundant. *P. tonganus* was observed feeding on the fruits *C. odorata, Terminalia catappa* (Indian almond; talie), and *F. obliqua* and searching for food in banana plantations. There were no observations of feeding in *S. inophylloides*, but the strictly nocturnal behavior of *P. tonganus* at this time would have made such observations difficult to obtain. Also, though a number of *S. inophylloides* trees were in flower, many had been heavily damaged by the storm, and—unlike most species—were showing a slow recovery, with only small clusters of flowers and leaves on most trees. At the same time, *P. samoensis* was observed feeding primarily on the fruits of *C. odorata* and *F. obliqua* and on the leaves of an epiphytic orchid *(Eria robusta)*. Although there were no direct observations of *P. samoensis* feeding on *F. reineckei*, the majority of these animals were feeding high in valleys, at elevations where *F. reineckei* is most abundantly distributed.

Reproductive Cycles

Although *P. samoensis* was observed with nonvolant young in January 1990, prior to Cyclone Ofa, the majority of females appear to have young outside the cyclone season in June-August. This is supported by observations in July 1987 and July-August 1988 of females carrying nonvolant young and by observations in January 1993 of a number of juvenile, volant *P. samoensis* that appeared to be 4–6 months old and no observations of females with nonvolant young.

The local reproductive cycles of *P. tonganus* have not been well documented, but females were observed with nonvolant young in July 1987 and January 1988. In January 1993, 86% (n = 84) of females observed in the Olovalu Crater had attached young, suggesting that this spe-

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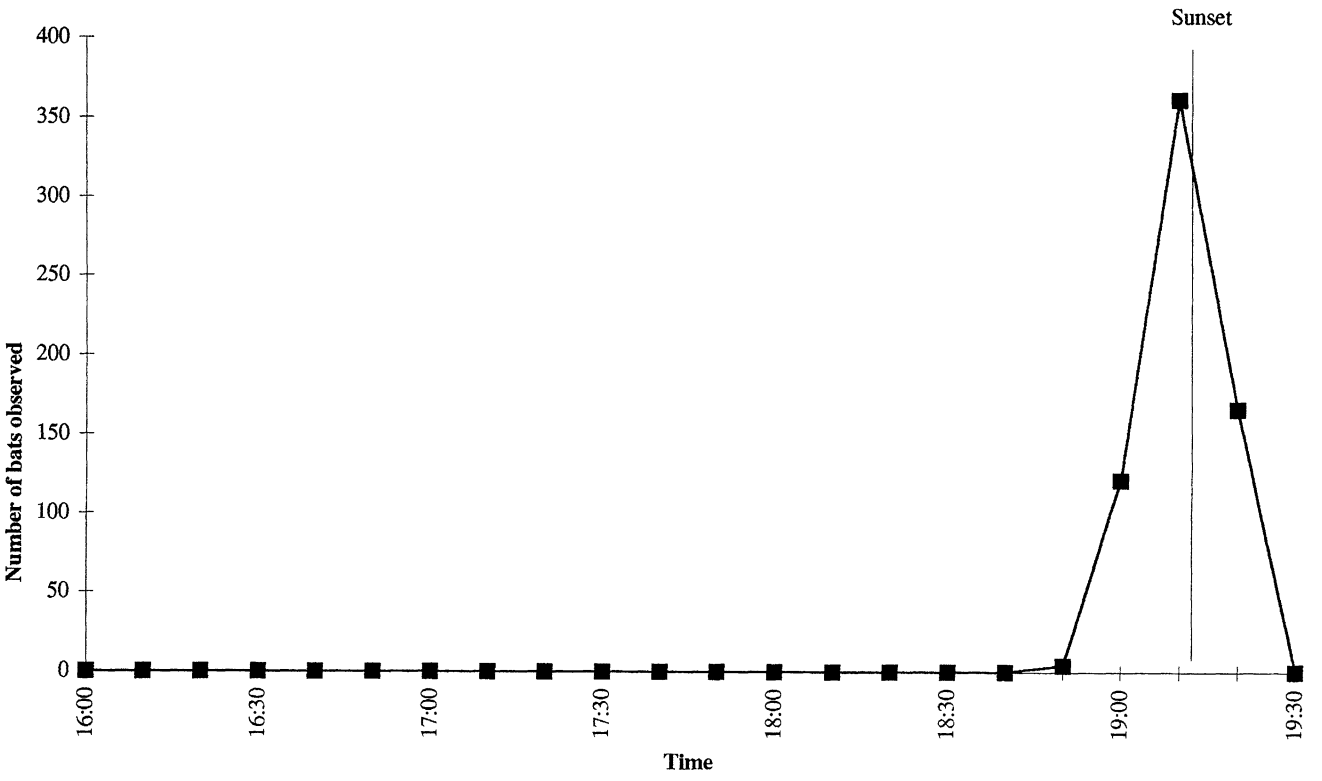


Figure 5. Emergence pattern from P. tonganus *roost site in Olovalu Crater, 4 January 1993, 13 months after Cyclone Val.*

cies has at least one birth peak during the cyclone season. It appears there was virtually 100% mortality of *P. tonganus* young after both storms. In May 1990, 3 months after Ofa, no juvenile animals and no females with attached young were observed. Only one highly weakened, immature animal was observed in January 1992, a few weeks after Val. Mortality of young *P. samoensis* also appeared to be high: no immature animals were seen in May 1990 and in January 1992 only a few immature individuals were seen. Although most appeared healthy, the one that could be most closely observed was in a weakened condition.

Discussion

Flying foxes, like most island-dwelling species within a tropical cyclone belt, are likely to have evolved strategies to cope with the recurrent hazard of cyclonic storms. Given their long life expectancy (~20 years), individual flying foxes may encounter several severe storms in a lifetime. In Samoa, for example, excluding Cyclones Ofa and Val, there have been two severe storms in the past 24 years.

Before Ofa in 1990, *P. tonganus* was by far the more abundant species in Samoa. Although definitive pre-cyclone population estimates are not available, it is likely that the *P. tonganus* population on Tutuila was as high as 12,000 (Wilson & Engbring 1992), and the numbers of *P. samoensis* were fewer than 700 (Engbring 1989). A similar abundance ratio for the two species was also likely for Western Samoa.

Given that *P. samoensis* was the rare endemic species, with perhaps more-restrictive habitat requirements, we expected that it would likely be more vulnerable to cyclonic storms than *P. tonganus*. Our data indicate, however, that populations of *P. tonganus* showed significantly larger reductions than those of *P. samoensis*. Most *P. tonganus* colonies declined 66–99%, whether inside or outside reserves. By contrast, *P. samoensis* populations, although showing severe declines in some areas outside reserves (Vai'a'ata and Alava Ridge), remained relatively stable in others (Falealupo, Afono, and Amalau) and increased (presumably through migration) inside some reserves (Tafua and Olovalu Crater). Our findings are consistent with those of Craig et al. (1994) and Wilson and Engbring (1993).

Although the storm induced short-term behavioral changes and left roost sites exposed, these factors did not significantly bias our population assessments. Some *P. tonganus* colonies dispersed immediately following the storm, making the animals more difficult to find, but aggregations reappeared within months. The absence or reduced numbers of animals in traditional roosting areas in January 1993, more than a year after the second storm, and the low numbers of animals observed at predictable

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favored foraging sites (e.g., flowering *Ceiba pentandra*; Elmqvist et al. 1992) in August 1994, more than two and a half years after Cyclone Val, suggest that the declines observed at established monitoring stations were due to storm effects, not local migration. On Tutuila, American Samoa, a number of traditional roosting sites for *P. tonganus* had been documented and monitored prior to the storms (Craig et al. 1994). The island's limited land area and high topographic relief make it difficult for aggregated animals to escape detection, so the observed population declines cannot be explained by changes in roosting patterns and must be attributed to storm-related losses.

For *P. samoensis* it can be argued that defoliation made roosting animals more visible. Ease of observation did not, however, bias our roost counts. Most monitored sites were discrete areas that had been thoroughly investigated prior to the storms. Also, both before and after the storms, roosting areas were most frequently identified and always confirmed by observations of animals circling in the vicinity of a roost (a characteristic behavior of *P. samoensis*), not solely by locating roosting animals.

We suggest that the differential patterns of mortality we observed for the two species can be explained by a combination of ecological and behavioral factors.

Foraging Behavior in Response to Cyclones

Our observations of foraging behavior indicate that in the current partially anthropogenic landscape *P. samoensis* is better adapted than *P. tonganus* to deal with severe resource depletion and, as a consequence, may be less prone to local extinction. Our initial assumption of a less restrictive feeding niche for *P. tonganus*, based on its consumption of agricultural crops, overlooked the greater tendency of *P. samoensis* to include leaves, petioles, and storm-resistant plants in its diet. Although folivory by leaf fractionation (Lowry 1989) has been observed in a number of frugivorous bats, including several *Pteropus* species (Richards & Provic 1984; Wiles 1987; Wiles et al. 1991; Kunz & Ingalls 1994; Kunz & Diaz 1995), its potential significance as a survival strategy in a cyclone-prone environment has been overlooked. Many plants, stripped by high winds of all flowers, fruits, and leaves, begin to leaf out within days after a storm, making leaves the only readily available food resource. Because under normal conditions flying foxes appear to rely on over-consumption of fruit to meet protein requirements (Thomas 1984) and because leaves generally have a higher protein content than fruit (Kunz & Diaz 1995), switching to folivory following a cyclone is highly adaptive. Although the leaves of some plants may be toxic (Kunz & Ingalls 1994), those leaves most readily available after the storms in Samoa (e.g., leaves of the banyan trees [*Ficus* spp.], and breadfruit) are known to be consumed by flying foxes under normal conditions (Kunz & Diaz 1995).

The majority of feeding observations of *P. samoensis* following both Ofa and Val involved folivory. This behavior was not totally unexpected because data gathered prior to the storms indicated that leaves constitute a regular but minor component in the normal diet (Kunz & Ingalls 1994; Kunz & Diaz 1995). We have pre-storm observations of *P. samoensis* feeding on the leaves of *A. altilis* and *E. robusta* and reliable reports of them feeding on the petioles of *C. papaya*. Our only observation of folivory for *P. tonganus* was an immature and clearly weakened individual on Ofu in January 1992, a few weeks after Cyclone Val.

One of the primary food resources for *P. samoensis* during the cyclone season (December-February) is flowering *F. reineckei* (Cox 1984*a*), which was much less storm-damaged than the native foods available to *P. tonganus* at this time. In January 1992 a number of flowering, slightly damaged *F. reineckei* were found on totally defoliated trees. Data gathered prior to the storms suggest that a primary food resource for *P. tonganus* during the cyclone season are the flowers of *Syzygium* (particularly *S. inophylloides*). These observations are consistent with those of Wodzicki and Felten (1975), who found *Syzygium* to be a key food resource for *P. tonganus* on Niue. Although *Syzygium* trees flower prolifically and thus provide an abundant food resource (including its fruit at other times of year), the flowers are delicate and vulnerable to wind damage. Also, the number of *S. inophylloides* trees has declined dramatically with the loss of lowland forests. Although *S. inophylloides* is distributed from coastal to montane forests, much of what is left on Tutuila is concentrated on exposed slopes and ridges, where storm damage was particularly severe.

Reproductive Consequences of Cyclones

Although disruption of roosting patterns has been reported for other flying fox species after storms (*Pteropus conspicillatus* in Australia [Richards 1990]), our observations indicate that disruption was more severe for *P. tonganus* than for *P. samoensis*. *P. tonganus* abandoned a number of traditionally used roost sites in the periods immediately following the storms, whereas *P. samoensis* was still found in most pre-storm roost sites, even those that were heavily damaged.

The storms also appeared to be more disruptive of the reproductive patterns of *P. tonganus*. For *P. samoensis* the peak reproductive period—when most nonvolant young are observed—appears to be June-August, outside the cyclone season. Although it is still not clear what the reproductive patterns are for *P. tonganus*, observations both prior to the storms and in January 1993 indicate the populations have one birth peak during the cyclone season. Although immature *P. samoensis* are presumably at greater risk than adults from post-storm food restriction, apparently healthy young *P. samoensis* were

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observed in January 1992. Because no infant *P. tonganus* and only one weakened juvenile were observed in January 1992, virtually 100% mortality of young for this species seems likely. Given the high nutritional demands of late lactation on the mother and the limited foraging skills of newly volant young at a time of acutely reduced food availability, a high juvenile mortality during and after the storm is highly plausible. It is not known to what extent the loss of a dependent young and hence termination of lactation could lead to a compensating initiation of ovulation in *P. tonganus*, and hence to an increased reproductive potential.

Post-cyclone Mortality within and outside Reserves

The post-cyclone numbers of *P. samoensis* were the same or higher inside reserves and generally lower outside reserves, whereas populations of *P. tonganus* showed comparable declines inside and outside reserves. This can be explained partially by differences in foraging ranges and behaviors. Both the Tafua and Olovalu Crater populations of *P. tonganus* traveled considerable distances and foraged outside the reserves, where they were not protected from hunting. In addition, this species showed a much greater tendency than *P. samoensis* to enter villages to feed on fallen fruit, where they were killed by domestic animals, and outside reserves, where they were targets of human hunters.

Although the foraging range of *P. samoensis* has not been thoroughly studied, behavioral observations at roosting areas suggest that many individuals frequently feed within 1–2 km of their roosts. Thus, it is likely in the larger reserves (Falealupo and Tafua) that individuals did not leave protected areas to feed. *P. samoensis* received additional protection from its tendency to avoid villages and agricultural areas and to feed primarily in forest.

The severe defoliation caused by cyclones leaves roosts highly exposed and far more vulnerable to hunting pressure at a time when human food resources are also depleted. Surveys in the Northern Marianas (Lemke 1992; Stinson et al. 1992) and observations from Vanuatu (Chambers & Esrom 1988; Bani 1992) suggest that the primary source of storm-related mortality for flying foxes is intensive post-storm hunting. Although mortality of juvenile, nonvolant individuals may be high as a direct result of the storms, all available information indicate that hunting by humans and predation by domestic animals were the main post-cyclone mortality factors for both flying fox species in Samoa (Daschbach 1990; Craig & Syron 1992; Craig et al. 1994).

Cyclones, Conservation, and Reserve Design

One important consideration for existing and future reserves in the area is whether adequate habitat will be secured for flying foxes during periods of acute resource scarcity. Our study suggests that the reserve areas on Savai'i (ca. 10,000 ha total area), although likely not sufficient for insuring the long-term survival of *P. samoensis*, are adequate for short-term maintenance of small populations, even after severe sequential cyclones. In the Tafua Reserve the numbers of censused *P. samoensis* actually increased after both storms, reflecting the combined effects of a ban on hunting, the relative abundance of food in a large tract of native forest, and the persistence of relatively undamaged forest patches inside the two volcanic craters. Also, interspecific competition for food was dramatically reduced because populations of other frugivores (*P. tonganus*, pigeons, and doves) were much reduced and remained at extremely low levels in January 1993.

The reserves did not effectively protect *P. tonganus* populations. Given the various behavioral traits that make this species differentially vulnerable to hunting after a storm (such as its tendency to travel large distances from roosting to feeding areas and to come into agricultural areas to feed), hunting bans and protection of roosting areas may be essential for maintaining viable populations.

Wind damage was patchy and not consistent between storms. In general, however, the interiors of volcanic cones received some protection from the wind and served as critical refugia for bats after the storms. Future reserves in Savai'i should target areas with high topographic complexity (like volcanic cones or deep valleys) that, based on satellite-pictures and aerial inspection, remained largely intact through both cyclones. As more native forest is lost to logging, agricultural conversion, and development, there is less assurance that enough forest will remain to support the variety of frugivorous, nectarivorous, and folivorous species during the period of resource depletion following severe cyclonic storms.

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on his land. We also thank all the Samoan people, including many children, who on their own initiative protected and fed hungry flying foxes.

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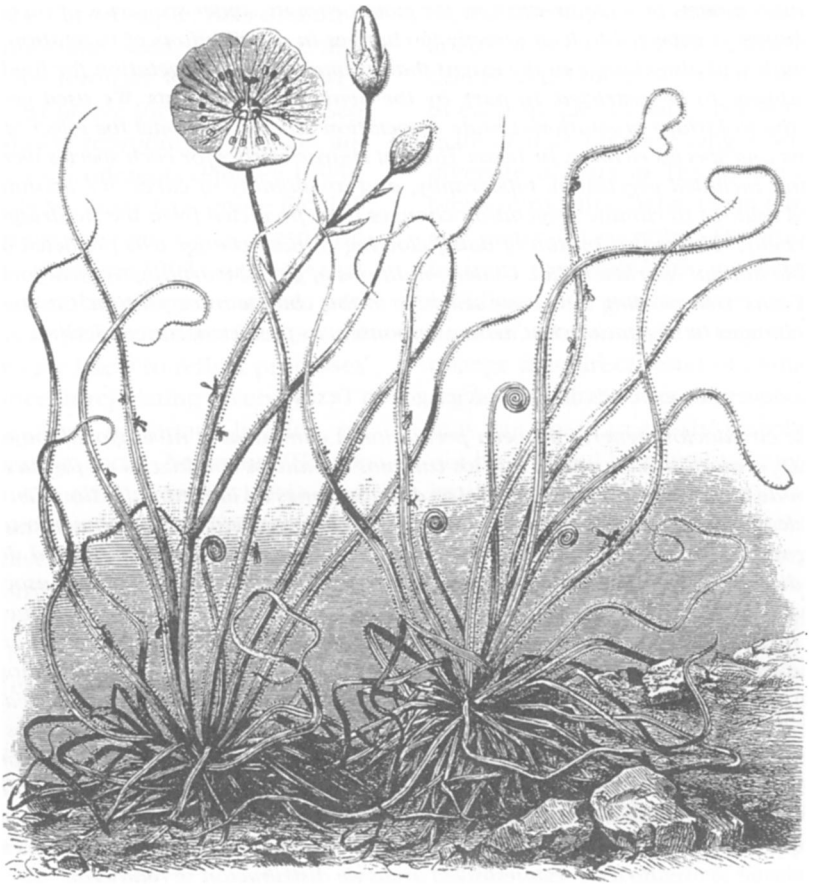
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