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Effects of Cyclone Waka on flying foxes (*Pteropus tonganus*) in the Vava'u Islands of Tonga

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Abstract: Severe tropical cyclones are a major cause of episodic mortality for Pacific Island flying foxes (large fruit bats). Many flying foxes starve after forests are stripped of food sources, and hunting by humans may also increase in the post-cyclone period. In December 2001, Cyclone Waka passed directly over the Vava'u Islands in the Kingdom of Tonga, western Polynesia. We visited the islands 6 mo later to survey the flying fox (*Pteropus tonganus*) population and assess availability of potential food items (fruit and flower) in primary, secondary and plantation forests. Less than 20% of the pre-cyclone bat population (surveyed in 1999–2001) remained 6 mo after the storm. The density of potential food trees in flower or fruit at this time was only 15% of pre-cyclone density, and the main species available were different in the two time periods. The highest density of potential food trees occurred in secondary forest (26 flowering or fruiting trees ha^{-1}) and plantations (23 ha^{-1}); primary forest offered the least food (18 ha^{-1}). Since 65–70% of the land area has been converted to agricultural plantations, this vegetation type had the highest absolute number of food-bearing trees – almost seven times that of primary forest. Flowering coconuts (*Cocos nucifera*) were the most abundant food source overall and we suggest that this species may be important in sustaining flying foxes following severe storms.

Key Words: Cyclone Waka, disturbance, flying fox, frugivory, *Pteropus tonganus*, Polynesia, Tonga

INTRODUCTION

Cyclones occur frequently in the tropical Pacific, passing through most island groups at irregular intervals ranging from < 1 to 50 y (Holland 1993). Cyclones kill some trees and strip branches, leaves, fruits and flowers from others. The sudden loss of food resources (typically fruits and flowers) can be a major cause of mortality for flying fox (large fruits bats) and bird populations (Daschbach 1990, Elmqvist *et al*. 1994, Flannery 1989). Following a cyclone in Samoa, population densities of the flying fox *Pteropus tonganus* Quoy & Gaimard declined by 80–90% (Craig *et al*. 1994, Pierson *et al*. 1996). Many bats starved and the lack of food also forced bats to forage on the ground where they were vulnerable to predation by humans and domestic animals (Craig *et al*. 1994, Daschbach 1990, Pierson *et al*. 1996). Substantial population reductions have also been noted for several other *Pteropus* species following cyclones, although no detailed surveys were done (Carroll 1984, Cheke & Dahl 1981, Flannery 1989). Where cyclones are frequent, they could act as a major limiting factor on flying fox populations. Large-scale (up to 90% in some areas) conversion of native forests to agricultural plantations consisting of food crops beneath an open overstorey of coconuts (*Cocos nucifera*) may further limit the recovery of bat populations, since they preferentially forage in primary forest (Banack 1998).

Cyclone Waka passed directly over the Kingdom of Tonga on 31 December 2001. This intense tropical cyclone had sustained winds estimated at 185 km h^{-1} and gusts of up to 230 km h^{-1}. The worst damage occurred in the Vava'u Islands in northern Tonga, which were affected by maximum winds for 6 h. Waka was reported to be Tonga's most severe cyclone since 1961 (http://weather.unisys.com/hurricane/s_pacific/2001/).

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Tonga's only flying fox species, *Pteropus tonganus*, is one of the most widespread *Pteropus* species in the Pacific, occurring from the Cook Islands to Papua New Guinea (Miller & Wilson 1997). Prior to cyclone Waka, flying foxes were abundant in Vava'u (Grant 1998, McConkey & Drake 2002). We visited the Vava'u Islands 6 mo after cyclone Waka (June 2002) to assess flying fox numbers and availability of potential food items and compare them to pre-cyclone data we gathered during a study on seed dispersal by flying foxes (McConkey & Drake 2002) conducted from 1999–2001. We had three specific aims: (1) estimate the decline in the flying fox population; (2) evaluate the extent of potential food loss for the bats, and (3) assess the relative importance of plantations, secondary forest and primary forest in providing potential food trees for bats.

STUDY AREA

The Vava'u archipelago (19° S, 174° W) is in the northern part of the Kingdom of Tonga in Western Polynesia. Maximum elevation of the largest island, 'Uta Vava'u (96 km^2), is 200 m. South of this island lie 57 smaller islands, ranging up to 9.3 km^2 and 40 m elevation. Primary forest covers 10–12% of the land in Vava'u, persisting mainly in areas too steep for cultivation; secondary forest and plantation cover 20% and 65–70% of land, respectively (Bolick 1995, Steadman *et al.* 1999). Coastal forest is widespread as small remnants on a number of islands, and consists almost exclusively of native trees (Steadman *et al.* 1999). Nothing has been documented on the fruiting and flowering times of plants in Tonga. We have not observed any strongly seasonal pattern during our research periods in Tonga. Some individuals of most species mentioned in this paper were fruiting or flowering on some islands in most of the months sampled (February–May, October, November) and this is consistent with Smith's (1979–1991) observations in Fiji.

METHODS

Flying fox decline

Pre-cyclone counts of commuting flying foxes were made for six islands (Table 2) in the Vava'u archipelago between 1999–2001 (see map in Franklin *et al.* 2004 and McConkey & Drake 2002). Post-cyclone counts were repeated for the same islands in June 2002, 6 mo after cyclone Waka. The selected islands were spread throughout the full geographic range of the archipelago; hence, the decline estimates should be representative of the region.

In both periods, flying foxes were observed continuously from the same (usually coastal) vantage points for 2 h before dark, which is the period of highest bat activity whilst they are still visible to the observers (K. McConkey unpubl. data). From these points, we counted all bats that could be observed commuting between islands. Watches from Utula'aina Point (situated in the largest forest patch on 'Uta Vava'u), only included bats flying within the main bay since no nearby islands occurred. These counts are likely to underestimate actual bat numbers, because foraging bats were not included (due to the difficulty in distinguishing individuals; Morrell & Craig 1995). However, given that the same method was used in both the pre- and post-cyclone period, an estimate of bat decline can be generated.

Counts were done over two, usually consecutive, evenings for each site, both before and after the cyclone and the mean count used for each site, during each visit. Some sites were sampled on multiple visits (5–13 mo between visits) before the cyclone and the mean of these visits was used for the comparison. To estimate the decline in bat numbers following cyclone Waka we compared mean pre-cyclone and post-cyclone counts for each individual site and calculated a mean decline.

Potential food loss

Pre- and post-cyclone measures of the availability of potential food for bats were done for the six sites for which bat counts were made both before and after the cyclone, and eleven other sites visited while estimating vegetation damage after the cyclone only (Franklin *et al.* 2004). Ten estimates of food availability were taken in primary forest and seven in secondary forest. Food availability transects (500 m long) were located in areas surveyed earlier (using stratified sampling) for collection of vegetation data (Franklin *et al.* 1999), and in many cases islands and habitat patches on islands were small enough that transects traversed most of the targeted habitat. Potential food availability was estimated by determining the proportion of trees at each site that offered potential food resources. Not all trees offer equal amounts or quality of food and we did not have information on how important different sources were to the flying foxes; however, this method provides a comparative estimate of potential food availability between time periods.

At each site, the number of fruiting and flowering trees present were counted from 100 canopy-height trees selected using the point-centred-quarter method (Mueller-Dombois & Ellenberg 1974). Trees with $\geq$ 10 cm dbh (diameter at breast height, measured at 1.3 m) were selected from 25 points at 20-m intervals along a roughly straight line, except when topography did not allow for this. For fruits, only species known to be consumed

Table 1. Per cent land area, total land area and post-cyclone tree density in three vegetation cover types on the 13 largest islands in Vava'u, Tonga.

Forest type	% land area[a]	Total land area (ha) (% land area × 12 006)	Post cyclone tree density (trees $ha^{-1} \pm 1$ SD)
Primary	11	1321	732 ± 196^{b}
Secondary	20	2401	948 ± 176^{b}
Plantation	65	7804	74^{c}

[a] From Steadman *et al.* (1999) and Bolick (1995).
[b] Post-cyclone density of trees ≥ 10 cm dbh, estimated from Franklin *et al.* (1999) and Franklin *et al.* unpubl. data. (secondary forest density based on their early and mid-successional plots (n = 6) and primary forest plots based on their late-successional plots (n = 13).
[c] Coconut density from Burrows & Douglass (1996) and corrected for average cyclone-related mortality in secondary forest (19%; Franklin *et al.* unpubl. data). No mortality estimates were done for plantations due to insufficient time.

by flying foxes were used in the final estimate of food availability. Because flower sources used by bats are less well known, all flowering trees (except for common species which never had feeding signs) were included in the estimate. Food species were determined from our own observations of feeding bats, feeding signs left under plants (bat teeth marks in the pulp of discarded fruit), and the literature (reviewed in Banack 1998). Pre-cyclone food availability was compared with post-cyclone abundance for the seven revisited sites, all of which were in primary forest.

Food availability in different habitats

The numbers of trees (and species) with food for flying foxes after the cyclone were compared among plantations, secondary and primary forest. The proportion of trees in primary and secondary forest with potential food items were generated from our potential food source transects. Crops in Vava'u are usually grown in plantations beneath an overstorey of coconuts (Steadman *et al.* 1999), and coconut flowers were virtually the only potential food present in plantations at the time of our study. We sampled 10 current or abandoned plantations with an overstorey of coconuts. All coconuts in 20-m-wide belt transects were checked for the presence of flowers. Transect length varied, but we aimed to count 100 coconut trees at each site.

We used published tree densities (from Burrows & Douglass 1996, Franklin *et al.* 2004) and our post-cyclone data on proportion of trees with food to estimate the density of available food trees in each forest type at the time of our post-cyclone survey (Table 1). Densities were then extrapolated to estimate total numbers of available food trees in each vegetation type on the 13 largest islands in Vava'u for which cover data are available (together these comprise 12 006 ha, or > 95% of the total land area). This assumes that our surveyed islands are representative of the cyclone damage inflicted on these 13 islands, which is reasonable, given that our surveys include 'Uta Vava'u, which comprises > 80% of the total land area.

RESULTS

Flying fox decline

Estimated flying fox abundance among survey sites ranged from 2–151 animals h^{-1} before the cyclone (across islands, seasons and years), and 0–8.5 animals h^{-1} 6 mo after the cyclone (Table 2); this represents a decline of 80 ± 10% (mean across all sites ± 1 SD). Because young bats (born after the cyclone) were present during our counts, thereby inflating post-cyclone numbers, actual cyclone-related mortality rate was probably underestimated. Some sites had estimated declines of 100%, but foraging bats were seen on these islands, indicating some flying foxes were present.

Potential food loss

The number of food trees in the primary forest sites declined substantially after the cyclone (Table 2). Before the cyclone, we found between 4–24% of sampled trees at each site provided food for the bats (n = 1500 trees). After the cyclone only 0–4% of sampled trees had food suitable for bats (n = 1600 trees). This represents a mean decline of 85 ± 12% (Table 2).

During the post-cyclone visit, flying foxes were observed feeding on the fruits of six species and the flowers (nectar or pollen) of three species (Table 3). Before the cyclone, the most numerous food trees were fruiting *Pleiogynium timoriense, Neisosperma oppositifolium* and *Pandanus tectorius* (Figure 1). Fruits from these species were difficult to find after the cyclone. *Cocos nucifera* flowers were the most abundant potential diet item after the cyclone; an estimated 79% of all potential food sources (208 443 stems projected from sampled density and the total area of each forest type on the 13 main islands) were coconuts with flowers (Table 3). The other most frequently available food sources were trees with the ripe fruit of *Morinda citrifolia*, and the flowers of *Maniltoa grandiflora, Hibiscus tiliaceus* and *Leucaena leucocephala*. Most fruiting *Terminalia catappa* and *T. litoralis* had evidence bats were consuming the pulp of the fruits and these species were conspicuously fruiting at most coastal sites. However, data were not gathered for these species because they are restricted to the immediate coast and hence did not feature regularly in the sampling transects.

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Table 2. Extent of flying fox and food decline in the Vava'u Islands, Tonga, after cyclone Waka.

Island	Flying foxes (h^{-1})[a] Pre-cyclone (number of visits)	Flying foxes (h^{-1})[a] Post-cyclone	% flying fox decline	% of plants bearing food Pre-cyclone	% of plants bearing food Post-cyclone	% food plant decline
A'a island	29.0 (2)	8.5	70.7	16.0	0.0	100
Euakafa island	2.5 (1)	0[b]	(100)	13.0	4.0	69.2
Foelifuka island	12.7 (3)	2.5	80.3	19.2	3.0	84.3
Fua'amotu island	2 (1)	0[b]	(100)	24.0	3.0	87.5
Utula'aina Point	151 (3)	6.5	95.7	16.1	1.0	94.2
Vaka'eitu island	20 (1)	5.5	72.5	4.0	1.0	75.0
Mean (± SD) of all sites			79.8 ± 9.9			85.0 ± 11.8

[a] Figures represent the mean number of commuting bats counted over two consecutive nights. Pre-cyclone counts are also averaged across multiple visits.
[b] Foraging bats were seen. Per cent decline in these sites is not included in overall mean.

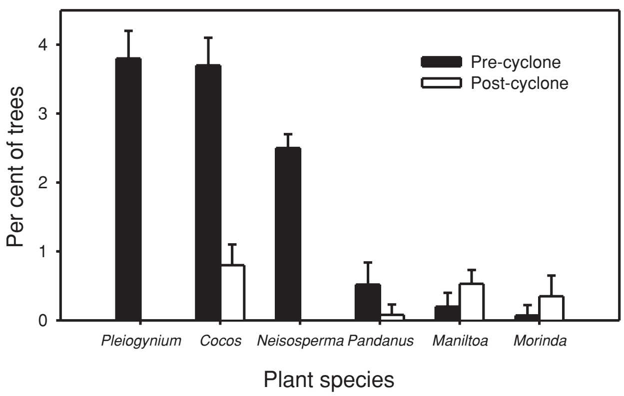

Figure 1. Mean percentage of trees bearing food (expressed as a percentage of all trees). Species shown represent the most numerous food sources (across all sites and months) available before and 6 mo after cyclone Waka. *Pleiogynium timoriense, Neisoperma oppositifolium, Pandanus tectorius* and *Morinda citrifolia* provided fruit and *Cocos nucifera* and *Maniltoa grandiflora* provided flowers. Standard error bars are shown.

Food availability in different habitats

Of the three vegetation types surveyed, the type that had the highest percentage of its trees bearing food was plantation (Table 3). Of 910 coconuts surveyed (10 sites), 26% had flowers (range, 9–34%). Food was borne on 1.9% of the sampled trees in primary forest and 2.7% of the trees in the secondary forest. Primary forest had a higher diversity of food species (10) than secondary forests (6) and plantations (1). A higher percentage of food trees bore flowers (3.2% excluding coconuts, 29.5% including coconuts) than fruit (1.7%).

The highest density of post-cyclone potential food sources was in secondary forest (26 trees ha^{-1}), followed closely by plantations (23 trees ha^{-1}) (Table 3). Primary forest had the lowest density (18 trees ha^{-1}). However, if total land area is considered, most potential food was in plantations (176 510 potential sources) – nearly three times that in secondary forests and almost seven times that in primary forest.

DISCUSSION

Flying fox numbers declined by 70–96% on the study islands after the cyclone. If this trend is representative of the Vava'u archipelago this suggests that only 20% of Vava'u's pre-cyclone flying foxes remained 6 mo after cyclone Waka. Although cyclone-related forest damage varied across the island group (Franklin *et al.* 2004), we believe we surveyed a sufficiently wide geographic spread of sites to gain a representative sample. Tonga's Ha'apai Island group lies 100 km south of Vava'u and was also affected by the cyclone. However, as cyclone Waka passed to the north of Ha'apai (http://weather.unisys.com/hurricane/s_pacific/2001/), damage was probably less extensive. *Pteropus* species similar in size to *P. tonganus* have been observed flying as far as 40 km without landing (Wiles & Glass 1990) and it is feasible that some flying foxes may have reached the Ha'apai group during or after the storm. However we believe it is unlikely that such dispersal would account for 80% of the previous population, particularly as food sources were probably also reduced in Ha'apai, and suggest that the observed decline represents mortality.

Flying fox mortality may have been direct (during the storm) or due to starvation and hunting of bats by humans in the weeks following the cyclone. Direct storm mortality has never been assessed for flying fox populations, although a lack of eyewitness accounts suggests mortality is low during cyclones (Pierson *et al.* 1996). In Vava'u, large numbers of flying foxes were seen floating in the water of a sheltered lagoon immediately after cyclone Waka passed over (S. Campbell *pers. comm.*), but dead bats were not reported from other areas until several weeks later.

In American and Western Samoa, most mortality occurred in the weeks following the cyclone (Craig *et al.* 1994, Pierson *et al.* 1996). Widespread defoliation of trees (90–99% in Western Samoa) caused a significant food shortage for flying foxes (Elmqvist *et al.* 1994). Bats entered villages looking for food 3 wk after cyclone Val

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Table 3. Food abundance after cyclone Waka in different forest types estimated for the 13 largest islands in Vava'u (see Table 1). The species confirmed to be eaten by the flying foxes after the cyclone are noted. Species with available parts assumed to be consumed but not confirmed are indicated by parentheses. Percentage in each forest type refers to the number of trees of that species (with the part eaten) compared with the total number of trees sampled in the forest type.

Species	Part eaten (or only available)	Primary forest			Secondary forest			Plantation			Total number of sources (% of all sources)
		%	trees ha^{-1}	total no.	%	trees ha^{-1}	total no.	%	trees ha^{-1}	total no.	
Cocos nucifera L.	Flower	–	–	–	1.4	13.3	31 933	26.3	22.6	176 510	208 443 (79%)
Cycas seemannii A. Br	(Seed)	0.3	2.2	2906	–	–	–	–	–	–	2906 (1%)
Ficus obliqua Forst. f.[a]	Ripe fruit	–	–	–	–	–	–	–	–	–	–
Hibiscus tiliaceus L.	(Flower)	–	–	–	0.3	2.8	6723	–	–	–	6723 (3%)
Leucaena leucocephala (Lmk) de Wit	(Flower)	–	–	–	0.4	3.8	9124	–	–	–	9124 (4%)
Maniltoa grandiflora (A. Gray) Scheffer[b]	Flower	0.5	3.7	4888	–	–	–	–	–	–	4888 (2%)
Melodinus vitiensis Rolfe[a]	Ripe fruit	–	–	–	–	–	–	–	–	–	–
Morinda citrifolia L.	Ripe fruit	0.5	3.7	4888	0.4	3.8	9124	–	–	–	14 012 (5%)
Pandanus tectorius Park.	Ripe fruit	0.1	0.7	925	–	–	–	–	–	–	925 (0.4%)
Pouteria (Planchonella) grayana (H. St. John) F. R. Fosberg[c]	Ripe fruit	0.4	2.9	3831	–	–	–	–	–	–	3831 (2%)
P. membranacea (H. St. John) Baehni[c]	Ripe fruit	0.1	0.7	925	–	–	–	–	–	–	925 (0.4%)
Pleiogynium timoriense (DC.) Leenh	(Flower)	0.2	1.5	1982	–	–	–	–	–	–	1982 (1%)
Terminalia catappa L.	Ripe fruit	–	–	–	0.1	0.9	2161	–	–	–	2161 (1%)
Terminalia litoralis Seem.	Ripe fruit	0.1	0.7	925	–	–	–	–	–	–	925 (0.4%)
Xylosma simulans A. C. Sm.	(Flower)	0.2	1.5	1982	–	–	–	–	–	–	1982 (1%)
Zanthoxylum pinnatum (J. R. Forst. & G. Forst) W. R. B. Oliv.	(Flower)	0.1	0.7	925	0.1	0.9	2161	–	–	–	3086 (1%)
Total (no. species)		1.9 (10)	18.3	24 177	2.7 (6)	25.5	61 226	26.3 (1)	22.6	176 510	261 913

[a] These species were not found in the vegetation transects.
[b] Young leaves were also consumed but abundance was not measured.
[c] These species were handled by flying foxes, but not fed on extensively.

and many died of starvation (Pierson *et al.* 1996). In Vava'u, local people reported 100% defoliation of trees and the trees took several weeks to begin resprouting (S. Cesare, P. McKee, *pers. comm.*, F. Tonga, *pers. obs*). Food resources must have been extremely limited during this time and flying foxes were seen foraging on the ground (S. Campbell, *pers. comm.*, F. Tonga, *pers. obs.*); thus we suggest that starvation was a major factor in the decline in bat numbers.

Flying foxes that are forced to forage on the ground are susceptible to predation by humans and domestic animals (Craig *et al.* 1994, Daschbach 1990, Pierson *et al.* 1996), and harvest rates more than doubled in the 3 mo following cyclones Val and Ofa in American Samoa (Craig *et al.* 1994). Predation was also reported to occur in Vava'u, including a small colony (fewer than 50 bats) that people killed for food (F. Tonga, *pers. obs.*), but estimates of predation-caused mortality could not be made. Overall mortality was higher in Samoa (80–99%) than in Vava'u (70–96%) and this difference may reflect different levels of hunting. The absence of villages from most islands in Vava'u (43 of the 58 islands are uninhabited) probably meant that hunting was relatively localized and a large proportion of the population was not at risk.

Average tree mortality due to cyclone Waka among lowland rain-forest sites was quite low (6%, Franklin *et al.* 2004), compared with Samoa (28–33%, Elmqvist *et al.* 1994). However, 6 mo after cyclone Waka, food was still scarce for the bats in comparison with before the cyclone. We report a reduction of 85% of the total food sources available to the bats after the cyclone. However, actual food loss may be substantially higher since many trees had lost part of their crown (Franklin *et al.* 2004); thus a single post-cyclone tree probably had less food than a single pre-cyclone tree.

Coconuts may provide important sustenance for flying foxes after cyclones. Flying foxes were reported feeding on young fruit in Vava'u when nothing else was available (S. Campbell, *pers. comm.*). In American Samoa coconut flowers were available 4 wk after cyclone Val (Craig *et al.* 1994). Six mo after cyclone Waka, coconut flowers were still the most abundant food source available, providing 80% of all potential food sources.

Native fruits tend to be more nutritious than cultivated species (Nelson *et al.* 2000) and flying foxes preferentially feed in primary forests (Banack 1998). Consequently, the widespread deforestation and land conversion that has occurred in Vava'u would be expected to limit the ability of flying foxes to recover from cyclones. Indeed, primary forest had the highest diversity of available food during our post-cyclone visit, but given coconuts were the most prolific, single food item available, recover quickly from cyclone damage, and occur at high density in plantations, coconut plantations may still play an important role in recovery of bat populations.

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