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Flying Foxes Prefer to Forage in Farmland in a Tropical Dry Forest Landscape Mosaic in Fiji

Matthew Scott Luskin[1]

Department of Environmental Science, Policy, and Management, University of California at Berkeley, Berkeley, California 94720, U.S.A.

ABSTRACT

To test flying fox adaptations to a habitat mosaic with extreme deforestation, the abundance, habitat choice and feeding behavior of the Pacific flying fox, *Pteropus tonganus*, were investigated across 16 islands of the Yasawa archipelago, Fiji. The habitat mosaic is formed by 4.3 percent tropical dry forest and 3.3 percent farmland, leaving exotic grasslands and stands of *Leucaena leucocephala* to overrun the vast majority of land. *Pteropus tonganus* abundance was high (5757 bats) despite deforestation and hunting. Roosting sites were restricted to native forest fragments. Grasslands and stands of *L. leucocephala* were completely void of bats at all times. The mean foraging density in farmland was four times higher than in forests and foraging competition was routinely observed in farmland but was extremely rare in forests. The author suggests that during the study, extensive foraging in farmland was supporting the high *P. tonganus* population. Additionally, the preferential foraging in farmland was responsible for the low foraging densities within forests and dramatically less intraspecies competition for forest resources. Further research is needed on seed dispersal within forests and to test for seasonal variations in bat abundance and feeding.

Key words: Chiroptera; fruitbats; Pacific Islands; Pteropodidae; *Pteropus tonganus*; tropical dry forest; Yasawa.

FLYING FOXES ARE CRUCIAL POLLINATORS and seed dispersers on oceanic islands (McConkey & Drake 2002). However, habitat destruction and hunting are threatening flying foxes and their ecological roles across the Pacific (IUCN 2009). Understanding the effects of habitat conversion on flying foxes and their ecological niches is important for the conservation of forest ecosystems.

Small and isolated oceanic islands generally have impoverished pollinator and seed dispersal guilds made up primarily of insects, birds and fruit bats (Fujita & Tuttle 1991). While various species contribute to small seed dispersal (< 30 mm diam.), prehistoric extinctions of large frugivorous bird species across the Pacific have left flying foxes as the keystone dispersers of large-seeded plants in the region (Cox *et al*. 1991, Fleming & Sosa 1994, Rainey *et al*. 1995, Steadman 1995, McConkey & Drake 2002). The loss of functional seed dispersal by flying foxes could lead to a cascade of linked extinctions of both plants and animals (Myers 1986, Fujita & Tuttle 1991).

Pteropus tonganus (Quoy & Gaimard 1830; Chiroptera: Pteropodidae; the pacific flying fox, insular flying fox, or *beqa*) is a large fruit bat widely distributed across the South Pacific and the only indigenous mammal of the Yasawa archipelago in Fiji. It is primarily nocturnal, congregates in large daytime roosts, and feeds on fruit, nuts and flowers in both native forests and cultivated land. Flying foxes travel up to 40 km a night foraging and are able to track food resources across land and water barriers (Richmond *et al*. 1998, McConkey & Drake 2007). Its diet, size and mobility enable *P. tonganus* to be an optimal seed disperser. Small seeds are dispersed whenever flying foxes feed; however, large seeds that cannot be ingested (≥ 4 mm diam.) must be carried away in the mouth for dispersal (Richards 1990). High foraging densities are necessary to instigate aggressive interactions that provoke bats to fly away with fruits, thus dispersing larger seeds (Richards 1990). McConkey & Drake (2006) found that in tropical rain forests, flying foxes cease to function as large seed dispersers long before they become rare because low foraging densities eliminate competition for resources.

Tropical dry forests once covered a broad area in western Fiji, including the Yasawa archipelago, due to the vast rain shadow cast by the mountainous interior of Viti Levu (Keppel 2005). Today, tropical dry forests in Fiji have suffered deforestation exceeding 99 percent of their historic extent and are critically endangered (Janzen 1988, WWF & IUCN 1995, Keppel 2005). Anthropogenic burning for easier overland transportation and farmland has devastated forests on the Yasawas. Sporadic fires and grazing by feral goats, cows and pigs now inhibits the growth of young forest plants. Exotic grasses or single species stands of *Leucaena leucocephala* have almost completely replaced native forests. *Leucaena leucocephala* (Fabaceae), common names leucaena, coffee bush, false koa or hedge acacia, is an invasive tree valued for its straight and rapid growth (Thaman & Tuiwawa 1999). Leucaena grows into thick impenetrable stands that are lacking in wildlife. On the Yasawas, steep cliffs and valleys far from villages often harbor the only remaining native forest fragments (Thaman & Tuiwawa 1999).

This study focuses on flying fox adaptations to the described landscape mosaic. Because of the deforestation on the Yasawas, flying foxes were expected to be persisting in low numbers. Further, the remaining *P. tonganus* population was expected to show roosting and feeding adaptations to nonnative landcover. Additionally, the premise was that flying foxes would be subsisting in low densities due to the naturally lower fecundity of dry forests and would be highly competitive for the limited dry forest resources (Banack & Grant 2002, McConkey *et al*. 2004). To test these hypotheses, data were collected on (1) the habitat mosaic of the Yasawa islands; (2) the *P. tonganus* abundance; and (3) the *P. tonganus* roosting and feeding habits.

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[1]Corresponding author; e-mail: tropic.luskin@gmail.com

METHODS

STUDY SITES.—The fieldwork was completed over 3 mo between June and August 2007. Fiji's Yasawa archipelago consists of over 30 volcanic islands northwest of Viti Levu (Fig. S1). Data were collected from the 16 largest islands (all > 40 ha), the largest island being Naviti (34.2 km^2) and the highest Waya (579 m). The average size of the 16 islands studied was 8.8 km^2; however, nine islands were < 2 km^2. This study identified four habitat types: native tropical dry forest, farmland and two types of exotic species coverage: grasslands and stands of the exotic tree, *L. leucocephala*. Tropical dry forest is defined as forest in a frost-free zone with annual precipitation of 500–2000 mm and a pronounced dry season (Murphy & Lugo 1986). Native forest quality was not differentiated although it is known that *P. tonganus* prefers minimal disturbance (Banack 1998, Nelson *et al*. 2000).

FIELD METHODS.—To measure *P. tonganus* abundance, roost counts and counts of diurnally active bats were conducted on all islands (Grant 1998, Brooke *et al*. 2000). Roosting bats were counted by visiting all roosts during 0800–1700 h by foot or boat. Roosts were characterized by tens to hundreds of individuals congregating in one or a few overlapping trees. Roosts were easy to locate because they were limited to small forest fragments and bats were vocal when roosting. The Yasawas are small islands with good overland accessibility so all roosts could be located and studied. Exact counts of bats at each roost site were made with binoculars (8×42) and a tick-counter (Bookhout 1996). Counting diurnally active bats was only necessary when a small island had no roosts yet did have migrating individuals. On such islands, abundance was determined by carefully surveying the entire island on foot and/or boat during 0800–1700 h. Roosting sites were visited one to three times on one or more days and islands lacking roosts were surveyed two to three times on the same day.

Feeding behavior was studied by counting foraging bats along one-way transects (40×500 m; McConkey & Drake 2006). Nocturnal bat abundance and feeding were synonymous as all bats observed along evening transects were foraging. *Pteropus tonganus* became active at dusk, and so transects were walked in the remaining 1.5 h before sunset and until light ran out (1700–1830 h). Forty meters (20 m each side) was the maximum width along transects where foraging bats could be accurately identified across all habitats and in poor light. Aggressive feeding behavior, characterized by fighting and vocalizations while foraging, was recorded for all transects (McConkey & Drake 2007). Aggressive interactions can be instigated by a multitude of situations including mating and juvenile–adult interplay, but only interactions arising from food competition were counted (Richards 1995). Only one feeding interaction was recorded for a particular site despite the number of bats involved. Between two and 10 transects were recorded for each landcover type on each island, yielding a total of 190 transects over the entire study (104 in forests, 86 in farmland). Transects were also walked in grassland and stands of *L. leucocephala*, yet no bats were observed, and so they were excluded from the analysis.

GEOGRAPHIC INFORMATION SYSTEMS.—The islands were mapped with satellite images from Landsat ETM+, acquired on 8 May 2003 (path 75, row 72), Google Earth, and on site with a GPS (Garmin, Olathe, KS, U.S.A.). The islands and habitat mosaic were digitized into custom geo-referenced polygons (regions of interest) in ArcGIS using bands 3, 4 and 5. An algorithm to calculate the area of the polygons was applied for forests and farmland (Jensen 2000, Feeley *et al*. 2005).

STATISTICS.—From the transect data, the mean feeding density (abundance/ha) was calculated for each landcover type on each island. The total island feeding abundance was estimated for each island by multiplying the mean feeding density in each landcover type by the total area of that habitat per respective island. All variables were normally distributed. The correlations between diurnal abundance, feeding density and abundance, island size and land cover types were tested with linear regression models (Jongman *et al*. 1995, Wheater & Cook 2000, StataCorp 2007).

RESULTS

The Yasawa archipelago's total forest coverage was 4.3 percent (6.1 km^2) and farmland was 3.3 percent (4.6 km^2), with the remaining 92.4 percent (130.2 km^2) exotic grassland or *L. leucocephala*. Native forest ranged from 0.5 percent of island area on Yasawa Island (14.5 ha) to 36 percent on Sau-i-lau (30.8 ha). The largest area of native forest on an island was 115.9 ha on Waya (5.4 percent), while the most farmland was on Naviti with 152.2 ha (4.4 percent; Table 1).

Pteropus tonganus was present on every island surveyed and there was a total of 5757 bats across all 16 islands. The mean density was 0.41 bats/ha of total island area, 5.35 bats/ha of useable habitat (forest and farmland combined) and 9.51 bats/ha of forest. *Pteropus tonganus* remained exclusively in native forest fragments in daylight but migrated into both farmland and forests from dusk till dawn. Bats were completely absent from grasslands and *L. leucocephala* stands over the entirety of the study. Yasawa Island and Nanuya Lailai had no diurnal population, likely due to the lack of forest on those islands, while Wayasewa had the largest population (1143 bats). Roosts were only located in forests and appeared permanent throughout the study. Roost size varied from 22 to 750 bats, averaging 157, and comprised 96 percent of the total diurnal population (Table 1).

Diurnal bat abundance per island was correlated with native forest per island ($r = 0.74$, $P < 0.01$). However, diurnal bat abundance was not correlated with island size or farmland. The strongest indicator of evening feeding abundance was farmland ($r = 0.95$, $P < 0.01$), followed by native forest ($r = 0.51$, $P = 0.045$; Table 2).

The total estimated evening feeding population was 89.9 percent of the observed diurnal population, with the decrease partly explained by bats that were still roosting or in flight. The mean feeding density in forests was 2.72 bats/ha and the mean feeding density was 8.81 bats/ha in farmland. The highest feeding density in a single transect was 45 individuals and the lowest was 0 (Table 1).

TABLE 1. *Summary data of island geography and flying fox population, roosting, and feeding.*

Island	Area (km^2)	Human pop (1996)	Forest (ha)	Farmland (ha)	*P. tonganus* population estimate		Roosts (> 20 bats)	Average feeding density (/ha)	
					Diurnal	Nocturnal/feeding		Forests	Farmland
Kuata	1.3	8	36.2	1.0	289	312	4	6.67	35.0
Wayasewa	6.3	206	55.3	9.2	1143	198	3	1.50	12.5
Waya	21.6	1001	116	62.4	480	567	4	1.67	6.00
Narara	0.4	0	12.5	0.0	45	0	1	3.00	0
Nanuya Balavu	0.7	14	20.5	0.6	750	49	1	2.00	12.0
Nokocuvu	0.5	0	13.2	0.4	85	31	2	2.00	10.3
Drawaqa	0.6	0	7.2	0.0	24	0	0	3.00	0
Naviti	34.2	1485	50.6	152	266	1065	2	1.50	5.50
Yaqeta	7.3	102	67.7	39.2	791	409	3	2.67	12.0
Matacawalevu	9.8	512	87.2	28.1	689	509	6	3.50	12.3
Nanuya Levu	1.6	60	10.8	23.5	133	65	3	4.33	8.00
Nanuya Lailai	1.2	120	9.2	3.4	0	10	00	0.67	4.00
Tavewa	1.5	112	4.9	13.7	188	189	1	1.33	13.3
Nacula	22.3	548	68.8	68.4	554	720	4	3.50	7.00
Sawa-i-lau	0.9	0	30.8	0.0	320	0	1	5.67	0.00
Yasawa	30.6	1064	14.5	61.7	0	7	0	0.50	7.00
Total	140.9	5232	605	464	5757	4131	35	439	141
Average	8.8	327	37.8	29.0	360	258	2.2	2.72	10.9*

*Mean of the 13 islands that contained farmland.

In farmland, there were 41 aggressive interactions including fighting and vocalizations over food. Interactions in farmland occurred at densities of 4–25 bats/ha. Only one aggressive interaction in forest was observed between feeding bats over the entire study. This occurred while feeding on flowers of the rare *Cynometra falcate* at a density of 31 bats/ha. In farmland, *P. tonganus* fed predominantly on papaya fruits, *Carica papaya*, breadfruit fruits, *Artocarpus altilis*, and mango flowers, *Mangifera indica*. In forests, bats fed primarily on coral tree flowers, *Erythrina variegata*, and coconut flowers, *Cocos nucifera*.

DISCUSSION

Severe deforestation totaling 95.7 percent of the Yasawa's total island area has yielded the overwhelming majority of land useless to flying foxes. Bats were absent from grasslands and *L. leucocephala* stands because they lacked both food and suitable roosting sites. *Pteropus tonganus* showed no adaptation to transformed landscapes, except to feed nocturnally in farmland trees. Local people hunted bats on every island, yet the lack of firearms has protected *P. tonganus* from the large-scale hunting problems experienced on other pacific islands (Palmeirim *et al.* 2005). Avoiding human predation restricted diurnal habitat and roosting sites to remote forests (Palmeirim *et al.* 2005; M. Luskin, pers. obs.).

Interestingly, bat abundance was high considering the extent of deforestation (Banack & Grant 2002, McConkey & Drake 2007). Nonetheless, the feeding density in forests was low and aggressive behavior indicating resource competition within forests was almost absent. The hypothesized responses to the extensive deforestation were: (1) small population of flying foxes; (2) adaptation to nonnative habitats; and (3) increased feeding competition within

TABLE 2. *Adjusted* R^2 *between island size (IS), habitat type (FA, forest area; FLA, farmland area), feeding and diurnal (DFFA)/nocturnal (NFFA) flying fox abundance.*

Variables	Correlation between variables				
	IS	FA	FLA	DFFA	NFFA
FA	0.16*				
FLA	0.83***	0.14*			
DFFA	0.07	0.34**	0.07		
NFFA	0.49***	0.45***	0.68***	0.05	
Abundance of bats feeding in farmland	0.51***	0.25**	0.80***	0.02	0.91***

Significance is indicated as follows:
$^{*}P < 0.1$; $^{**}P < 0.05$; $^{***}P < 0.01$.

the remaining forests fragments. The data show the exact opposite to be true: a large bat population, few adaptations and low feeding competition within forests. I propose that the driving rationale for these unpredicted results is *P. tonganus*' extensive foraging in farmland, which both support the abundance of bats and decreases the necessity of forest food resources. However, forest is shown to be a critical requisite for sustaining flying foxes since they serve as the sole roosting sites.

Feeding density in farmland (8.81 bats/ha) was four times that in native dry forest (2.72 bats/ha), illustrating a strong preference for foraging in farmland. Based on the relative feeding densities, farmland resources were the staple of *P. tonganus*' diet and responsible for supporting the high abundance. While *P. tonganus* has been observed feeding in farmland in many studies, the scale observed on the Yasawas is unreported. The likely rationale behind *P. tonganus*' preferential feeding behavior is the higher fecundity than in forests. In this study, bats were observed feeding mainly on fruit in farmland, but flowers in forests. The relative unproductiveness of tropical dry forest contrasted with the fruit trees cultivated in farmland created a sensible partiality by *P. tonganus* to forage in farmland (Murphy & Lugo 1986, Nelson *et al.* 2000, Keppel 2005).

The lack of aggressive feeding interactions in forests despite the large diurnal population demonstrates that roosting density does not equate to aggressive feeding interactions. Mass migration from forest to farmland each evening reduced forest densities below the threshold that would stimulate aggressive feeding interactions. This conclusion follows McConkey & Drake's (2006) deduction that aggressive feeding interactions between flying foxes are dependent on some threshold localized feeding density. Because aggressive feeding interactions are a requisite for flying foxes to disperse large seeds, the data suggest there is insufficient dispersal of large seeds by flying foxes on the Yasawas.

This study is limited by its short duration. Also, seasonal variations in fruiting plants could change the observed feeding behavior (McConkey & Drake 2007). Although bat migration between islands within the Yasawa is well within *P. tonganus*' nightly capabilities, it is unlikely that there are migrating bats from Viti Levu or other island groups based on the Yasawas remoteness (Banack & Grant 2002, McConkey & Drake 2007). Thus, the bat population is most likely stable and the results for roosting bats and diurnal counts consistent year round. It should be noted that there had not been a significant cyclone in the region for several years preceding the study.

The overall effects from *P. tonganus*' extensive feeding in farmland are both positive and negative. Farmland is supporting a high flying fox population in a region where extensive deforestation would otherwise have decimated their levels. Furthermore, a large abundance of flying foxes enables nutrient cycling, especially into forests where bats roost. The large population also facilitates pollination and small seed dispersal (Cox *et al.* 1991, Fleming & Sosa 1994). Concurrently, farmland appears to be *P. tonganus*' favored food source, diminishing resource competition within forests, which thus reduces large seed dispersal. Maintenance of viable flying fox populations is important to the longevity of forests in all of the regions they inhabit and is crucial in areas of low biodiversity such as oceanic islands (Richards 1990, Cox *et al.* 1991, Fleming & Sosa 1994, Kunz & Fenton 2003). The loss of flying foxes' ecological roles could jeopardize the critically endangered tropical dry forests of the Pacific (Myers *et al.* 2000, IUCN 2009). In particular, Fijian dry forests are a conservation priority because they are home to an array of rare species including the critically endangered Fijian crested iguana (*Brachylophus vitiensis*; Keppel 2005, IUCN 2009).

Conservation efforts to maintain the current population of bats on the Yasawas should focus on maintaining roosting sites (*i.e.*, forest fragments) and monitoring hunting. More importantly, immediate conservation efforts should focus on preventing any further destruction of forests, and then aim at fostering regrowth. Future research is needed on seasonal food resources and the flying foxes' response to such any changes. Farmed fruit is known to be nutritionally unequal to forest resources for flying foxes and the possible effects from widespread farmland foraging could be significant (Nelson *et al.* 2000). Finally, large-seeded dry forest plants species of the Yasawas should be investigated in light of the flying foxes adapted feeding patterns.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Map of the Yasawa islands.

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