Ecology and conservation of bats in Temotu Province, Solomon Islands and Torba Province, Vanuatu

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Abstract. Bats are essential to the functioning of many island ecosystems. A large proportion of Pacific Island *Pteropus* are endemics, limited in their distribution to single paleotropical islands or close island groups. This subset is also highly threatened by hunting and habitat disturbance. Further exacerbating these threats is a dearth of scientific knowledge that makes long-term management and conservation planning difficult. We aimed to gather data on seven bat species from Nendö, Reef Islands, Tinakula, and Vanikoro (Solomon Islands), and Vanua Lava and Mota (Vanuatu). Between 1990 and 2019 we surveyed bats using walked transects, mist nets and camp counts, and collected data on diets and roosting sites. Data collection targeted four limited range endemics (Nendö tube-nosed bat (*Nyctimene sanctacrucis*), Banks flying-fox (*Pteropus fundatus*), Temotu flying-fox (*Pteropus nitendiensis*) and Vanikoro flying-fox (*Pteropus tuberculatus*), and three more widespread species (Vanuatu flying-fox (*Pteropus anetianus*), Pacific flying-fox (*Pteropus tonganus*) and Fijian blossom bat (*Notopteris macdonaldi*). *Notopteris macdonaldi*, *P. nitendiensis*, *P. tonganus* and *P. tuberculatus* were the most common species recorded on transects and mist net surveys. Transect encounter rates were 0.1–4.5 km^{-1} (*P. nitendiensis*), 0.2–20.0 km^{-1} (*P. tonganus*) and 0–7.2 km^{-1} (*P. tuberculatus*). *Pteropus fundatus* was rarer, we did not detect this species during daytime searches, and it was the least common mist net capture. We documented 65 *Pteropus* food plants in our study area. *Nyctimene sanctacrucis* was not detected on Nendö, Tinakula and Reef Islands despite considerable effort. We consider this bat is likely extinct, if in fact it is a distinct species.

Additional keywords: archipelago, bats, biodiversity hotspot, conservation, Critically Endangered, ecology, endemic, extinction, habitat disturbance, hunting, island, IUCN Red List, keystone species, mist netting, *Notopteris*, *Nyctimene sanctacrucis*, Pacific, paleotropical, *Pteropus*, rare, threatened, Vulnerable.

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Introduction

Throughout large parts of the Pacific, bats are the only native terrestrial mammals present. They are essential to the functioning of island ecosystems, pollinating plants and spreading seeds and nutrients among and between islands (Cox *et al.* 1992; Banack and Grant 2002; McConkey and Drake 2006). Flying-foxes (*Pteropus* spp.) naturally extend into the Pacific further than any mammalian lineage and clearly harbour the ability to transit long distances between isolated islands and mainlands (Flannery 1995). Despite their ability for long-distance flight, the bulk of *Pteropus* are island endemics limited in their distributional ranges to single paleotropical islands

or archipelagos (Mickleburgh *et al.* 2002; Lavery *et al.* 2016; Vincenot *et al.* 2017).

Island *Pteropus* are a valuable source of protein to Indigenous people, are conspicuous and relatively easy to hunt, have low rates of reproduction and can be the source of valuable cultural commodities (Mickleburgh *et al.* 2002; Lavery and Fasi 2017; Vincenot *et al.* 2017). Therefore, they are a highly threatened subset of bats. In fact, 28 of the 31 species of Critically Endangered, Endangered or Vulnerable flying-foxes on the IUCN Red List are from islands (Mickleburgh *et al.* 2002; Vincenot *et al.* 2017). Many of these occur in the western Pacific where scientific research has been limited. Basic distributional

and ecological data and population trends are severely lacking for many endemic Pacific Island *Pteropus*. This basic lack of knowledge further endangers island flying-foxes by limiting capacity to plan for long-term conservation and threat management.

Temotu and Torba provinces comprise some of the most geographically remote islands in the Solomon and Vanuatu archipelagos respectively. They support a depauperate mammalian fauna relative to larger islands closer to New Guinea. However, at least three endemic flying-foxes from the '*samoensis*' species group occur there (Flannery 1995; Almeida *et al.* 2014). All three are threatened (Endangered or Critically Endangered) on the IUCN Red List (Helgen and Hamilton 2008; Leary *et al.* 2008*a*, 2008*b*).

Banks flying-fox (*P. fundatus*) is a small species with reduced molars, a greyish-brown head, a red-brown mantle and brown body. Little is known about the diet, habitat preferences or reproductive biology of *P. fundatus*. The presumed distribution of is primarily based on the locations of the 1963 collections of H. Bregulla (Felten and Kock 1972). Bregulla's collection included 13 specimens from Mota; a single adult male from both Vanua Lava and Mota Lava; and two male specimens from the 'Banks Islands' (Felten and Kock 1972). In 1992, P. German collected extensively throughout the Banks Islands for the Australian Museum, and only captured *P. fundatus* on Mota (referred to in Flannery 1995, p. 258). The Australian Museum specimens were collected from village gardens and plantations, suggesting it is a species capable of exploiting disturbed environments.

Vanikoro flying-fox (*P. tuberculatus*) is a medium-sized species, uniform dark brown in colour with a crown and mantle of slightly lighter brown fur. Originally collected in 1828 during the voyage of the *Astrolabe* and described in 1869 (Peters 1869), the correct type locality remained confused until Troughton (1927) collected eight specimens and fixed the locality to Vanikoro. Subsequently, it was feared extinct after surveys in the 1990s failed to detect the species (Leary and Aujare 1994). Nothing has been reported of the species other than the collection of an additional four specimens including a juvenile in August 1926 (Sanborn 1931).

Temotu flying-fox (*P. nitendiensis*) is endemic to the Santa Cruz islands, Temotu Province, Solomon Islands (Troughton 1930). It is a medium-sized flying-fox weighing between 185 and 230 grams, yellow to golden brown in colour with a darker mantle on the dorsum of the neck and shoulders on males (Flannery 1995). One of two female specimens collected in October 1990 were pregnant (T. Leary, unpubl. data; Flannery 1995).

The Nendö tube-nosed bat (*Nyctimene sanctacrucis*) is known from a single specimen presumed to have been collected from Nendö in 1892 and held in the collections of the Australian Museum (Parnaby *et al.* 2017). Forearm length is approximately 75 mm, the fur of the back is described as 'mottled wood and buffy-brown with a washing of cinnamon drab, and wings and ears are marked with yellow or dark brown spotting' (Troughton 1931). Mickleburgh *et al.* (1992) erroneously claim that it was last seen in 1907, but there is no evidence of the species other than the holotype. Flannery (1995) regards *N. sanctacrucis* extinct, likely a result of habitat disturbance.

Each of these limited range bats co-occur with Pacific flying-fox (*P. tonganus*), which is among the most widespread species of

the genus. Two more species Vanuatu flying-fox (*P. anetianus*), and Fijian blossom bat (*Notopteris macdonaldi*) are sympatric with *P. fundatus* and *P. tonganus* in the Banks Islands (Flannery 1995). Specimens of *P. anetianus* were collected from Gaua, Mota Lava, Ureparapara and Vanua Lava by the Whitney South Sea Expedition, by H. Bregulla in 1963, and by P. German in 1992 (Sanborn 1930; Felten and Kock 1972; Flannery 1995). *Notopteris macdonaldi* is a relatively widespread species recorded from a number of islands in Fiji and Vanuatu (Fig. 1).

We aimed to describe the distributions of pteropodid bats in Temotu Province, Solomon Islands and the Banks Islands, Torba Province, Vanuatu between 1990 and 2019. We also sought to estimate species abundances and roost sizes, document behaviour, diets and ecology and collate information on species threats and conservation status.

Materials and methods

Study area

Field surveys were completed between 1990 and 2019 in Solomon Islands and Vanuatu on Nendö, Malo and Tömotu Noi (referred to collectively herein as Nendö); Fenualoa, Makalom, Matema, Nagawa, Niupani, Ngalo (Lomlom), Nifiloli, Nukapu and Pileni, (referred to collectively herein as the Reef Islands); Baine and Tevai (referred to collectively herein as Vanikoro); Tinakula; Mota; and Vanua Lava (Table 1). These islands are positioned in a complex geological region between the larger islands of Solomon Islands and Vanuatu in the East Melanesian Islands Biodiversity Hotspot (Mittermeier *et al.* 2004) (Fig. 2).

Tinakula is an active stratovolcano that has remained uninhabited since erupting with lava flows and ash explosions in 1971 (Global Vulcanism Program 2020). A more recent ash explosion occurred in October 2017 (Global Vulcanism Program 2017). Nendö and Vanikoro are predominantly built of Pliocene volcanic materials of basaltic origin (Coleman *et al.* 1969). The Reef Islands and the southwest lowlands of Nendö are uplifted Pleistocene reef limestone (British Solomon Islands Deptartment of Geological Surveys 1969; Coleman *et al.* 1969; Müeller-Dombois and Fosberg 2013). Many of the Reef Islands are being extensively eroded and reduced in size by sea-level rise (R. Pierce, pers. obs.). Rainforest is the prevailing vegetation type on the volcanic islands, dominated by *Campnosperma brevipetiolata*, *Calophyllum vitiense*, *Gmelina solomonensis*, *Parinari corymbosa*, *Pterocarpus indicus* and *Endospermum medullosum* (Walker 1948; Müeller-Dombois and Fosberg 2013). Apart from mangroves, the vegetation of the Reef Islands is almost entirely human-modified, consisting of coconut plantations, agroforest and subsistence gardens and small remnants of highly disturbed lowland rainforest and littoral forest/scrub (T. Leary, pers. obs). Temotu Province is wetter and more prone to cyclones than the remaining Solomon Islands and phytogeographically the islands are more akin to those of Vanuatu (Walker 1948; Müeller-Dombois and Fosberg 2013). Villages and areas of shifting subsistence cultivation and fallow are concentrated along coastlines. Commercial logging operations have converted large areas of Nendö and Vanikoro to secondary forest in various stages of succession.

Vanua Lava and Mota are similarly dominated by rainforest of medium stature with emergent trees (including figs) and the
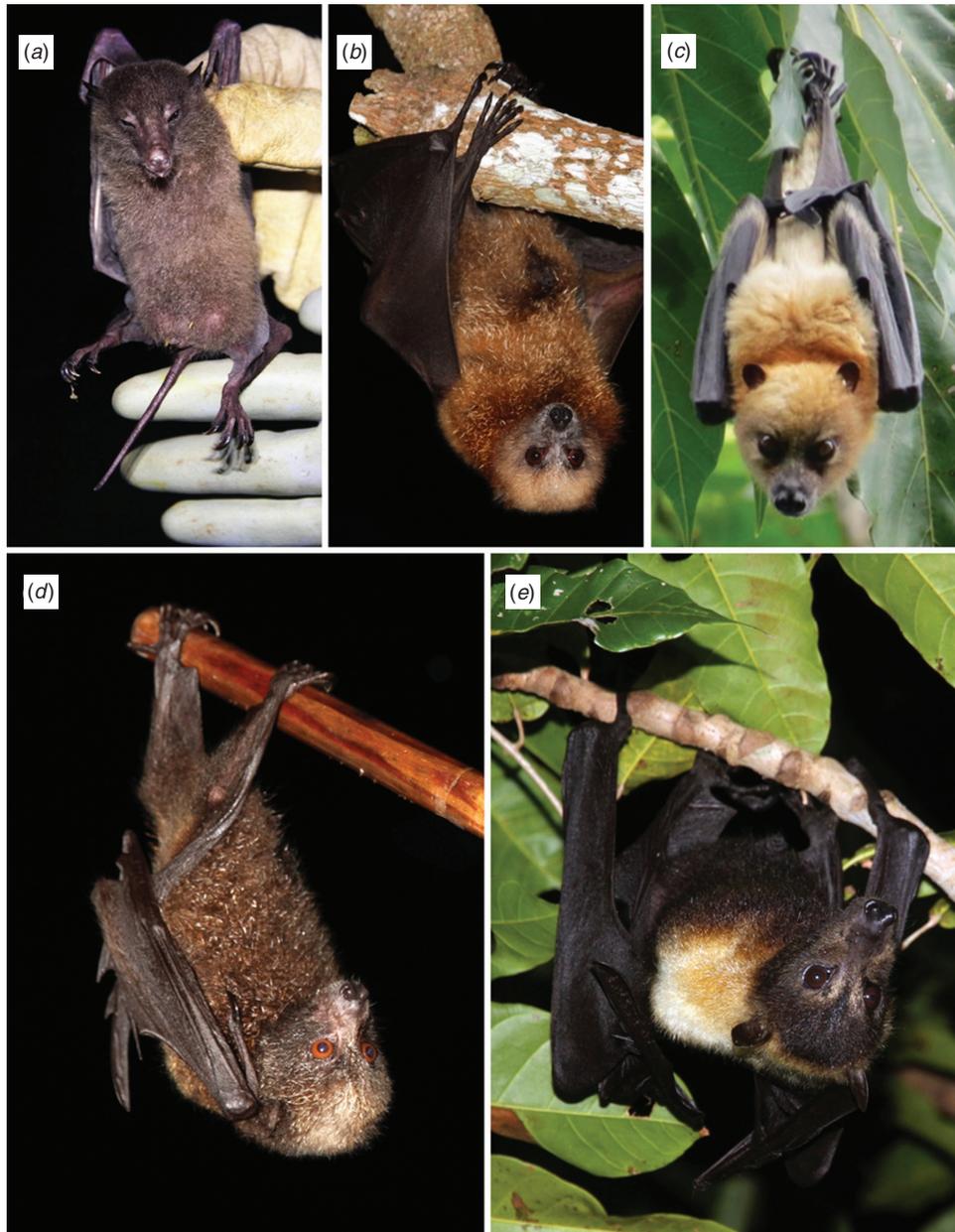
Fig. 1. (*a*) Fijian blossom bat (*Notopteris macdonaldi*), Mota (Photo: T. Lavery); (*b*) Banks flying-fox (*Pteropus fundatus*), Mota (Photo: T. Lavery); (*c*) Temotu flying-fox (*P. nitendiensis*), Nendö (Photo: R. Pierce); (*d*) Vanikoro flying-fox (*P. tuberculatus*), Vanikoro (Photo: T. Lavery); (*e*) Pacific flying-fox (*P. tonganus*), Mota (Photo: T. Lavery).

eastern side of Vanua Lava supports small areas of herbaceous and woody freshwater swamps (Müeller-Dombois and Fosberg 2013). Agroforestry gardens, small–scale agricultural plots and shifting subsistence garden plots are concentrated in the coastal lowlands and lower slopes. These islands are free from the widespread commercial logging present on Nendö and Vanikoro.

Mist net surveys

We surveyed bats using black 16 mm mesh, 12×2.5 m nylon mist nets (Ecotone Series 1000, Sopot, Poland) in 2018; and 38 mm mesh (12 or 18×2.7 m), or 31 mm mesh (9 or 6×2.7 m) (Australian Bird Study Association), in the 1990s and 2015. Nets were configured individually within the forest understory and subcanopy. We placed them on wooden poles up to 10 m from the ground or suspended on ropes up to 15 m above the ground spanning roads, or across natural forest or garden gaps, creeks or 'flyways' to maximise the number of species and individuals captured. Surveys commenced before dusk and finished at midnight or dawn. Survey effort was calculated as square metre mist net hours (net-m^2 h^{-1}), whereby one 12×2.5 m net deployed for 1 h gives an effort of 30 net-m^2 h^{-1}.

Table 1.   **Study island size, maximum elevation and survey dates**

Island Group	Island	Size (km^2)	Elevation (m)	Survey dates
Banks	Mota	10.9	411	8–12 May 2018
	Vanua Lava	350.3	946	4–6 May 2018
Santa Cruz	Nendö	543.8	549	27 September–5 October 1990
				3–10 October 1992
				6–13 October 1993
				23 October–26 November 1993
				18 September–1 October 2014
				12–18 and 26–29 September 2015
				26 April–2 May 2018
	Tinakula	8.3	851	8–12 October 2014
				30 September–2 October 2015
				28–30 August 2019
Reef	Fenualoa	4.8	17	7–9 September 1993
				18–22 October 1993
	Makalom	0.02	<3	1 September 2019
	Matema	0.2	~5	21–22 September 1993
	Ngalo	14.5	~21	10–15 September 1993
	Ngawa	5.8	~9	10–15 September 1993
	Nifiloli	0.4	19	16–20 September 1993
	Niupani	0.3	3	12–14 October 2017
	Nukapu	0.3	3	2 September 2019
	Pileni	0.2	3	30 August–1 September 2019
Vanikoro	Tevai	20.2	~450	23–28 September 2014
				20–25 September 2015
	Baine	184.6	924	20 and 23 September 2015
				27 April–2 May 2018

Transects and counts

We used diurnal (08:00–12:00 hours) and nocturnal (18:30–20:00 hours) walked line transects to estimate roosting and feeding densities of flying-foxes. Two to eight observers walked informal forest trails and vehicle roads and searched for flying-foxes in the lower canopy. In 2018 we recorded the sighting angle and radial distance of each flying-fox observed to allow densities to be estimated. Sighting angle was recorded using a sighting compass and radial distance using a laser rangefinder (Leupold RX-650, Beaverton, OR, Canada). Perpendicular distance from the transect was recorded for each individual observed using the sighting angle and radial distance. We assumed our surveys would have imperfect detection, i.e. targets on the transects were sighted with 100% probability, and the probability of missing targets was assumed to increase with distance away from our transect. We used the packages *Distance* version 0.9.6 (Miller 2016) and *Rdistance* version 2.2.1 (McDonald *et al.* 2018) in R version 3.3.2 (R Core Team 2016) to estimate flying-fox densities and generate effective strip widths (ESW). We pooled data across islands to generate detection functions, and estimated densities for individual species.

We counted stationary roosting camps of *P. tonganus* (Mota, Nendö, Reef and Vanikoro), or tallied individuals in five-minute intervals as they departed the roost at dusk (Nendö). One to six observers counted individuals using hand tally counters (Ktrio, Pearland, TX, USA). Where counts from multiple observers were available, we averaged these to estimate camp size and counting error.

Additional data on flying-fox food plants and roosting habits were recorded via informal discussions with local residents,

direct observations, or by identifying the remains of fruit adhering to animals. Plants were identified to species or genus level using Henderson and Hancock (1988) and Hancock and Henderson (1988), or in the 1990s also by Solomon Islands National Herbarium staff. Diameter at breast height (DBH) of roost trees was measured with a diameter tape (Richter, Speichersdorf, Germany) to the nearest mm in 1993 and for accessible trees in 2015. In other years (and for inaccessible trees) diameter was visually estimated to the nearest centimetre. In 1993 we also compared diameter of roost trees with the diameter (at breast height) of surrounding trees (>10 cm DBH) in randomly placed 10 × 10 m plots adjacent to the roost trees.

Results

Distributions and abundance

We recorded *P. nitendiensis* on Nendö and Tinakula (comprising a total land area of approximately 590 km^2). *Pteropus tuberculatus* was recorded on Tevai and Baine (total land area 204 km^2). Although not documented in this study, *P. tuberculatus* may also exist in low numbers on nearby Utupua Island (J. Gamou, pers. comm.). *Pteropus fundatus* was recorded on Mota but was not detected at our single survey site on Vanua Lava. We detected *N. macdonaldi* in large numbers on Vanua Lava and Mota. *Pteropus tonganus* was documented on all islands, and we did not detect *N. sanctacrucis* or *P. anetianus*.

Mist net captures

We achieved a total of 32253 net-m^2 h^{-1} across Mota, Nendö, Reef, Tinakula, Vanikoro and Vanua Lava Islands, and captured 97 individual bats from 5 species (Table 2). The
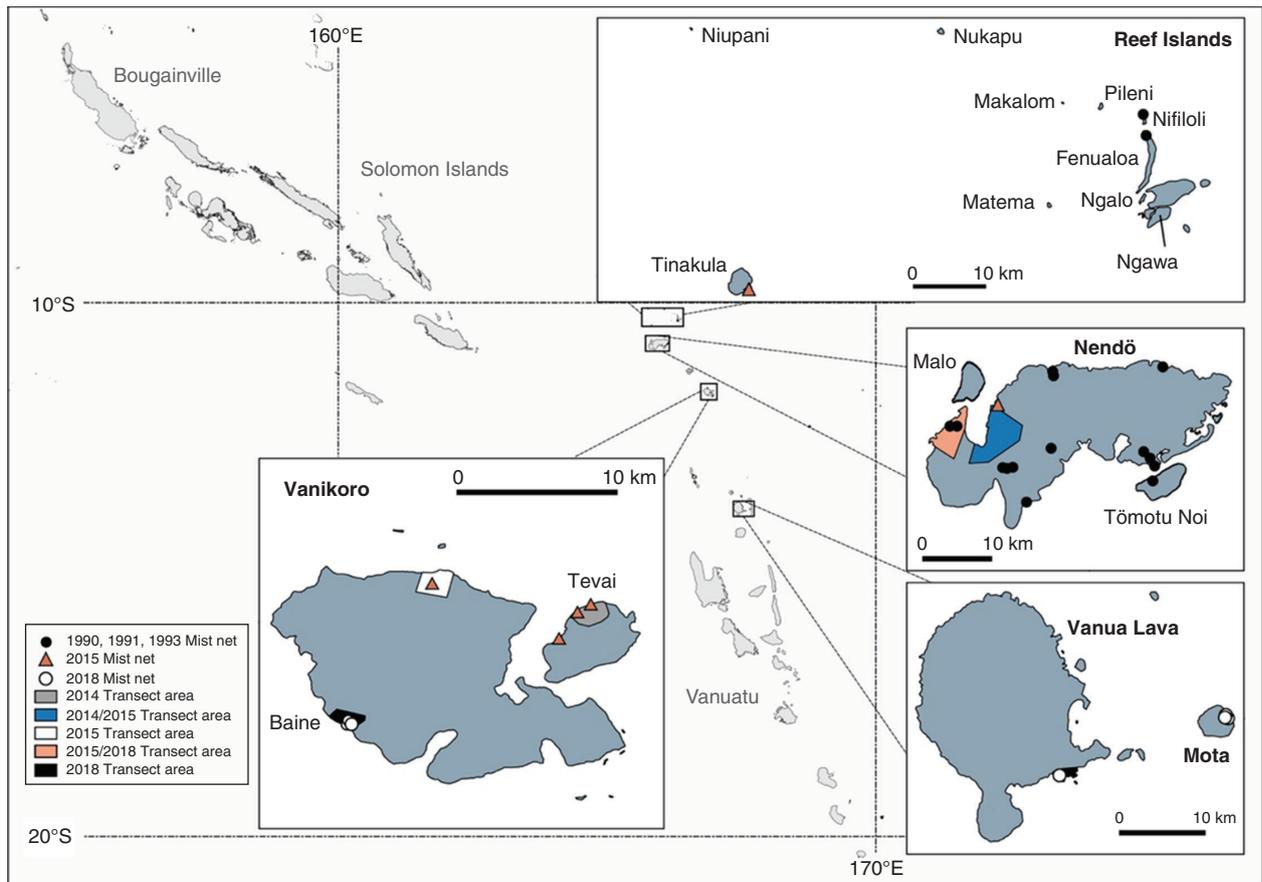
Fig. 2. Locations of Mota, Nendö, Reef, Tinakula, Vanikoro and Vanua Lava Islands, transect and mist net localities. Transects on Tinakula in 2014, 2015 and 2019 and Pileni and Nukapu in 2019 not shown due to scale of map.

Table 2. Capture rates of *Pteropus nitendiensis, P. tuberculatus, P. fundatus, P. tonganus* and *Notopteris macdonaldi* from Mota, Nendö, Reef, Tinakula, Vanikoro and Vanua Lava Islands

Island	Date	Mist net-m^2 h^{-1}	Species	Individuals	Capture rate (1000 net-m^2 h^{-1})
Mota	May 2018	2106	*N. macdonaldi*	28	13.3
			P. fundatus	4	1.9
			P. tonganus	8	3.8
Nendö	September–October 1990	7371	*P. nitendiensis*	1[A]	0.1
			P. tonganus	5	0.7
	October 1992	3758	*P. nitendiensis*	6	1.6
			P. tonganus	4	1.1
	October–November 1993	6415	*P. nitendiensis*	19	3.0
	September 2015	1652	*P. nitendiensis*	1	0.6
Reef	September 1993	3208	–	0	0
Tinakula	September 2015	1871	–	0	0
Vanikoro	September 2015	3451	–	0	0
	May 2018	1701	*P. tonganus*	1	0.6
			P. tuberculatus	7	4.1
Vanua Lava	May 2018	720	*N. macdonaldi*	14	18.1

[A]Three additional animals obtained from village hunters.

most commonly captured species was Fijian blossom bat (*N. macdonaldi*), the least commonly captured species was Banks flying-fox (*P. fundatus*).

Notopteris macdonaldi and *P. fundatus* were captured in subsistence gardens adjacent to areas of secondary forest and close to villages. *Pteropus tuberculatus* was captured in substance gardens and in mixed secondary forest and agroforest. Our highest capture rates of *P. nitendiensis* on Nendö were in primary lowland rainforest and subsistence gardens in 1992 and 1993 respectively, and we did not capture them in recently logged or plantation forests in 1990.

Transects

We walked a total of 101.7 km of transects in 2014 (52 km), 2015 (24.3 km), 2018 (12.5 km) and 2019 (12.9 km) across six study islands, and encountered a total of 272 individuals of three study species (Table 3). In 2014 and 2015, *P. nitendiensis* was encountered on Nendö and Tinakula at relatively similar rates on garden, secondary forest and primary forest transects (0.3–1.2 km^{-1}). In 2018, we encountered this species within gardens and secondary forests in the vicinity of Lata township at a much higher rate than in 2014 and 2015 (encounter rate 4.5 km^{-1}). In 2019, we encountered *P. nitendiensis* on Tinakula, 2 years after a volcanic eruption had coated the island in several centimetres of volcanic ash and defoliated most trees, nearly all of which had recovered. The highest encounter rate of *P. tuberculatus* in 2014 was in coconut plantations (7.2 km^{-1}), compared with 0.3 km^{-1} in primary forests. In 2018 we encountered *P. tuberculatus* on transects through gardens and secondary forests at a rate of 2.5 km^{-1}. We did not record this species on 2015 and 2018 transects through recently logged forest.

Overall, we encountered an average of 1.0 ± 1.5 (s.d.) *P. nitendiensis* per kilometre of transect and an average of 2.0 ± 3.1 *P. tuberculatus* per km of transect (Table 3). In nocturnal surveys on Vanikoro and Vanua Lava we encountered *P. tonganus* at a rate of 6.7 per km of transect compared with an encounter rate of 1.4 ± 1.5 during diurnal surveys of Vanikoro and Nendö. In diurnal surveys on Vanikoro, Tinakula and Nendö we recorded *P. tonganus* at a rate of 0.2–4.6 animals per km of transect. Using the perpendicular distances recorded on our 2018 transects we calculated effective strip widths of 16.9 m for diurnal surveys and 32.4 m for nocturnal surveys and estimated diurnal and nocturnal densities of flying-foxes (Table 3).

Camp counts

During 2015 and 2018, we counted the number of individuals in six *P. tonganus* camps on Nendö (two camps), Mota (three camps) and Vanikoro (one camp) (Table 4). On Nendö in 2018 we made counts of animals as they left the camp on dusk. Animals began to leave the roost at approximately 16:50 hours and we counted until 18:05 hours when it became too dark to reliably see bats. At this time, we estimated three-quarters of the camp had departed. The vast majority flew in a northwest to westerly direction towards the centre of the island. On Nendö in 2015 near the Luetopulelo River we made a daytime count of bats roosting on six trees in disturbed secondary rainforest.

On Mota, counts of the three camps were made during daytime when bats were roosting. All three camps were on large fig trees (*Ficus* spp.), isolated from forested areas. The camp at Mission Harbour was the largest of the three and was situated within a *tabu* area where access and hunting are prohibited. The camp at Lotawora Village was spread along the coastline and comprised three smaller groups each of 20–30 individuals. The camp in Lotawora garden was on a large, emergent fig tree situated in a matrix of secondary forest and garden plots.

On Vanikoro, counts were made during the daytime when bats were roosting in secondary forest within a matrix of agroforests and subsistence gardens. The camp was on three large (DBH range 60.4–176.8 cm) emergent trees. All bats roosted on the exposed upper canopy.

In 1993 we visited 18 camp locations known to local guides on the Reef Islands - Nifiloli Island (six camps), Fenualoa Island (eight camps), Ngalo Island (three camps), and Matema Island (one camp). Only 13 camps were occupied at the time (Table 4), and pregnant females or females with young were identified in three of these. The thirteen occupied camps were on between one and nine large remnant trees (primarily *Ficus* sp.). We compared the diameter of roost trees at six of the camp sites with the diameter of surrounding trees. Roost trees were of significantly greater diameter (mean 93.3 ± 48.2 cm (s.d.); DBH range 45.3–250 cm) than surrounding trees (mean 24.5 ± 8.3 cm; DBH range 10–42.8 cm) (two-sample *t*-test unequal variance assumed $t = 7.3711$; $P < 0.001$). All camps were located within 100 m of the shoreline, with the majority less than 20 m from the water in highly disturbed remnant littoral forest or lowland rainforest. The camps were not continually occupied between months, and counts differed between September and October 1993 for some locations. For example, one camp near Moloa'a Pt supported approximately 100 animals on 8 September 1993, but greater than 3500 individuals on 19 October 1993. Island residents advised us the mangroves between Ngalo and Ngawa islands (Manuopo Channel) and Ngatendo Island were important roost sites, but during our dinghy-based searches of these areas we only saw scattered individuals and small groups. We did not attempt to quantify numbers. Single camps were encountered on Niupani Island in 2017, and Pileni and Nukapu Islands in 2019. Each camp contained less than 20 individuals. Signs that *P. tonganus* had been gnawing on coconuts were found on the tiny, rapidly eroding Makalom Island in 2019 and Matema Island in 1993.

In November 1993 we visited nine reported *P. tonganus* camps on Nendö but only seven of these were occupied, four within mangroves and three in disturbed secondary rainforest (Table 4). Except for the largest mangrove island roost, *P. tonganus* were roosting on between three and five trees at each camp. On the mangrove island in Luemonda Bay *P. tonganus* were roosting on almost every tree. We measured the diameter of roost trees at five of these camps, three within mangroves and two within secondary rainforest. The diameter (DBH) of roost trees in mangrove camps were in significantly smaller (mean 44.7 ± 9.8 cm; range 32–65 cm) than the roost trees at non-mangrove sites (mean 88.2 ± 11.2 cm; range 70–100 cm) (two-sample *t*-test $t = -8.0837$; $P < 0.001$). The vegetation surrounding the three camps in the south-west of Nendö had been badly damaged by cyclone Nina in January 1993 and roost trees were the only large

Table 3. Walked density transects on Nendö, Nukapu, Pileni, Tinakula, Vanikoro and Vanua Lava Islands, total bats encountered, and density estimates derived from Distance Version 0.9.6

ESW, effective strip width

Island	Date	Transect type	Habitat	Total length of transects (km)	ESW(m)	Species	No.	Encounter rate/km	Estimated density/km² (±s.e.)
Nendö	Sept 2014	Diurnal	Primary and secondary forest	19.0	–	*P. nitendiensis*	16	0.8	–
						P. tonganus	4	0.2	–
			Gardens and secondary forest	6.0	–	*P. nitendiensis*	7	1.2	–
						P. tonganus	5	0.8	–
	Sept 2015	Diurnal	Primary and secondary forest	9.0	–	*P. nitendiensis*	6	0.7	–
						P. tonganus	40	4.4	–
			Gardens and secondary forest	6.0	–	*P. nitendiensis*	2	0.3	–
						P. tonganus	7	1.2	–
	May 2018	Diurnal	Gardens and secondary forest	7.1	16.9	*P. nitendiensis*	32	4.5	146.7 s.e. ±90.7
					–	*P. tonganus*	33	4.6	–
Nukapu	Sep 2019	Diurnal	Gardens and secondary forest	2.2	–	*P. tonganus*	15	6.8	–
Pileni	Aug–Sep 2019		Gardens and secondary forest	1	–	*P. tonganus*	4	4	–
Tinakula	Sept 2014	Diurnal	Gardens & secondary forest	10.0	–	*P. nitendiensis*	1	0.1	–
					–	*P. tonganus*	2	0.2	–
	Sept 2015	Diurnal	Primary and secondary forest	3.5	–	*P. nitendiensis*	1	0.3	–
					–	*P. tonganus*	4	1.1	–
	Aug 2019		Primary and secondary forest	9.7	–	*P. nitendiensis*	1	0.1	–
Vanikoro	Sept 2014	Diurnal	Primary forest	12.0	–	*P. tuberculatus*	4	0.3	–
					–	*P. tonganus*	3	0.3	–
			Coconut plantation	5.0	–	*P. tuberculatus*	36	7.2	–
					–	*P. tonganus*	18	3.6	–
	Sept 2015	Diurnal	Recently logged forest	5.8	–	*P. tuberculatus*	0	0	–
					–	*P. tonganus*	7	1.2	–
	May 2018	Diurnal	Recently logged forest	0.8	–	*P. tuberculatus*	0	0	–
		Diurnal	Gardens and secondary forest	1.6	16.9	*P. tuberculatus*	4	2.5	66.7 s.e. ±36.6
		Nocturnal	Gardens and secondary forest	0.7	32.4	*P. tonganus*	14	20.0	348.7 s.e. ±36.6
Vanua Lava	May 2018	Nocturnal	Gardens and secondary forest	2.3	32.4	*P. tonganus*	6	2.6	30.4 s.e. ±26.2

Table 4.   *Pteropus tonganus* camp counts on Nendö, Reef, Vanikoro and Mota Islands
Camp locations noted for 1993 surveys were derived from map grid references and are approximate only. Locations in other years were obtained using handheld GPS

Island	Site	Location (in decimal degrees)	Survey date	No. of individuals ± s.d. (no. of counts)
Nendö	Carlisle Bay Camp 1	−10.65512°, 166.05244°	2 November 1993	~100 (1)
	Carlisle Bay Camp 2	−10.65529°, 166.05472°	2 November 1993	~200 (1)
	Mangrove island Luemonda Bay.	−10.75932°, 166.01500°	4 November 1993	2784.5 ± 304.8 (2)
	Luemonda Bay	−10.75774°, 166.01784°	4 November 1993	~300 (1)
	Nambalue River	−10.83327°, 165.87616°	9 November 1993	188.5 ± 16.3 (2)
	Near Mala Village	−10.83374°, 165.87949°	9 November 1993	165.0 ± 49.5 (2)
	Near Monan Village	−10.83340°, 165.79909°	24 November 1993	~100 (1)
	Near Luetopulelo River	−10.72345°, 165.83441°	14 September 2015	192.5 ± 17.7 (2)
	Lata	−10.71506°, 165.79252°	26 April 2018	260.5 ± 45 (3)
Reef	Fenualoa Island – SE of Mola'a Pt	−10.20419°, 166.30109°	8 September 1993, 19 October 1993	~100 (1) 3628.5 ± 525.4 (2)
	Fenualoa Island – NE of Takwaiaro Village	−10.20781°, 166.30492°	8 September 1993	264.5 ± 14.9 (2)
	Fenualoa Island – NE of Takwaiaro Village	−10.20964°, 166.30599°	8 September 1993, 9 September 1993, 19 October 1993	~100 (1) ~120 (1) ~100 (1)
	Fenualoa Island – NE of Malapu Village	−10.21782°, 166.31093°	9 September 1993	13 (1)
	Fenualoa Island – E of Mbangala Village	−10.25810°, 166.30496°	9 September 1993	10 (1)
	Ngalo Island – W of Nyimoa Village	−10.26603°, 166.33068°	10 September 1993	35 (1)
	Ngalo Island – E of Ngana'a Village	−10.26399°, 166.35439°	13 September 1993	60 (1)
	Ngalo Island – N of Nganimbanea Village	−10.27103°, 166.36126°	13 September 1993	74.5 ± 36.1 (2)
	Nifololi Island (five northern camps)	−10.18191°, 166.29603°	8 September 1993	148 (1)
	Nifololi Island (southern camp)	−10.19219°, 166.30120°	19 September 1993	150 (1)
Vanikoro	Near Buma Village	−11.61622°, 166.96812°	24 September 2015	191 ± 9.9 (2)
Mota	Lotawora Village	−13.82989°, 167.69774°	9 May 2018	105 ± 10.6 (2)
	Lotawora Garden	−13.84594°, 167.69968°	11 May 2018	76.1 ± 7.2 (13)
	Mission Harbour	−13.83723°, 167.68309°	12 May 2018	602.8 ± 135.6 (5)

trees still standing. Five *P. nitendiensis* were observed roosting on the periphery of the *P. tonganus* Camp1 at Carlisle Bay on three separate understory trees.

Diet and behaviour

We documented diverse assemblages of plants that provide food in the form of fruits, flowers and nectar, or leaves for *P. nitendiensis* (44 species), *P. tonganus* (56 species) and *P. tuberculatus* (24 species). For *P. fundatus*, five food plants were identified (Supplementary Table S1).

Pteropus nitendiensis was frequently observed foraging during the daylight hours, with most individuals seen mid to late afternoon. Direct foraging observations of *P. nitendiensis* were: flowers/nectar of *Mucuna* sp., fan palm (*Licuala* sp.) and coconuts (*Cocos nucifera*); and fruits of nutmeg (*Horsfieldia spicata*), mango (*Mangifera indica*), breadfruit (*Artocarpus altilis*), Malay apple (*Syzygium malaccense*), and cutnut (*Barringtonia edulis*). During our 2015 surveys, an individual took a half-ripe fruit *Terminalia catappa* in its mouth and flew off into the forest. The single individual mist-netted at Neödun in 2015 had *Piper betle* seeds/fruit adhering to its belly and in its cheek pouches. In 2018 *P. nitendiensis* was regularly observed foraging in breadfruit trees in the early evenings. Animals would chew the fruit and eject a wad of fibrous material onto the ground.

We observed *P. nitendiensis* roosting in nine tree species: breadfruit (*Artocarpus altilis*) (8); rosewood (*Pterocarpus indicus*) (2); *alite* (*Terminalia catappa*) (1); wild mango

(*Mangifera* minor) (1); sandpaper fig (*Ficus wassa*) (2); white beech (*Gmelina* sp.) (2); *Ketekete* (*Campnosperma brevipetiolata*) (1); and two unidentified trees known in local language by the names *nola* (3) and *nonabutbir* (1). The mean DBH of eight roost trees measured in 2015 was 45.6 cm ± 22.3 (range 35–100 cm) and height ranged from 12 to 30 m. Six of eight trees had a DBH <40 cm. Animals primarily roosted in the lower-mid levels of the canopy (5–12 m above ground) in positions that offered overhead cover, and near the terminal ends of branches causing leaves to partially envelop them.

On our April 2018 transects, we regularly encountered pairs of roosting *P. nitendiensis*, and local guides suggested these were male and female mating pairs. By mimicking the species' vocalisations, guides were able to attract the bats, which flew in from the forest and circled low underneath the thick canopy, responding to the calls before returning to their roost (C. Posala, pers. obs.).

In 2014 and 2018 we observed *P. tuberculatus* foraging during daylight between 16:00 and 18:00 hours before *P. tonganus* became active. In September–October 2014, *P. tuberculatus* was most frequently encountered on transects conducted in coconut plantations where the species was seen feeding on coconuts and fan palm flowers and nectar. In April 2018, we frequently observed *P. tuberculatus* arriving at fruiting breadfruit trees prior to dusk.

Pteropus tuberculatus was primarily observed roosting singularly, and occasionally in pairs. Animals were observed

roosting on the lower–mid branches of subcanopy trees, approximately 10–12 m above the ground in primary forests and agroforests. Betel nut palms (*Areca catechu*), coconuts, and breadfruit were common in these areas. Roost trees observed were breadfruit, coconut, mango, mangroves (*Rhizophora apiculata*), and teak (*Tectona grandis*). All sites provided good overhead cover, but the animals often clung to relatively bare branches. The estimated DBH of roost trees ranged between 40 and 50 cm. *Pteropus tuberculatus* appeared to avoid interactions with *P. tonganus* and repeatedly left their roosts or feeding trees when this larger flying-fox came within close proximity.

On Mota, residents indicated the roosts of *P. fundatus* are located beneath the dead fronds of *Pandanus* trees along the steep coastal hillsides. We searched for roosts in *Pandanus* trees along a section of coastline adjacent to Lotawora Village in May 2018 but were unable to verify these reports. Coconut and *Pandanus* flowers were identified as important food sources by Lotawora Village residents who also reported that *P. fundatus* commonly visits village subsistence gardens at night.

On all islands, people identified *P. tonganus* as the primary hunting target rather than *P. anetianus*, or small range endemics (*P. fundatus*, *P. nitendiensis* and *P. tuberculatus*). On Vanikoro, *P. tuberculatus* is not hunted for food as it reportedly has an unpleasant taste and/or it is too small for eating. However, the species is occasionally killed to prevent damage to coconuts and other garden fruits, and younger men occasionally hunt them for sport or leisure.

Discussion

This study has provided a much-needed update on the distributions of flying-foxes in Torba Province, Vanuatu and Temotu Province, Solomon Islands. Over a 29-year period between 1990 and 2019 we have accumulated important ecological, abundance, dietary, and behavioural data for some of the world's most data-deficient flying-foxes.

Despite over 24000 mist net-m^2 h^{-1} across Nendö, Tinakula and Reef Islands we failed to detect *N. sanctacrucis.* Species of *Nyctimene* are usually easy to detect with mist-nets set in a range of habitats including primary and secondary forests and subsistence gardens, or adjacent to flowering trees and shrubs. We specifically targeted the range of suitable habitats for this species and expect *N. sanctacrucis* would have been encountered if indeed present on the study islands. We conclude the taxon must be extinct in Temotu Province. Moreover, whereas *N. sanctacrucis* has generally been viewed as a distinct species, it may in fact be better regarded as a subspecies or synonym of *N. major* (Burgin 2019).

The distribution of *P. nitendiensis* has been confirmed as including Nendö and Tinakula Islands. The distribution of *P. tuberculatus* includes Baine and Tevai (Vanikoro), and reports that it may also exist on Utupua Island should be further investigated. We found both species to be relatively abundant in surveys conducted in 2014 and 2018. Flannery (1995) noted how unusual it is that *P. anetianus, P. fundatus* and *P. tonganus* coexist on small islands such as Mota, when remaining islands in Vanuatu (and Temotu Province) support only two sympatric species. We suspect the distributions of *P. anetianus* and *P. fundatus* in the Banks Islands may in fact

be more complex than currently perceived. A cursory review of museum databases suggests the two species have not been recorded in sympatry on Mota. Australian Museum expeditions did not record *P. fundatus* outside of Mota in the early 1990s (P. German, pers. comm.). We did not record *P. anetianus* on Mota and we did not encounter *P. fundatus* or *P. anetianus* on Vanua Lava.

There are three possible explanations for discrepancies in species distributions in the Banks Islands. First, our 2018 surveys were brief and limited to single sites on Mota and Vanua Lava and thus survey effort may not have been sufficient to detect all species. Second, contractions or shifts in species distributions could have occurred since the collections made by H. Bregulla in 1963 (Felten and Kock 1972) in response to vegetation changes, shifting land uses, or increased hunting pressure. Third, errors in specimen collecting localities could have arisen due to similarities in the names of some of the Banks Islands (i.e. Mota vs Mota Lava vs Vanua Lava). Additional surveys in the Banks islands (Gaua, Mota, Mota Lava, Ureparapara and Vanua Lava) and a detailed review of existing museum specimens should be priorities for all species, but especially to provide confident resolution of the distribution and conservation status of *P. fundatus*.

The encounter rates we derived across all species and sites ranged between 0.4 and 20.0 km^{-1}, and density estimates were between 30.4 and 348.7 individuals km^{-2}. A number of Asia-Pacific *Pteropus* studies have reported abundance estimates that fall within these ranges. On Iriomotejima, Japan, Lee *et al.* (2009) encountered Ryuku flying-fox (*P. dasymallus*) at a rate of 2.5 ± 0.6 per km of transect. On Ulithi Atoll, Caroline Islands Wiles *et al.* (1991) calculated a minimum average density for *P. mariannus* of 210 bats km^{-2} and on Sarigan, Mariana Islands, Wiles and Johnson (2008) estimated densities of 25–47 bats km^{-2} for the same species. In comparison, counts of camp dispersal columns by Brooke and Tschapka (2002) provided population estimates of *P. tonganus* on Niue equivalent to 11.2–22.4 animals per km^2 of forested habitat, that were below the range of density estimates obtained in this study. Engbring (2007) estimated densities of *P. samoensis* at 1.5–19.5 animals km^{-2} on four Samoan islands and Brooke (2001) reported 6.1 individuals km^{-2} (range = 0.9–18.5 km^{-2}) on Tutuila, American Samoa. However, these Samoan estimates were generated using an alternate method of counting bats from a fixed vantage point as they flew over areas of land of known size. This technique can lead to underestimates of bat density, rendering comparisons with estimates from walked transects problematic.

All our transects were conducted at low elevation in coastal areas surrounding villages where cultivated fruiting trees that attract flying-foxes were common. Our encounter rates and density estimates are thus unlikely to be representative of the range of habitats found on our study islands that include large areas of more remote primary and secondary forests, with elevations up to a maximum of 946 metres on Vanua Lava. In order to obtain robust population estimates across these species range, expansion of transects to encompass a wider range of habitat types and elevations is needed.

Coconut and pandanus flowers were identified as important food sources for *P. fundatus* and Flannery (1995) relayed that one specimen collected in 1992 "was shot at 8:50 pm while it fed

on *Vaveli* [*sic – naveli, Barringtonia edulis*], which was then in flower". This apparently nectarivorous diet is consistent with inferences made from the reduced dentition of *P. fundatus* (Flannery 1995). *Pteropus nitendiensis*, *P. tonganus* and *P. tuberculatus* were found to consume the fruit and nectar from broad assemblages of plants. Of the food plants identified for these species, 56–67% were targeted for fruit, and 30–41% were targeted for their flowers/nectar. In September–October 2014, *P. tuberculatus* was most frequently recorded on transects through coconut plantations on Tevai, but during September 2015, no animals were seen in this habitat type. In 2018 breadfruit was in season and *P. tuberculatus* was observed daily in late afternoons visiting the fruiting trees around the village.

Temporal shifts in diet and foraging range in response to food availability are common amongst island flying-foxes (Banack and Grant 2002; Tidemann and Nelson 2004; Epstein *et al.* 2009). Dietary studies of *P. samoensis* and *P. tonganus* in Samoa found that although animals consumed the fruits and flowers of 78 species, they were not generalists but sequential specialists, preferring resources produced by plants in primary forests rather than those in agroforest or secondary forests (Banack 1998).

A change in the use of coconuts between 2014 and 2015 could reflect variation in flower abundance, as production can vary between months and years in response to climatic variables (Ranasinghe *et al.* 2015). Alternately, cultivated plants may simply provide secondary resources that increase in importance when preferred resources are unavailable. In Samoa, agroforest plants became diet staples for flying-foxes during periods when primary forest resources were restricted (Banack 1998). Shifts in foraging sites used by flying-foxes with food availability have been frequently documented (e.g. Tidemann and Nelson 2004).

A fascinating observation made in this study was that *P. nitendiensis* may be socially monogamous, roosting in male and female pairs. Imitations of the vocal calls seemed to elicit a territorial response where the animals flew in from their roosts to investigate. This behaviour was apparently seasonal, being observed in April–May of 2018 but not in September–October 2014 or 2015. Monogamy is rare among mammals (approximately 5%) and the proportion of monogamous species among bats is similarly low at 3% (McCracken and Wilkinson 2000; Lukas and Clutton-Brock 2012). However, one of the few known examples (*P. samoensis*) both roosts and forages in pairs and coincidently belongs to the same species group as *P. nitendiensis* (Cox 1983; Pierson and Rainey 1992; Almeida *et al.* 2014). There are several hypothesis for the evolution of monogamy including the need for biparental care to raise off-spring, and an inability for males to monopolise multiple females because of their sparse distribution (Komers and Brotherton 1997). However, Komers and Brotherton (1997) instead showed that the most common trait among monomogmous mammals was the occurrence of females that are solitary and occupy small and exclusive ranges, enabling them to be monopolised by males.

Vanikoro residents indicated that the meat of *P. tuberculatus* is unpleasant to eat and few people reported hunting the species. Given this, a smaller body size and sympatry with the larger *P. tonganus*, hunting is unlikely to pose the significant level of threat that is common to island endemic *Pteropus* globally (Vincenot *et al.* 2017). In fact, our informal discussions about flying-fox hunting practices indicated *P. tonganus* was the preferred target on all islands. We are unable to infer anything about the current sustainability of hunting regimes or population trends of *P. tonganus*, but our data will hopefully serve as a useful reference for future research in this region. *Pteropus tonganus* is extremely important to the functioning of island ecosystems and should be an important component of any future studies focussed on the small range endemics (Cox *et al.* 1992). For example, even small population declines in this species have been shown to result in major shifts in ecological functions important for island ecosystems, with the potential for flow on effects for sympatric *Pteropus* (McConkey and Drake 2006).

Pteropus fundatus, P. nitendiensis and *P. tuberculatus* are all exposed to considerable extinction risk purely as a result of their tiny distributions and exposure to stochastic events such as cyclones. This is likely to be further exacerbated by habitat disturbance and climate change. Both Nendö and Vanikoro are subject to extensive, ongoing commercial logging and the lowlands of Mota have been extensively cleared and converted to subsistence gardens or commercial crops (Global Witness 2018). In 2018 we encountered *P. tuberculatus* in small pockets of intact forest close to recently logged areas, but the species appeared to be absent in forests logged in 2015 and 2018. In the Western Province of Solomon Islands, commercial logging over an extended period was shown to impact only small-range endemics bats, because of their specialised ecology and small distributions (Lavery *et al.* 2020). Thus, logging and other forms of habitat disturbance on our study islands will potentially have the greatest impact on threatened endemics. Additional monitoring of population trends, raising local awareness of endemism, and collaborative conservation efforts led by communities, will be important next steps in ensuring long-term survival of these unique flying-foxes.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

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