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Variation in the nocturnal foraging distribution of and resource use by endangered Ryukyu flying foxes *(Pteropus dasymallus)* on Iriomotejima Island, Japan

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Abstract

The nocturnal distribution and resource use by Ryukyu flying foxes was studied along 28 transects, covering five types of habitats, on Iriomote Island, Japan, from early June to late September, 2005. Bats were mostly encountered solitarily (66.8%) or in pairs (16.8%), with a mean linear density of 2.5 ± 0.6 bats/km of transect/night. Across the island, however, bat densities were distributed non-randomly among transect-nights, not correlated with transect length, and showed a slightly clumped distribution (variance/mean = 3.3). Outskirt trails contributed higher values to the relative importance of bat abundance, but the highest mean abundances occurred mostly at village sites on the west coast, which on average devoted only a quarter of their land area to agriculture/husbandry compared to those on the east coast. This supports our prediction that higher bat abundances are found in areas with less anthropogenic interference and more forest. Among habitats, the mean total abundance and density were lower in cultivated areas than in villages and inland forests. Bat perches in cultivated areas were also lower, and were in correspondence with lower shrub and canopy heights, and less canopy coverage. Flying fox abundance was correlated moderately with the heterogeneity of the tree composition, and strongly with the density of major fruiting trees. Thirty-nine species of plants and some animal items were used by Ryukyu flying foxes, including at least 31 species of fruits, 13 species of flowers, and leaves of seven species, with 14 species new to the record. *Ficus septica* and *F. variegata* were the most frequently encountered and dominant items in both fecal and rejecta/dropped samples, followed mostly by other figs and mulberries in the former, but by larger-seed non-Moraceae plants in dropped samples. Our results suggest that for conservation of flying foxes undisturbed forests providing an adequate resource basis are of major importance.

Contents

Introduction

Mutual relationships between plant-eating animals and their food plants, where animals may play a role as seed dispersers, pollinators, or both, represent one of the key ecological interactions (Howe and Westley, 1988). This is supported by phytophagous bats in the Neotropics (*e.g.*, Galindo-Gonzalez, 2000) as well as in the Old World tropics (Marshall, 1983; Hodgkison *et al.*, 2003). They are recognized as essential keystone species for maintaining ecological integrity in some areas, and are also beneficial for the human economy (Fujita and Tuttle, 1991; Wiles and Fujita, 1992; Shilton *et al*., 1999; Nyhagen *et al*., 2005). On the other hand, many species in this category and their delicate ecological attributes have been under threat to different degrees and warrant conservation attention (Racey and Entwistle, 2003), notably Old World pteropodid fruit bats (Cox *et al*., 1991; Rainey *et al*., 1995; Thiriet, 2005; Welbergen *et al*., 2008).

The Ryukyu flying fox (*Pteropus dasymallus* Temminck, 1825), together with the Bonin flying fox (*P. pselaphon* Lay, 1829) on Ogasawara Islands, and the Japanese flying fox (*P. loochoensis* Gray, 1870) of Okinawa, are the most northerly distributed pteropodids on the Pacific islands (Mickleburgh *et al*., 1992). Ryukyu flying foxes have the widest latitudinal distribution of these species, ranging along the West Pacific island chain from southern Japan south to Batan and other northern Philippine islets (Heaney *et al*., 2008), and five subspecies are recognized. These include (1) Erabu fruit bats *P. d. dasymallus* on Kuchinoerabu and most of the Tokara Islands; (2) Orii's fruit bats *P. d. inopinatus* on Okinawa; (3) Daito fruit bats *P. d. daitoensis* on Kita-daito and Minami-daito; (4) Yaeyama fruit bats *P. d. yayeyamae* on Tarama of the Miyako Islands and most of the Yaeyama Islands; and (5) Formosan fruit bats *P. d. formosus* occurring on Lutao (Green Island), Taiwan (Yoshiyuki, 1989; Ota, 1992).

All five subspecies had been classified as endangered, mainly due to limited distribution and threats of deforestation and hunting (Ota, 1992; see the current status for the species level as "Near Threatened"; IUCN, 2008). Some information is available for a few colonies of the three northern subspecies (Erabu, Daito, and Orii's fruit bats) at limited sites (*e.g*., Funakoshi *et al*., 1993, 2006; Izawa *et al*., 2001; Nakamoto *et al*., 2007a). Yet, little is known about the two southern subspecies, except for some anecdotal or sporadic notes (Lin and Pei, 1999; Nakamoto *et al*., 2007b). The paucity of critical data on their distribution, abundance, and ecological needs has spurred an urgent call recommending a top priority for assessing the southern-most islands off the main islands of Japan and in Taiwan (Mickleburgh *et al*., 1992).

Previous studies on Ryukyu flying foxes have been concentrated either in few adjacent village sites (Funa-

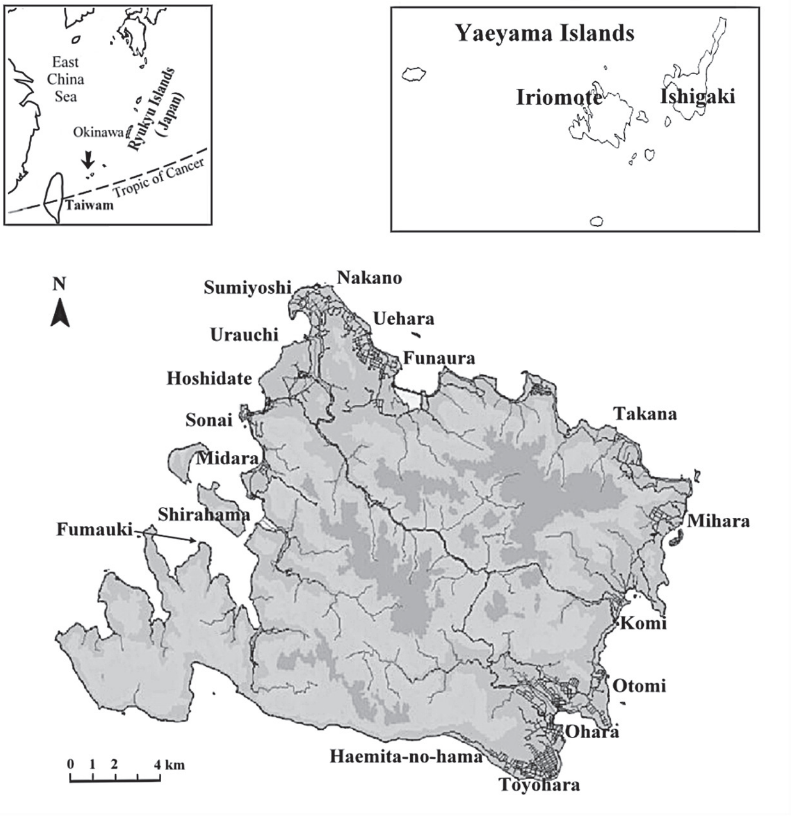

Fig. 1. Study site map showing Iriomote and the census sites, Ryukyu Islands of Japan in the left panel, and the Yaeyama Islands indicated by the arrow in the left panel, and enlarged in the right panel.

koshi *et al*. 1991, 1993), in an urban area (Nakamoto *et al*., 2007a), or focused on few bats on a small islet (Funakoshi *et al*., 2006). Flying foxes, however, can use various habitats with different degrees of dependence (*e.g*., Brooke *et al*., 2000; Vardon *et al*., 2001; Banack, 2002). Our study reports the first attempt to investigate the nocturnal distribution, relative abundance, and resource use by the least-studied Yaeyama subspecies on one of the largest inhabited islands. We tested the hypothesis that habitat modification and food availability will affect bat foraging, and predicted that bats will be less abundant in more-populated and anthropogenically modified areas where they potentially would experience greater disturbance (Wiles *et al*., 1989; but see work in Australia suggesting the opposite, Parris and Hazell, 2005; Williams *et al*., 2006). Flying foxes may travel distances up to 50 km for foraging (*e.g*., Marshall, 1985; Banack, 2002; Marcus and Hall, 2004); the availability of fruiting plants appears to be a key factor affecting their abundances and movements (Eby, 1991; McConkey and Drake, 2007). Hence we examined diets and food resource use of Yaeyama fruit bats, and predicted that the nocturnal dispersion and foraging of fruit bats should be positively correlated to the density of their major food plants.

Materials and methods

Study sites

Iriomote (24°15’-25’N, 123°40’-55’E; an area of 289 km^2, the highest elevation at 470 m above sea level) is the largest among the nine islets of the Yaeyama Islands, at the southernmost tip of the Ryukyu Islands, Japan (Fig. 1).

Together with nearby islands (*e.g*., Ishigaki and Taiwan), they are central to the northern West Pacific island arc, between the rest of the Ryukyu Islands and the main islands of Japan to the north, the East China Sea to the west, and the Philippines to the south. Hot-humid summers and warm winters typify Iriomote (Japan Meteorological Agency data), with a mean annual rainfall exceeding 2300 mm, and a mean temperature of c. 23°C from April to October, peaking at c. 29°C in July but descending to 17-18°C in January. Over 80% of this mountainous inland is covered by intact primary or secondary subtropical broadleaf forests (Schmidt *et al*., 2003), and is dominated by *Quercus miyagii* Koidz., Chinquapins *Castanopsis sieboldii* (Makino) Hatus., figs (*Ficus* spp.), and *Schima wallichii* (Schima). Lowlands below 100 m are distributed along the 130 km or so of shoreline and around a few major rivers, where human settlements and cultivated areas are located; these are more prominent on the eastern and northern coasts. *Hernanadia nymphaeifolia* (Presl) Kubitzki and horsetail pines *Casuarina equisetifolia* L. are common in coastal forests, but mangroves of *Bruguiera gymnorrhiza* (L.) Lam, *Rhizophora mucronata*, and *R. stylosa* prevail along estuaries and rivers. Figs (*e.g*., *F. superba* Miq. and *F. virgata* Reinw. ex Blume) are interspersed with *Cerbera manghas* L., *Heritiera littoralis* Dryand, hanging-flower checkerboard foot *Barringtonia racemosa* (L.) Blume *ex* DC, and screwpines *Pandanus odoratissimus* L. f. in swampy wetland forests (Walker, 1976).

Bat and habitat census

From early June to late September 2005, we conducted 48 nocturnal censuses along 28 transects at 14 sites (1-3 transects/census; Fig. 1). Each transect was assessed at least four times. Seven sites were located in the eastern and the other seven in the western half of the island, except the southwestern-most corner, Funauki, due to its inaccessibility by land. Site-to-site distances were c. 2 km in the west, and c. 3-4 km in the east. Sites covered five major types of habitats over most lowlands and ranged up to 5 km from the coast into inland areas, where fruit bats are known to fly for nightly foraging (M. Matsumoto, pers. comm.). Each site had two transects separated by 200 m or farther, and the length of each transect varied depending on accessibility (mean, 1.24 ± 0.19 km/transect; 34.79 km in total).

At each site, one transect circled around or penetrated a village, running through residential and cultivated areas, whereas the other meandered along the outskirts and toward more inland areas, representing natural habitats and some smaller fields. Between censuses we alternated sites in the west and east and randomly picked transects until the entire transect set was completed in a period of 2-3 weeks. We also alternated the nightly sequence among transects, so that each transects got surveyed at different times of the night. We arrived at a site 30 min before sunset to observe arrivals or passing of bats until sunset. A census began within 30 min after sunset and ended when all designated transects had been surveyed for the night, usually within 4 h. We walked each transect at roughly an equal pace of about 1 km/h, and travelled by vehicle between transects.

Bats were searched for with binoculars (Leica 10 × 42 BN, Solms, Germany), aided with spotlights or headlights, and by listening to their sounds while feeding or interacting with each other. Upon each encounter, we tallied the number of bats present, and recorded the species of plants on which a bat perched, the perch height, and the distance from the transect (DFT). We measured vegetation-related habitat variables on site or later in the daytime, including height variables, i.e., top (TCH) and bottom (BCH) heights of tree canopy, shrub height (SH), herb height (HH), and coverage variables, i.e., canopy coverage (CC) and ground coverage (GC). Types of behaviors displayed, such as flying, non-flying moves, and feeding, were recorded, and the food eaten determined. We restricted our searches to a strip of 30 m on either side and assumed a complete census. Our prior tests indicated that this is a suitable distance in most habitats, but in inner forests we acknowledge that our observations were more limited.

Feeding traces and dietary analysis

Flying foxes can swallow small seeds of fruits, but often spit larger seeds and fibrous wads (Richards, 1990), thus we searched for feeding traces by bats, including feces, rejecta pellets, and dropped fruit remains or vegetative parts (Thomas, 1989; Banack, 1998), along the surveyed transect lines during daylight hours. Throughout the study period we surveyed each transect at least four times, amounting to c. 150 working hours. Traces were clumped or also widely scattered along transects, presumably due to aggregation, feeding roost spots, or flying of bats. Any two adjacent feces or pellets of a similar freshness and within a distance of 5 m were treated as if they were from the same site location. Dropped fruits were recorded on site, but each retrievable fecal item or pellet was collected, sun-dried, and then stored in a single labelled envelope for later analysis. Along transect lines we further investigated the tree composition and abundances of fruiting trees at each of those sites. The heterogeneity of the tree composition and the density of major fruiting trees were estimated.

We identified seeds in fecal/pellet samples to the lowest taxonomic level possible, mostly to species, and counted seed numbers, whereas animal items were sorted and identified to order, under a dissecting microscope (Zeiss Stemi 2000-C, 10 × 5 magnification, Oberkochen, Germany). The dry mass of each species of seed and each animal item in each sample was measured to the nearest 0.01 g with an electronic balance (Precisa XS3250C, Dietikon, Switzerland). We determined the relative frequency of occurrence (FO) and proportion of mass (PM) of each food item in fecal/pellet samples. We calculated the FO as the number of samples in which a particular food item was identified divided by the sum of the numbers of samples containing each food item that was identified. This provides a standardized measure, ranging from 0% to 100%, of the commonness of each food item in the diet. We averaged the PM of a food item across all samples to provide an index of the proportional contribution in mass of each food item to the diets of bats.

Data analyses

Data are presented as the mean ± standard error (SE). We arcsine-transformed data on proportions to meet the normality requirement (Zar, 1999). The statistical significance level α was set to $P < 0.05$, using Statistica 6.0 (StatSoft, 2001). A χ^2 test was used to determine if the frequency distribution was random among abundance levels. For each site, a relative importance value was estimated by incorporating the FO and relative abundance (RA) of bats (Lee *et al*., 2007). We assessed the correlation (Pearson's R) between FO and RA of bats, FO with the mean bat linear density (per km of transect) for both habitat type and among census nights, and the mean linear density with tree heterogeneity and density of major fruit plants. We performed multiple regression analysis to examine the relationship of bat density with canopy variables and coverage variables among habitat types. During our study, three typhoons formed and passed through or close to Iriomote, including strong typhoons 0505 Haitang (with winds at 198 km/h at its center) and 0513 Talim (190.8 km/h at its center), which coincided with our census periods of every 2-3 weeks. We used analysis of variance (ANOVA) to examine the difference in mean bat linear density among the four periods, divided by typhoons. Multiple analysis of variance (MANOVA) was used to examine the effects of site location and habitat types on variances in total bat abundances, mean density, perching height, and distance to the transect. We adopted MANOVA to examine location differences (west vs. east) in the mean human population size, number of residences, village area, population/ha of village area, and residences/ha of village area (Ministry of Internal Affairs and Communications Statistics Bureau data; N. Nakanishi, aerial-photo data). When significant differences emerged, we used additional multiple-range comparisons (Fisher's PLSD) to locate the differences. A *t*-test was applied to compare the area devoted to cultivation between eastern and western parts of the island. We also used the converted Simpson index to assess the heterogeneity of fruit trees. A higher index value indicates a more-diverse tree composition with a more-even proportional distribution (Krebs, 1999).

Results

Spatio-temporal variation in nocturnal distributions and relative abundances

We recorded 650 bats (2.2 ± 0.18; range, 1-20) in 298 encounters during 120 transect-nights of field censuses. A single bat was observed in 66.8% of encounters, followed by pairs of bats (16.8%), and in only 3% of cases were bats detected in groups larger than 10 ($\chi^2 = 426.5$, d.f. = 4, $P < 0.001$). On average, we had 6.2 ± 0.53 (range, 0-14) encounters of 13.4 ± 1.43 bats (range, 0-43) per night; or 2.7 ± 0.24 encounters (range, 0-12) and 5.5 ± 0.57 bats (range, 0-32) per transect night, at an overall encounter probability of 75%. Mostly, we recorded five or fewer (72.5%), and rarely over ten (9.2%), bats per km of transect. Bat abundances were not randomly distributed among transect nights ($\chi^2 = 75.75$, d.f. = 4, $P < 0.001$) and were not correlated with the length of the transect ($r = 0.135$, $F_{1,\,26} = 0.35$, $P < 0.6$). After incorporating the length of each transect, our data translated into a mean linear density of 2.5 ± 0.6 bats/km of transect/night, with a ratio of the variance to the mean of 3.3 ($\chi^2 = 89.3$, d.f. = 27, $P < 0.001$).

Mean density of bats were similar among the 4 periods (2.3 ± 0.66, 2.0 ± 0.54, 2.9 ± 0.76, and 2.3 ± 0.73 bats/km of transect/night) interrupted by three typhoons ($F_{3,\,116} = 0.16$, $P > 0.5$). Among transects, the outskirt trails of Shirahama, Otomi, Midara, and Komi contributed the index values of highest relative importance, followed by Hoshidate Village and Toyohara trail. Each one led in either of the frequency of occurrence, the total relative abundance, or both, and together they accounted for over 54% of the RI value (Table 1).

These two measures were correlated to each other ($R = 0.795$, $F_{1,26} = 44.65$, $P < 0.001$). The highest mean linear density, however, occurred mostly at villages, i.e., Hoshidate, Mihara, Shirahama, Sonai, and Urauchi-Sumiyoshi (Table 1). All villages with higher bat densities, except Mihara, are located on the west coast (W), whereas five villages and three outskirt

Table 1. Relative frequency of occurrence, abundance, importance value, and mean linear density (± SE) per kilometer of transect, of flying foxes at different sites on Iriomote.

Site/Transect§	FO/RA	RI (%)	Mean density (bats/km)	Habitat‡
^{w}Shirahama^{1}	3.96/7.74	5.85	6.89 ± 3.11	v
^{w}Shirahama^{2}	13.65/11.98	12.81	5.45 ± 1.19	i, c
^{w}Midara^{1}	0.44/0.25	0.34	1.25 ± 1.25	u
^{w}Midara^{2}	9.68/7.49	8.59	3.19 ± 0.61	i, c, u
^{w}Sonai^{1}	3.05/6.52	4.79	5.94 ± 1.28	v, c
^{w}Sonai^{2}	2.86/2.50	2.68	1.35 ± 0.78	i, c, u
^{w}Hoshidate^{1}	3.12/13.29	8.20	11.83 ± 2.41	v, c
^{w}Hoshidate^{2}	4.58/2.80	3.69	2.15 ± 1.01	i, m, u
^{w}Urauchi-Sumiyoshi^{1}	4.23/4.39	4.31	5.03 ± 1.68	v, c
^{w}Urauchi-Sumiyoshi^{2}	2.47/1.60	2.03	0.80 ± 0.41	c, u
^{w}Nakano-Uehara^{1}	0.35/0.20	0.28	0.32 ± 0.32	v
^{w}Nakano-Uehara^{2}	5.58/3.99	4.79	2.86 ± 1.09	i, u
^{w}Funaura^{2}	6.69/5.79	6.24	1.33 ± 0.47	i, c, m, u
^{e}Mihara^{1}	4.58/4.39	4.49	7.10 ± 3.13	v
^{e}Mihara^{2}	3.87/3.20	3.54	1.42 ± 0.59	i, m, u
^{e}Komi^{1}	2.47/1.40	1.93	2.80 ± 1.50	v
^{e}Komi^{2}	8.45/8.19	8.32	3.95 ± 1.62	i, c, m, u
^{e}Otomi^{1}	1.06/0.80	0.93	1.29 ± 0.88	v
^{e}Otomi^{2}	11.01/8.24	9.62	3.93 ± 1.50	i, u
^{e}Haemita-no-hama^{2}	7.92/5.24	6.58	1.71 ± 0.64	c, u

§w: west, e: east; 1: villages, 2: outskirts; eight sites with zero values, i.e., Funaura^{1}, Takana$^{1,\,2}$, Ohara$^{1,\,2}$, and Toyohara, were unlisted. ‡v: village; i: inland forest; c: coastal forest; m: mangrove; u: cultivated land trails contributed no bat records, seven of which are along the east coast (E). Villages in the east and west did not differ in mean area (ha; E, 12.8 ± 3.3; W, 10.2 ± 0.9), number of residences (E, 78.2 ± 25.2; W, 87.6 ± 10.6), population size (E, 157.5 ± 51.5; W, 163 ± 20.7), population/ha of village land (E, 17.1 ± 3.3; W, 16.4 ± 2.1), or residences/ha of village land (E, 8.8 ± 2.0; W, 8.8 ± 1.1; MANOVA: Wilks' $\lambda = 0.353$, $F_{5,7} = 2.57$, $P = 0.125$). Each village in the east, however, had over a four-fold larger surrounding land area (82.93 ± 19.8 ha) used for agriculture or husbandry activities than in the west (20.21 ± 5.03 ha; $t = 3.07$, d.f. = 10, $P < 0.05$). Sites in the west also had higher fruit-tree density (47.14 ± 11.13/ha; $t = 2.11$, d.f. = 12, $P < 0.05$) and heterogeneity of tree composition (5.39-6.99) than eastern sites (22.15 ± 4.13/ha; 1.5-4.52, except 7.51 for Komi).

Mean linear densities were positively correlated to frequencies of occurrence of bats both among census nights ($R = 0.837$, $F_{1,40} = 89.03$, $P < 0.001$; Fig. 2a), and also among habitat types ($R = 0.772$, $F_{1,3} = 4.44$, $P < 0.15$; Fig. 2b) but with a larger variation. Occurrence and spatial distribution of bats were affected by both the site location (Wilks' $\lambda = 0.161$, $F_{4,70} = 2.82$, $P < 0.05$) and the associated habitat types (Wilks' $\lambda = 0.147$, $F_{4,70} = 2.69$, $P < 0.05$). The mean total abundance (Fisher's LSD, $P < 0.05$) was higher in villages than in other habitats except inland forests, and the mean linear density ($P < 0.05$) was higher in villages than in mangroves and cultivated land (Fig. 3). Bats perched at lower heights in cultivated areas than in inland forests ($P < 0.05$), at lower heights on the east coast than on the west ($P < 0.05$), and were further distances from trails when occurring in mangrove

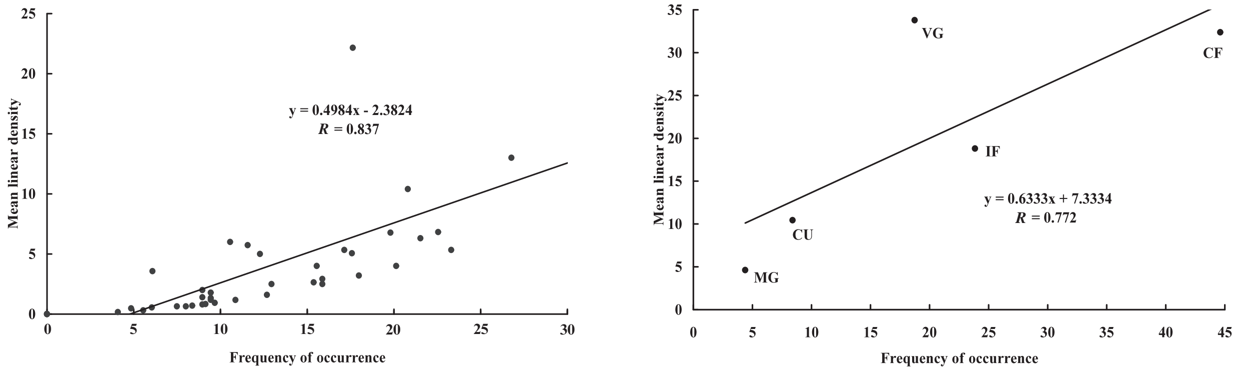

Fig. 2. Arcsin-transformed frequency of occurrence of flying foxes and mean linear density (bat/km of transect) of flying foxes (a) during 48 nights of censuses and (b) in the five different types of habitats, on Iriomote, i.e. mangroves (MG), cultivated fields (CU), villages (VG), inland forests (IF) and coastal forests (CF).

Fig. 3. Mean (± SE) total abundance (■), linear density (⊡) of flying foxes, the height (□) of a bat perching, and its distance from the trail (DFT; ▨), in the 5 types of habitats. A letter and an asterisk (*) indicate significant differences in abundance.

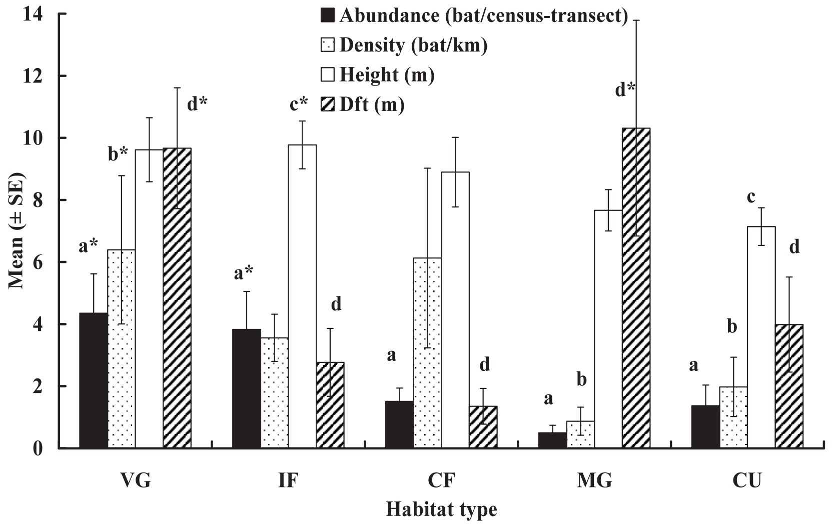

Table 2. Mean values (± SE) of six habitat variables measured for five types of habitats (N = sample size), and relationships between habitat variables and the abundance of flying foxes examined by a multiple regression, followed by respective t values. The total encounter and abundance of flying foxes for each habitat are in parentheses. VG, villages; IF, inland forests; CF, coastal forests; MG, mangroves; CU, cultivated fields. Habitat variables include height variables (m): TCH, top canopy height; BCH, bottom canopy height; SH, shrub height; HH, herb height; and coverage variables (%): CC, canopy coverage and GC, ground coverage. Values with different letters within a variable indicate a significant difference as determined by Fisher's PLSD multiple range comparisons.

	VG (N = 12) (81, 313)	IF (N = 10) (114, 152)	CF (N = 13) (54, 95)	MG (N = 6) (6, 10)	CU (N = 12) (43, 80)	t	P
TCH	11.88 ± 0.63^{a}	10.24 ± 0.53^{a,b}	8.0 ± 0.46^{a}	15.63 ± 4.46	7.39 ± 0.68$^{a, b}$	1.15	NS
BCH	5.81 ± 0.75	5.66 ± 0.63^{b}	4.32 ± 0.55	6.0 ± 1.0	2 .95 ± 0.50^{b}	4.17	***
SH	2.92 ± 0.81	4.67 ± 0.59^{b}	3.07 ± 0.66	5.0 ± 2.0	2.24 ± 0.47^{b}	-3.2	**
HH	1.91 ± 0.8	3.56 ± 0.6	2.27 ± 0.66	3.75 ± 0.75	1.54 ± 0.40	0.4	NS
CC	46.0 ± 3.18$^{c, d}$	59.4 ± 2.68^{c}	36.9 ± 4.77$^{c, d}$	46.7 ± 8.82	23.7 ± 3.59$^{c, d}$	0.1	NS
GC	66.1 ± 4.13	63.7 ± 2.97^{e}	47.0 ± 4.95^{e}	87.5 ± 9.47	73.3 ± 4.73^{e}	2.78	*

NS = not significant; $P < 0.01$; ** $P < 0.005$; *** $P < 0.001$;
^{a} VG > IF, $P < 0.05$, VG > CF, $P < 0.005$, VG > CU, $P < 0.001$; ^{b} IF > CU, $P < 0.05$; ^{c} IF > VG, CF, CU, $P < 0.005$; ^{d} VG > CU, $P < 0.001$, CF > CU, $P < 0.05$; ^{e} IF > CF, $P < 0.01$, CU > CF, $P < 0.001$.

forests than in inland and costal forests ($P < 0.05$; Fig. 3). Among the five types of habitats, bottom canopy height and ground coverage were positively correlated, but shrub height was negatively correlated, with the numbers of bats occurring (multiple regression R = 0.49, $F_{6, 170} = 8.93$, $P < 0.001$; Table 2).

On average, bat perches in cultivated land had lower top- and bottom-canopy heights, lower shrub height, and less canopy coverage than those of most other habitat types, especially inland forests. While top canopy heights were higher in villages than in inland and coastal forests, perches in inland forests had greater canopy coverage, and ground coverage of bat perches was lower in coastal forests than in inland forests and cultivated land (Table 2). The heterogeneity of trees (TH) at the < 3 m range was higher in cultivated fields (6.55) and villages (6.19) than in other forested habitats (3.43-4.39). Yet, cultivated fields had the lowest TH at ranges of 3-5 (4.50) and > 5 m (3.79) compared to all other habitats (3-5 m, 5.26-5.78; > 5 m, 4.61-6.19), whereas that of inland forests was highest at both levels (3-5 m, 5.78; > 5 m, 6.19). The bat densities were correlated both with heterogeneity of tree composition ($r = 0.655$, $F_{1, 12} = 9.04$, $P < 0.05$; Fig. 4a), and strongly with the density of major fruiting trees (R = 0.893, $F_{1, 12} = 47.12$, $P < 0.001$; Fig. 4b).

Diets and patterns of resource use

Yaeyama fruit bats fed on at least 31 species of fruits, 13 species of flowers, and seven species of leaves, of a total of 39 species, 21 families, and 28 genera of plants (Table 3). We found feces more frequently (360 locations, 5.1 ± 0.71 locations /transect-day, N = 70) than

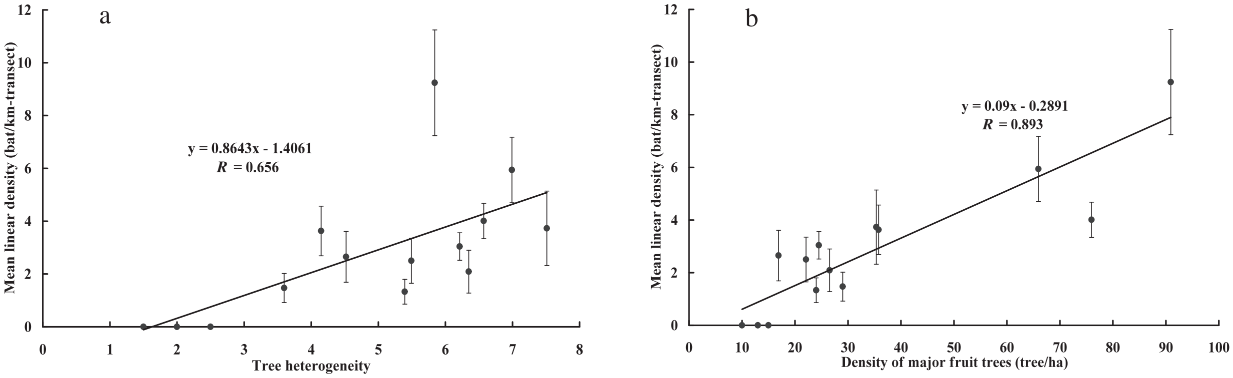

Fig. 4. Relationships of mean (± SE) linear density (bat/km of transect) of flying foxes with (a) the heterogeneity of tree composition and (b) the density of major fruiting trees.

Table 3. Species of plants and types of parts taken by Yaeyama fruit bats on Iriomote Island, with respective common names in parentheses if applicable. The percent pile site indicates the relative frequency of occurrence of a particular species beneath which at least two traces of food uses were retrieved beneath.

Family	Species	% pile site	Type[*]
Actinidiaceae	*Actinidia arguta*[a]		1
Anacardiaceae	*Rhus succedanea* (Japanese Wax Tree)		1, 3
Bromeliaceae	*Ananas comosus* (Pineapple)[b, c]		
Caricaceae	*Carica papaya* (Papaya)[b, c]		1
Combretaceae	*Terminalia catappa* (Indian Almond)[b]	3.8	1
Ebenaceae	*Diospyros maritime* (Coast Persimmon)[b]		1, 2
	D. egbert-walkeri (Ebony)		1
Euphorbiaceae	*Macaranga tanarius* (Parasol Leaf Tree)		1, 3
	Melanolepis multiglandulosa		1, 2
Gramineae	*Saccharum officinarum* (Sugar cane)[b, c]		4
Guttiferae	*Calophyllum inophyllum* (Alexandrian Laurel)[a, b]	1.9	1, 2
	Garcinia subelliptica (Happiness Tree)[b]	24.5	1, 2
Fabaceae	*Erythrina variegata* (Tiger's Claw)[b, c]		2
	Mucuna membranacea Hayata (Kasho Modama)[a]		2, 3
	Pueraria montana (Taiwan Kudzu)[a]		3
Meliaceae	*Melia azedarach* (China Berry)	1.9	1
Menispermaceae	*Stephania japonica*[a]		1
Moraceae	*Ficus ampelas*	1.9	1
	F. Benguetensis (Weeping Fig)		1
	F. erecta[b]	3.8	1
	F. irisona		1
	F. microcarpa (Banyan)[b]		1, 3, 4
	F. Nipponica		1
	F. septica[b]	15.1	1
	F. superba (Large leaved Banyan)[b]	7.6	1, 3
	F. variegate (Variegated Fig)[b]	1.9	1
	F. virgata Reinw. (White Fig)		1
	Morus australis (Small-leaved Mulberry)[b]	3.8	1
	M. alba (White Mulberry)	1.9	1
Musaceae	*Musa liukiuensis* (Plantain)[b, c]		1, 2
Myrtaceae	*Psidium guajava* (Guava)[b, c]	7.6	1, 2
Palame	*Arenga tremula* (Philippine Dwarf Sugar Palm)[b]		2
	Livistona chinensis (Chinese fan palm)[b]	5.7	1, 2
	Satakentia liukiuensis (Satake Palm)[b]	7.6	2
Podocarpaceae	*Podocarpus macrophyllus* (Podocarpus)[b]		1
Rotaceae	*Murraya paniculata* (Jasmin Orange)	1.9	1, 2
Sapotaceae	*Planchonella obovata* (Pouteria)		1
Sonneratiacea	*Sonneratia alba* (Maya-pushik)[a, b]		2
Ulmaceae	*Trema orientalis* (Charcoal Tree)	7.6	1, 3

[*] 1: fruits; 2: flowers; 3: leaves; 4: others; [a] N. Nakanishi, K. Yasuda, personal observations;
[b] Food plants also summarized in Nakamoto et al. (2007); [c] Plants that are cultivated on Iriomote

rejecta pellets (153, 2.5 ± 0.29, $N = 62$) and dropped fruits (17, 1.4 ± 0.19, $N = 12$) ($\chi^2 = 63.7$, d.f. = 2, $P < 0.001$). In contrast, the mean number of samples per locations recorded varied, with greater numbers of pellets (8.1 ± 1.25) and dropped fruit remains (5.7 ± 3.11), but lower numbers of feces (2.9 ± 0.17) at each location. We found 53 piles of feces or traces of food remains repeatedly or periodically directly beneath or very near trees of 16 species. The happiness tree *Garcinia subelliptica* and *Ficus septica* had the greatest proportions, followed by the large-leaved banyan *F. superba*, guava *Psidium guajava*, and charcoal tree *Trema orientalis*; leaves of the latter were most frequently consumed (Table 3).

Plants dominated the food composition, with seven cultivated species (17.9%). Animal items occurred in

Table 4. Food items identified in feces, and rejecta pellets and culled fruit drops, of Yaeyama fruit bats, and presented in relative frequency of occurrence (FO), proportion of dry mass (PM), and mean mass (MM) of retrieved seeds, on Iriomote Island.

Item	Feces			Pellets/Drops		
	FO	PM	MM	FO	PM	MM
Plant	**88.10**	**98.83**		**87.28**	**99.76**	
Ficus spp	79.93	92.54		60.12	73.66	
F. ampelas	0.17	0.18	[a]	0	0	0
F. benguetensis	8.16	5.25	0.014 ± 0.003	5.78	2.59	0.034 ± 0.018
F. erecta	0.85	0.47	0.001 ± 0.0008	1.16	0.14	0.002 ± 0.002
F. irisona	1.19	1.29	0.004 ± 0.003	2.89	0.57	0.008 ± 0.005
F. microcarpa	4.76	3.80	0.011 ± 0.003	8.09	3.43	0.046 ± 0.015
F. nipponica	0.17	[a]	[a]	0	0	0
F. septica	41.67	65.98	0.042 ± 0.006	21.39	42.62	0.567 ± 0.112
F. superba	0.68	0.11	[a]	5.20	5.63	0.076 ± 0.03
F. variegata	22.11	15.36	0.01 ± 0.002	15.61	18.69	0.249 ± 0.067
F. virgata	0.17	0.1	[a]	0	0	0
Morus spp.	3.40	1.91	0.005 ± 0.002	5.20	5.6	0.075 ± 0.04
Diospyros egbert-walkeri	0.17	0.22	[a]	4.05	3.72	0.050 ± 0.026
Garcinia subelliptica	0.51	0.62	0.01 ± 0.002	4.05	3.85	0.051 ± 0.026
Psidium guajava	0.34	0.16	[a]	2.31	3.94	0.053 ± 0.034
Melia azedarach	0	0	0	2.31	5.87	0.078 ± 0.039
Trema orientalis	1.02	0.05	[a]	0.58	0.44	0.006 ± 0.006
Others[b]	1.87	2.74	0.008 ± 0.004	3.47	1.48	0.020 ± 0.015
UN[c] Seeds	0.68	0.51	0.001 ± 0.001	2.89	0.41	0.005 ± 0.005
UN[c] Flowers	0	0	0	2.31	0.78	0.010 ± 0.006
UN[c] Fruits	0.17	0.07	[a]	0	0	0
Animal	**11.91**	**1.18**		**12.72**	**0.24**	
Coleoptera[d]	5.44	0.41	0.001 ± 0.0006	5.20	0.08	0.001 ± 0.0007
Hemiptera[e]	0.34	0.05	[a]	0.58	[a]	[a]
Hymenoptera[f]	2.89	0.08	[a]	1.73	[a]	[a]
Lepidoptera	0.34	0.03	[a]	0.58	[a]	[a]
Neuroptera	0.34	0.01	[a]	0.58	[a]	[a]
Orthoptera[g]	0.34	0.04	[a]	0	0	0
Crustacean	0.68	0.06	[a]	1.16	0.02	[a]
Unar[h]	0.85	0.31	[a]	1.16	0.11	0.001 ± 0.001
Vertebrate[i]	0.34	0.01	[a]	1.16	[a]	[a]
Others	0.34	0.18	[a]	0.58	0.03	0.0004 ± 0.0004

[a] values < 0.001; [b] other species or species groups of plants with a relatively higher proportion of seeds in samples, including *Melanolepis multiglandulosa*, *Rhus succedanea*, *Planchonella obovata*, Leguminosae; [c] plant materials of unknown identities; [d] Cerambycidae, Elateridae, Scarabaeidae; [e] Cicadellidae; [f] Agaonidae, Formicidae; [g] Acrididae; [h] unidentified arthropod fragments; [i] *Japalura polygonat*a (Agamidae).

lower frequencies and included mostly insects but also a vertebrate (Table 4). Figs were the major items, but with various importance values among the types of samples. *Ficus septica* and *F. variegata* were the most dominant items in both fecal and dropped samples. They accounted for over 63% of the FO and 81% of the PM in fecal/pellet samples, followed mostly by other species of figs, mulberries *Morus* spp., happiness trees, and charcoal trees in lower ranks. In dropped samples, *F. septica* and *F. variegata* also led in FO (37%) and PM (61.3%), but were followed, especially in mass proportion, by more non-Moraceae plants in higher proportions, such as chinaberry *Melia azedarach*, guava, and ebony *Diospyros egbert-walkeri* (Table 4).

Discussion

Variation in nocturnal distributions and relative abundances

Yaeyama fruit bats are solitary or form mostly very small groups while foraging, but at a larger scale, their nocturnal spatial distribution is slightly clumped. Among habitats, the mean abundance and density were lower in cultivated areas than in villages and inland forests. This explains the across-island variation in bat distribution, where higher abundances were found in western than in eastern village sites, and supported our predictions. Villagers appeared tolerant to flying foxes, including their excretion and sounds (Y.F. Lee, unpubl. data; M. Matsumoto, pers. comm.). On average, however, eastern villages devoted a four-fold larger area of land to agriculture/husbandry activities, areas presumably with a higher rate of disturbance and intensity of human activities. Eastern sites also had lower fruit-tree density and heterogeneity range in tree composition. On Daito Island, where a high intensity of cultivation has made mangrove forests one of the few remaining undisturbed habitats, fruit bats are consistently found roosting in the border of mangroves (Izawa *et al*., 2001).

The distribution of foraging bats was correlated with land use patterns, habitats, as well as with food supplies, which is consistent with that reported for grey-headed flying foxes *P. poliocephalus* in Australia (McConald-Madden *et al*., 2005). Bat density was correlated moderately with heterogeneity of tree composition, strongly with the density of major fruiting trees, and supported our predictions. Shifts in foraging sites by flying foxes for better food availability have been frequently documented and may occur between types of forests in an area (Banack, 2002), across various distances within a short period of time (Tidemann and Nelson, 2004; McConkey and Drake, 2007), or during migration (Hall and Richards, 2000). Nakamoto *et al*. (2007a) reported Orii's fruit bats using certain fruiting trees intensively in an urban area. On Iriomote, bats in larger groups were observed frequenting some village sites, such as Hoshidate and Sonai, where large fruiting trees and ample food supplies occurred.

We observed variation between habitats in the height and DFT of perching bats. Heights of bats were lower in cultivated areas, and were in correspondence with lower canopy and shrub heights, and less canopy coverage, in this habitat. The DFT of perching bats was probably, at least in part, due to environmental features that restrict accessibility, such as tidal patterns in mangroves, and paths tended to be narrower and tree boundaries closer to trails in inland and coastal forests. An alternative but not mutually exclusive explanation is that the height and DFT may reflect a perceived or actual risk of predation. Fruit bats may fall prey to snakes, raptors, and other mammals (Pierson and Rainey, 1992; Klose *et al*., 2009). On Iriomote these at least include Beauty Rat Snakes *Elaphe taeniura* (Cope, 1861), Japanese Lesser Sparrowhawk *Accipiter gularis* (Temminck and Schlegel, 1844), feral cats *Felis catus* Linnaeus, 1758, and Iriomote Cats *Prionailurus iriomotensis* (Imaizumi, 1967) (Watanabe *et al*., 2003). Lower perching heights may reduce the risk from aerial raptors, particularly at trees of less canopy coverage, and in more open cultivated areas; lower shrub heights may make terrestrial predators more difficult to conceal and less possible to approach a perching tree from surroundings. The latter is also supported by the negative correlation between shrub height and bat density. At greater distances from paths and often depending on tides, bats in mangroves may be free of predation pressure from most terrestrial predators. This is supported by the fact that with a generally higher mean upper-canopy layer, perching heights of bats in mangroves were among the lowest, where terrestrial predators are most restricted.

Diets and resource use

Food plants used by Yaeyama fruit bats, as previously reported based mostly on anecdotal and sporadic notes, include 16 species of fruits, ten species of flowers, and fibrous stalks of sugarcane, for a total of 25 species (Nakamoto *et al*., 2007b). This study added another 14 species of plants to this list. Overall, the diet was less diverse than that reported for Orii's fruit bats on Okinawa (fruit: 53 species, flower: 20 species, leaf: 18 species; Nakamoto *et al*., 2007a), but broader than that of Erabu (fruit: 19 species, flower: eight species, leaf: 11 species, bark: two species) and Daito fruit bats (fruit: 22 species, flower: nine species, leaf: six species; Funakoshi *et al*., 1993; Nakamoto *et al*., 2007b). Compared to other tropical pteropodids (*e.g*., Marshall, 1985), Funakoshi *et al*. (1993) attributed the broader diet of Erabu fruit bats to the warm-temperate seasonality in the food supply. This was not fully supported by our study conducted at a lower latitude near the Tropical of Cancer, and equally or more-diverse diets reported more recently in other paleo-tropical fruit bats (*e.g*., on American Samoa, Banack, 1998; Malaysia, Tan *et al*., 1998).

Instead, the latitudinal variation in the diet breadth of Ryukyu flying foxes, and the fact that our assessments were conducted only in the prime summer season, suggest a connection between diversity and variation in diets of fruit bats with food availability that is influenced by local phenology and the size of the distribution area where bats occur. This is confirmed by results for other species in the Pacific (*e.g*., McConkey and Drake, 2007). We observed asynchronous fruiting among individual trees of the same fig species, which also explains the high variation in abundances of bats recorded among transect-nights, and is an indication of local movements (Funakoshi *et al*., 1993). Food availability to frugivorous bats is often difficult and complicated to accurately estimate (Stashko and Dinerstein, 1988; but see Kalko, 1998), and it has not been quantitatively assessed for most subspecies of Ryukyu flying foxes. Our data provide evidence of a positive correlation between bat abundances and heterogeneity of tree compositions and the density of fruiting trees.

The Moraceae is the single most important family of food plants for Yaeyama fruit bats, and figs are the predominant food type, which was reported in almost all previous studies on diets of flying foxes (Marshall, 1985; reviews in Shanahan *et al*., 2001) and even other non-pteropodid fruit bats (Kalko *et al*., 1996; Korine *et al*., 2000). On Iriomote where the human population is low and mature primary forests remain intact on a large proportion of the land, bats feed mainly on native fruit plants (32 of 39 species of plants, 82.1%). This is a proportion closer to but higher than the one observed in Erabu fruit bats on Kuchinoerabu (22 of 29 species of plants, 75.9%; Funakoshi *et al*., 1993), and much higher than the one found in Daito fruit bats (15 of 26 species of food plants, 57.7%; Nakamoto *et al*., 2007b). Nakamoto *et al*. (2007a) concluded that the diverse diet of Orii's fruit bats results from adaptation to cultivated plants (30 of 78 species of food plants, 38.5%) in urbanized environments, as also has been noted in grey-headed flying foxes (McDonald-Madden *et al*., 2005; Williams *et al*., 2006). Yet, nutrient deficiencies may be the real drive why flying foxes feed on a more diverse group of plants, as high proportions of cultivated plants have replaced native species, especially figs (Nelson *et al*., 2000). Most of the major fruits identified in samples, i.e., figs and mulberries, contain small but many seeds, which is consistent with feeding behavior described for flying foxes (Richards, 1990). Common garcinia, which contains a few large seeds, is an exception and also a fruit found favored by Daito fruit bats (Kinjo *et al*. unpubl. data). The dropped fruit remains, retaining seeds, were often located beneath or very close to the trees where bats fed, and the distances the seeds were dispersed by bats appeared greatly reduced.

We found seven species of leaves in the diet, and various animals at a notable frequency (11.9%), but with a minute proportion in mass. These have not been reported previously in the Yaeyama subspecies (Nakamoto *et al*., 2007b). Leaves appear in an increasing number of species of fruit bats of both the Paleo- and Neotropics (*e.g*., Kunz and Diaz, 1995; Courts, 1998; Nelson *et al*., 2000), and support the idea that folivory provides essential nutrients (*e.g*., carbohydrates, proteins, and calcium) for daily requirements (Rajamani *et al*., 1999; Nelson *et al*., 2005). While animal items are not uncommon in diets of pteropodids (*e.g*., Barclay *et al*., 2006), they are often attributed to incidental ingestion. It requires further observations or experiments for us to fully verify this possibility or alternatives, such as a rare case of carnivory in megachiropterans (Courts, 1998).

Implications for flying fox conservation

Our study provides an opportunity to draw parallels for a comparison with another closer and less studied subspecies, and it offers insights important for the conservation of island flying foxes. Formosa fruit bats suffered a dramatic decline, starting over 30 years ago, from exploitation and habitat alteration and destruction, and remains extremely rare (Lin and Pei, 1999; Heaney *et al*. 2008; D.J. Lin, unpubl. data). The historical hunting episode on Lutao, lasting for 10-15 years, presumably arose from economic incentives, for most bats were snared and later exported (Lin and Pei, 1999), and coincided with significant trading during the same period in other Pacific islands (*e.g*., Guam and the Mariana Islands, Wiles and Payne 1986). Hunting has been officially banned and fruit bats are legally protected on Lutao, yet their future fate is far from certain due to other factors such as habitat alteration, lack of stable food availability, and possible human disturbance (Lin and Pei, 1999).

Unlike bats that inhibit Lutao (c. 17.3 km^2 at low tide), Yaeyama fruit bats occur among islands of a total land area exceeding 550 km^2. Typhoons frequent both areas, but have no apparent effects on flying foxes on larger islands, *e.g*., Iriomote (this study). Yet, remnant populations on small islands may still be vulnerable to disturbances, even by chance (Pierson *et al*., 1996). The resident density (c. 173.4/km^2) and annual tourist numbers (> 300,000) on Lutao are 25-fold and one- or two-fold those on Iriomote (Statistics Bureau data, Japan; National Statistics data, Taiwan), and cause inevitably more intensive habitat alteration or destruction. Ota (1992) noted a rapid decline in bat colonies on Hateruma after plantings replaced native forests. Plantations may provide substitution, but over time bats may still suffer from nutrient deficiencies (Nelson *et* *al*., 2000), or need to travel farther for more foraging options, which will be increasingly more difficult for bats on isolated or small islands (Meyer and Kalko, 2008; Meyer *et al*., 2008), and poses additional threats.

Concerning the status of Ryukyu flying foxes, and Pacific Island flying foxes in general, Yaeyama fruit bats on Iriomote are a good learning case. Human attitudes toward bats are extremely important conservation aspects (Y.F. Lee, unpubl. data; McCallum and Hocking, 2005; Thiriet, 2005). Habitat preservation and restoration, preferably through efforts by the local communities (Entwistle, 2001), to recover native forests and suitable food plants (*e.g*., figs) need to be implemented. Tourism and development should be carefully evaluated and tightly regulated, particularly for critical and small islands, such as Lutao. It remains unclear whether the currently few bats on Lutao are returnees of dwindling colonies that left Lutao for refuges, remnants of a formerly larger population, or immigrants from elsewhere. Further studies should focus on dispersal patterns and population dynamics on multiple islands over the entire or most of the distribution area of this species to achieve a deeper understanding of the ecology of the species in support of improved and more effective conservation strategies.

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