

Population and Conservation Status of *Pteropus dasymallus* in Taiwan

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Pteropus dasymallus is widely distributed on islands throughout the western edge of the Pacific Ocean. The Formosan flying fox, *P. d. formosus*, is an endemic subspecies in Taiwan found mainly on Lyudao; it was previously thought to have been extirpated. Since 2005, intensive surveys have been conducted to investigate the residency, population size and plant resource utilization of *P. dasymallus* in Taiwan. Interviews were carried out to investigate its former abundance and the causes of population decline. In Taiwan, *P. dasymallus* is in a state of ongoing oceanic dispersal and colonization and has considerably expanded its geographic range. In addition to remaining in its historic habitat on Lyudao, *P. dasymallus* has also established colonies on Gueishan Island and in Hualien on Taiwan's main island in the past few decades; the population size is estimated to be 240 individuals, and this number is on the rise. Approximately three-quarters of the entire population (73.64%) was found on Gueishan Island. The sex ratio was strongly skewed toward males. A total of 40 plant species were recorded as providing the flying fox with food, roosts or perches. More agricultural and horticultural plant species were used by the flying fox in urban Hualien. According to the interviews, flying foxes were abundant on Lyudao, but their number dramatically declined

from the 1970s to the mid-1980s, mainly due to commercial hunting. Maintaining a sufficient population size and genetic variability is fundamental to the long-term survival of the flying fox. Enforcing conservation laws, restoring habitat, controlling invasive species and improving public awareness are the main steps in the recovery and sustainability of the flying fox population.

Key words: Insular ecosystem, Interoceanic dispersal, Local extirpation, Pteropodidae, Ryukyu flying fox.

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BACKGROUND

Pteropus species (Chiroptera: Pteropodidae), known as flying foxes, are keystone species that play important roles in pollination and seed dispersal in Old World tropical and subtropical ecosystems (Aziz et al. 2021; Cox et al. 1991). They are ecologically distinct in their contribution to maintaining forest structure and diversity, particularly on islands with relatively depauperate assemblages of large frugivores and pollinators (Cox et al. 1992). Under the threats of habitat loss, forest degradation, and intentional use, many flying fox populations have rapidly declined over the past few decades. These threats are intensified on islands and increase the risk of extinction (Frick et al. 2020, Kingston et al. 2021, Mickleburgh et al. 2002). According to the IUCN Red List of Threatened Species, over half of *Pteropus* species are considered threatened (IUCN 2021). These threats could also impact flying foxes' ecological, evolutionary and economic contributions to ecosystem services (Cox and Elmqvist 2000; Florens et al. 2017; McConkey and Drake 2006). Given the high vulnerability and endemism of insular ecosystems, monitoring the status of flying foxes on islands is important for developing corresponding protection and management strategies.

Pteropus dasymallus (the Ryukyu flying fox) is widely distributed on islands throughout the western margin of the Pacific Ocean, extending 1,800 km from the Ryukyu Archipelago of southwestern Japan through Taiwan to the northern islands of the Philippines (Kinjo and Nakamoto 2015). Five subspecies, namely, *P. d. daitoensis*, *P. d. dasymallus*, *P. d. inopinatus*, *P. d. yayeyamae* and *P. d. formosus*, have been recognized based on their respective island groups (Yoshiyuki 1989). In addition, a Philippine population was discovered in the 1990s on the Batanes and Babuyan Islands. It has not yet been officially designated as a subspecies (Heaney et al. 1998). Although the subspecies are morphologically similar, significant genetic differentiation has been

detected among most of them, except between *P. d. yayeyamae* and *P. d. formosus*, reflecting historical vicariance events and restricted gene flow across deep, broad oceanic barriers (Chen et al. 2021).

Pteropus d. formosus (the Formosan flying fox) historically mainly inhabited Lyudao, with sporadic records of occurrences on the eastern part of Taiwan's main island and Lanyu (Mickleburgh et al. 1992). The flying fox was distributed island-wide on Lyudao, where the population was estimated to be over 2,000 individuals (Lin and Pei 1999). However, the population size rapidly decreased, likely due to intensive hunting since the 1970s. Subsequently, the flying fox was rarely observed and considered to have been extirpated or in the process of becoming extirpated. Therefore, it has been listed as an "Endangered Species" under the Wildlife Conservation Act (Taiwan) since 1989. Little was known about its status on Lyudao until 2005, when it was formally announced that the flying fox had been rediscovered (Chen et al. 2009). Also, flying fox individuals have occasionally been found on offshore islands or on the eastern part of Taiwan's main island in recent years. An updated review of its status is necessary.

To determine whether *P. dasymallus* currently resides in Taiwan, we surveyed its historical range, newly recorded locations, and potential habitat. We interviewed residents to gain a better understanding of the former abundance and population decline of the flying fox. In addition, we reviewed sighting records from the last 40 years to determine whether the flying fox was observed frequently. The aim of our study was to assess the status of *P. dasymallus* in Taiwan, including its presence, current population size, and utilization of plant resources, as well as to investigate residents' perceptions of the flying fox and identify potential critical threats to the flying fox.

MATERIALS AND METHODS

Study area

We conducted surveys of *P. dasymallus* on three islands, namely, Lyudao (Green Island, the main historical range), Gueishan Island (Turtle Island, a newly recorded location) and Lanyu (Orchid Island, a potential habitat with a few sighting records), and in Hualien (a newly recorded location) (Fig. 1, Table 1). Lyudao (area: 15.1 km²) is a volcanic island located 30.9 km off the southeastern coast of Taiwan. It is a popular tourist site during summer.

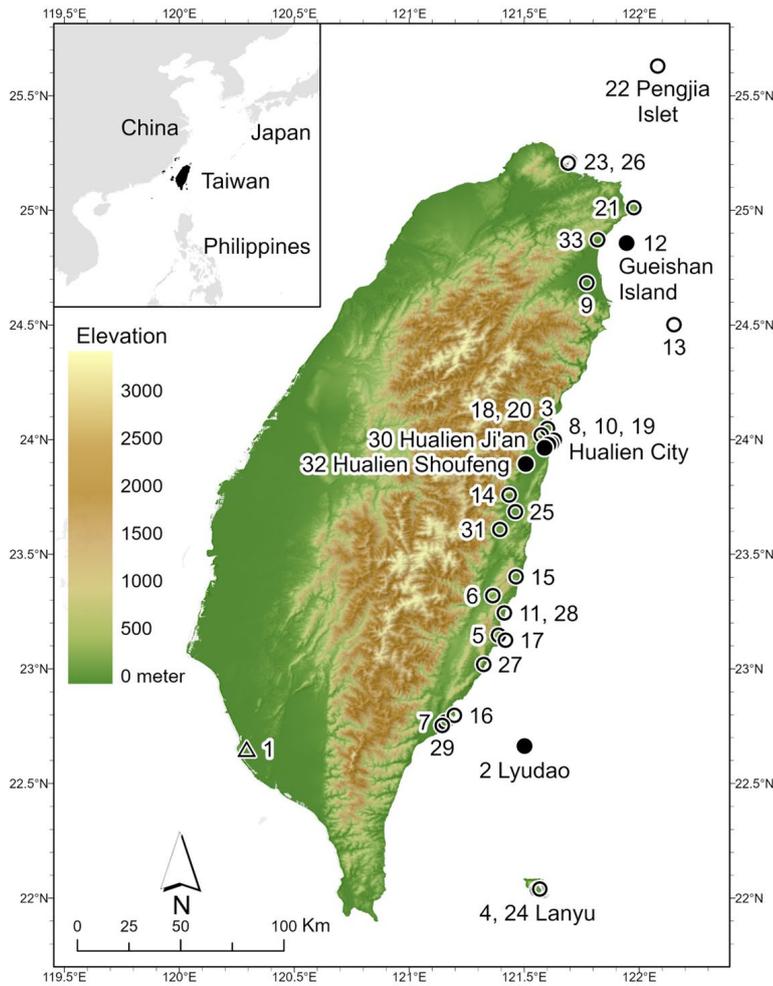


Fig 1. A map of Taiwan showing the occurrence records of *Pteropus dasymallus*. Full circles, empty circles and empty triangles represent resident populations and sporadic and dubious records, respectively. Approximate locations are presented for numbers 1-6, 9 and 21, where precise coordinates are unavailable (please refer to Table 1 for the details of localities).

Gueishan Island (2.8 km²) is a small volcanic island located 9.7 km off the northeastern coast of Taiwan. There are five trails on the island (see Chen et al. 2017). Residents were required to leave by 1977 when Gueishan Island was designated a military control area. Since then, except for the Coast Guard, no residents have inhabited the island. The island is open to the public from March to November during the day.

Table 1. Records of *Pteropus dasymallus* in Taiwan since 1873. The year of discovery, location, number of individuals, sex and reference are provided. Resident populations are displayed in bold

No.	Year (month)	Location	Number and sex ^a	Reference
1	1873	Kaohsiung ^b	1 M, 1 F	(Sclater 1873)
2	1920	Lyudao ^c	? N	(Kuroda 1920)
3	1932	Hualien (Sinchen)	1 N	(Horikawa 1932)
4	1933	Lanyu ^c	1 N	(Kuroda 1938)
5	1934	Taitung (Chenggong)	? N	(Kuroda 1938)
6	1969	Hualien (Yuli)	1 F	NMNH ^d
7	1985	Taitung (City)	1 N	(C.-Y. Lu pers. comm.)
8	1992	Hualien (City)	1 N	(M.-J. Liao pers. comm.)

9	1995 (or 1996)	Yilan (Luodong)	2 F, 4 N	(W.-L. Chi pers. comm.)
10	1995 (Mar.)	Hualien (City)	3 N	(T.-L. Yu pers. comm.)
11	1998	Taitung (Changbin)	1 N	(H.-D. Gu pers. comm.)
12	2004 (Sep.)	Gueishan Island ^c	2 N	(C.-C. Tsai pers. comm.)
13	2006 (Sep.)	Yilan (Su'ao) ^c	1 M	(C.-W. Lin pers. comm.)
14	2006 (Oct.)	Hualien (Fenglin)	1 M	(K.-C. Yeh pers. comm.)
15	2008 (Mar.)	Taitung (Changbin)	1 M	(J.-N. Hu pers. comm.)
16	2008 (Sep.)	Taitung (City)	1 N	(G.-D. Zhong pers. comm.)
17	2008 (Sep.)	Taitung (Chenggong)	1 N	(G.-D. Zhong pers. comm.)
18	2009 (Apr. or May)	Hualien (Xiulin)	1 N	(T.-P. Lan pers. comm.)
19	2009 (Nov.)	Hualien (City)	2 M	(C.-H. Wu pers. comm.)
20	2010 (Apr. or May)	Hualien (Xiulin)	1 N	(T.-P. Lan pers. comm.)
21	2015 (Sep.)	Taipei (Gongliao)	1 M, 1 F	(J.-Y. Lin pers. comm.)
22	2015 (Oct.)	Pengjia Islet ^c	1 N	(I.-F. Fu pers. comm.)
23	2015 (Oct.)	Taipei (Yehliu)	1 N	(P.-W. Chang pers. comm.)
24	2017 (Apr.)	Lanyu ^c	1 N	(Y.-R. Zhang pers. comm.)
25	2018 (Sep.)	Hualien (Fenglin)	1 N	(G.-Y. Lin pers. comm.)
26	2018 (Sep. and Oct.)	Taipei (Yehliu)	pellets	This study
27	2018 (Sep. and Oct.)	Taitung (Chenggong)	pellets	This study
28	2018 (Oct.)	Taitung (Changbin)	pellets	(H.-D. Gu pers. comm.)
29	2018 (Oct.)	Taitung (City)	pellets	This study
30	2019 (Jun.)	Hualien (Ji'an)	2 N	(W.-H. Li pers. comm.)
31	2020 (Aug.)	Hualien (Guangfu)	1 N	(K.-C. Yeh pers. comm.)
32	2020 (Oct.)	Hualien (Shoufeng)	1 N	(X.-C. Zhong pers. comm.)
33	2021 (Oct.)	Yilan (Toucheng)	2 N	(X. Li pers. comm.)

^a: "M" denotes males, "F" denotes females, "N" denotes unknown sex, "?" denotes an unknown number, and "pellets" indicate observation of masticated pellets only. ^b: A dubious record (please refer to text for the details). ^c: Outlying islets. ^d: National Museum of Natural History, USA. Accession no: USNM358143. ^e: This is a record of an individual found in the open ocean.

Lanyu (46.8 km²), another volcanic island, is located 60.8 km off the southeastern coast of Lyudao and 104.8 km north of the Batanes Islands, Philippines. Lanyu is part of the island chain where *P. dasymallus* is distributed; however, only one occurrence was formally recorded and was traced back to 1933 (Kuroda 1938). The residents of the island are indigenous Tao people. Hualien is on the east coast of Taiwan's main island, located between the Pacific Ocean and the Central Mountain Range. Hualien's natural habitats are relatively well preserved, except in the city center (29.4 km²).

Field survey

To assess whether the flying fox was resident and to monitor population changes, we conducted field surveys on Lyudao (August 2005–April 2008 and September 2018–October 2021) and Gueishan Island (March 2009–March 2013 and July 2018–October 2021) and in Hualien City (September 2018–November 2021). Surveys were performed monthly, seasonally or semiannually, depending on the objectives in different stages, with a higher survey intensity during 2005–2013 to verify the presence and foraging habitat of the flying fox. Each survey session lasted for 3–6 consecutive days. Surveys were performed along 12–18 500-m transects of potential habitats across Lyudao, along the five trails on Gueishan Island, and in 21 potential localities in Hualien City.

Night surveys were conducted from 6–10 PM to record the numbers, localities and behavior of the flying fox using direct observations (sight and sound). During the day, we also investigated feces and masticated pellets as indirect signs of the presence of the flying fox. All identified feces and pellets were removed to prevent duplicate records. A one-time 10-day survey was performed on Lanyu in April 2009 to detect the occurrence of the flying fox.

We applied the capture-mark-recapture method to estimate population size. Individual information was obtained via direct capture, observation and noninvasive genetic sampling of feces, pellets and food remains. Capture was carried out on Gueishan Island. Mist nets were placed in the flight paths of the animals before dusk and until midnight during March 2009–September 2012 and October 2019–October 2021. For each individual, wing membrane samples were collected using 3-mm biopsy punches and stored in 99.5% ethanol or silica beads for genetic analysis. Each individual was injected with a subcutaneous passive integrated transponder (PIT) tag between the scapulae or fitted with a uniquely numbered metal band around its thumb for individual identification. After being measured, sexed, sampled and marked, all flying foxes were released. Identification via direct observation was only applied on Lyudao during August 2005–April 2008, where the flying fox’s occurrence was relatively regular. Individuals were identified by color pattern, body size and sex. Fresh feces, pellets and food remains were collected on Lyudao and Gueishan Island and in Hualien City from May 2019 to October 2021. DNA extraction and amplification, sex determination and individual identification were performed following the methods described in Chen (2020) and Chen et al. (2021).

Population size was estimated using the Chao 2 estimator for replicated incidence data (Chao 1987, Chao and Chiu 2016), based on the following formulas: $\hat{S}_{Chao2} = S_{obs} + \left(\frac{m-1}{m}\right)\frac{q_1^2}{2q_2}$ for $q_2 > 0$ and $\hat{S}_{Chao2} = S_{obs} + \left(\frac{m-1}{m}\right)\frac{q_1(q_1-1)}{2}$ for $q_2 = 0$, where S_{obs} is the total number of distinct individuals observed in a study area, q_1 and q_2 are the numbers of individuals observed once and twice, respectively, and m is the number of surveys. The log-transformed 95% confidence intervals of population size are $\left[S_{obs} + \frac{(\hat{S}_{Chao2} - S_{obs})}{C}, S_{obs} + (\hat{S}_{Chao2} - S_{obs})C\right]$, where $C = \exp\left\{1.96 \left[\ln\left(1 + \frac{\text{var}(\hat{S}_{Chao2})}{(\hat{S}_{Chao2} - S_{obs})^2}\right)\right]^{\frac{1}{2}}\right\}$, where $\text{var}(\hat{S}_{Chao2}) = q_2 \left[\frac{1}{2}\left(\frac{m-1}{m}\right)\left(\frac{q_1}{q_2}\right)^2 + \left(\frac{m-1}{m}\right)^2\left(\frac{q_1}{q_2}\right)^3 + \frac{1}{4}\left(\frac{m-1}{m}\right)^2\left(\frac{q_1}{q_2}\right)^4\right]$ for $q_2 > 0$ and $\text{var}(\hat{S}_{Chao2}) = \left(\frac{m-1}{m}\right)\frac{q_1(q_1-1)}{2} + \left(\frac{m-1}{m}\right)^2\frac{q_1(2q_1-1)^2}{4} - \left(\frac{m-1}{m}\right)^2\frac{q_1^4}{4\hat{S}_{Chao2}^2}$ for $q_2 = 0$. We also estimated the intrinsic rate of natural increase (r_m) based on the female population on Gueishan Island, where more capture-mark-recapture data were available. We assumed that the small population experienced exponential growth on the recently successfully colonized island with abundant resources and few predators. The rate was calculated with the

formula $r_m = \left[\ln \left(\frac{N_t}{N_0} \right) \right] \frac{1}{t}$, where N_0 is the number of animals at time 0 and N_t is the number of animals at time t (McIlwee and Martin 2002).

To examine the utilization of plant resources, we identified the plant species in the feces, pellets and food remains of flying foxes according to seed size and shape, content texture and color, and the surrounding flora according to the plant checklists from the Red List of Taiwan Plants (Editorial Committee of the Red List of Taiwan Plants 2017), Plants of Taiwan (Institute of Ecology and Evolutionary Biology, National Taiwan University 2022), and World Flora Online (WFO 2022). Unidentified samples were taken back to the laboratory for detailed examination following the methods described by Chen et al. (2017).

Resident interviews

Interviews were conducted with elderly residents of Lyudao, Gueishan Island and Lanyu to determine the role of the flying fox in local communities. Interviewees from Lyudao and Lanyu, aged over 50 and 70 years, respectively, have lived on the islands since they were young; in contrast, interviewees from Gueishan Island, aged over 50 years, lived on the island until 1977. A semistructured in-depth interview was conducted to capture their knowledge of the flying fox, including past experiences with and memories of this species. For Lyudao residents, the questions included the flying fox's occurrence, ecological habits, and local customary uses, as well as possible reasons for its disappearance. For residents from Gueishan Island and Lanyu, the questions focused on their life and industry on the islands and whether they had ever heard or seen the flying fox. The interviews were conducted in 2009–2010. We repeated the interview survey of Lyudao residents aged over 60 years in 2021 to assess changes in public perception.

Historical records

Sighting records of flying foxes during the last 40 years and relevant literature were collected and reviewed. We interviewed or corresponded with some observers regarding their encounters with flying foxes and determined whether the events occurred frequently or rarely. Distances to the nearest coast were measured using Google Earth for locations that had precise coordinates. All interviews were conducted sporadically during 2009–2021.

In this study, we excluded subspecies names in data regarding newly discovered individuals/populations in Taiwan since *P. d. yayeyamae* and *P. d. formosus* are still indistinguishable by morphology and genetics.

RESULTS

Field surveys

Our surveys revealed that the flying fox is present on Lyudao and Gueishan Island and in Hualien year-round. On Lyudao, flying foxes were most frequently detected in a forest valley by the main road and on steep mountainsides by an open area during night surveys. All these areas were away from villages. Flying foxes often stayed in those areas to feed or rest, sometimes even throughout the night. A female carrying dependent young was observed in mid-April.

On Gueishan Island, flying foxes were mainly observed on ridge crests beside Lake Gueiwei. Flying foxes sometimes aggregated and interacted on a specific Taiwan date palm (*Phoenix hanceana* Naudin.) found in grasslands, with up to eleven individuals recorded. Copulation was observed in November. Females carrying young pups were recorded beginning in mid-May. Flying foxes have been regularly observed in Hualien City, Ji'an and Shoufeng since 2009, 2019 and 2020, respectively. They were recorded roosting or foraging at schools, parks, and along trails and riversides, in greater numbers and in an increasing number of locations (Table 1). Females carrying young were observed beginning in mid-April.

During 2009–2012, 22 individuals were captured on Gueishan Island. Two bats were recaptured in different surveys. The population size was approximately 114 individuals, according to the Chao 2 estimator. In the recent period (2019–2021), 60 individuals were captured or detected with fecal and pellet genetic analyses. Twelve individuals were recaptured or rediscovered. The estimated population was 176 individuals. The overall observed sex ratio was 1.96:1 (males: females), which was significantly different from parity (binomial test: $P < 0.01$). The estimated intrinsic rate of natural increase was 0.058 based on the change in the female population over a period of 9 years (2012–2021).

In Hualien City, 12 individuals were identified from genetic analyses of feces, pellets, food remains and carcasses. The estimated population was 60 individuals. The observed sex ratio was 3.5:1, which was not statistically significant (binomial test: $P = 0.180$). Only four and two individuals were identified on Lyudao in 2005–2008 and 2019–2021, respectively. The estimated populations were five and three individuals, respectively (Table 2).

In total, 40 species of plants were used as food, day roosts or night perches by the flying fox (Table 3). Eleven were nonnative plants (27.50%), including an invasive species, Indonesian cinnamon *Cinnamomum burmannii* (Nees) Blume, which was recorded in Hualien Ji'an; the other

species were agricultural or horticultural plants found on school campuses or in parks, secondary forests or beside streets.

Table 2. Estimated population size with log-transformed 95% confidence intervals of *Pteropus dasymallus* on Lyudao and Gueishan Island and in Hualien City. The number of identified individuals by sex (M: male, F: female, N: unknown) is also displayed^a

Location Sex	Lyudao			Gueishan Island			Hualien City		
	M	F	N	M	F	N	M	F	N
Years 2005-2013									
Number of identified individuals	1	1	2	14	8	0	-	-	-
Estimated population size	5 (4–17)			114 (44–407)			-		
Years 2019-2021									
Number of identified individuals	0	0	2	39	19	2	7	2	3
Estimated population size	3 (2–12)			176 (110–330)			60 (27–162)		

^a: Individuals were identified by multiple methods, including direct observations, capture and genetic analyses of feces, pellets and food remains, as described in the text.

Table 3. The plant resources used by *Pteropus dasymallus* for food (F), day roosts (R) or night perches (P) on Lyudao and Gueishan Island and in Hualien City

Species	Lyudao ^a	Gueishan Island	Hualien
Dicotyledons			
Anacardiaceae			
<i>Mangifera indica</i> L. ^b	F, P		F, P
Asteraceae			
<i>Wedelia biflora</i> (L.) DC.		F, P	
Bignoniaceae			
<i>Spathodea campanulata</i> Beauv. ^b			P
Caricaceae			
<i>Carica papaya</i> L. ^b	F, P		F, P
Casuarinaceae			
<i>Casuarina equisetifolia</i> L. ^b	F, P		P
Combretaceae			
<i>Terminalia catappa</i> L.	F, P		F, P, R
<i>Terminalia mantaly</i> H.Perrier. ^b			P
Ebenaceae			
<i>Diospyros blancoi</i> A. DC.	F, P, R	F, P	P
<i>Diospyros maritima</i> Blume	F, P	F, P	
<i>Diospyros morrisiana</i> Hance		F, P	
Euphorbiaceae			
<i>Macaranga tanarius</i> (L.) Müll.Arg.		P	
Calophyllaceae			
<i>Calophyllum inophyllum</i> L.			F, P
Clusiaceae			
<i>Garcinia subelliptica</i> Merr.	F, P		F, P
Lauraceae			
<i>Cinnamomum burmannii</i> (Nees) Blume ^b			F, P
<i>Cinnamomum camphora</i> (L.) J.Presl. var. <i>camphora</i>			F, P
Malvaceae			
<i>Bombax ceiba</i> L.			F, P
Moraceae			
<i>Broussonetia papyrifera</i> (L.) L'Hér. ex Vent.			F, P
<i>Ficus ampelas</i> Burm. f.		F, P	
<i>Ficus benjamina</i> L.		R	
<i>Ficus cumingii</i> Miq. var. <i>terminalifolia</i> (Elmer) Sata	F, P		
<i>Ficus fistulosa</i> Reinw. ex Blume	F, P	F, P	F, P
<i>Ficus microcarpa</i> L.f. var. <i>microcarpa</i>		P	F, P, R
<i>Ficus septica</i> Burm.f.	F, P	F, P	F, P
<i>Ficus</i> sp.		P	

<i>Ficus superba</i> (Miq.) Miq. var. <i>japonica</i> Miq.		P	F, P
<i>Ficus virgata</i> Reinw. ex Blume			F, P
<i>Morus australis</i> Poir.		F, P	
Primulaceae			
<i>Ardisia sieboldii</i> Miq.		F, P	
Myrtaceae			
<i>Psidium guajava</i> L. ^b		F, P	
<i>Syzygium samarangense</i> (Blume) Merr. & L.M.Perry ^b			F, P
Rosaceae			
<i>Rubus</i> sp.			F, P
Sapotaceae			
<i>Palaquium formosanum</i> Hayata	F, P, R		F, P
Staphyleaceae			
<i>Turpinia ternata</i> Nakai		F, P	
Pentaphylacaceae			
<i>Eurya japonica</i> Thunb.		F, P	
Monocotyledons			
Arecaceae			
<i>Livistona chinensis</i> R.Br. var. <i>subglobosa</i> (Mart.) Becc.		F, P	
<i>Phoenix hanceana</i> Naudin.		F, P	F, P
<i>Roystonea regia</i> (Kunth) O.F.Cook ^b	P		F, P, R
Musaceae			
<i>Musa</i> sp. ^b	F, P		F, P
Strelitziaceae			
<i>Ravenala madagascariensis</i> Sonn. ^b			P
Pandanaceae			
<i>Pandanus odoratissimus</i> L.f.	F, P		
Total number of species: 40	15	18	25
Number and percentage of nonnative species: 11 (27.50%)	5 (33.33%)	1 (5.56%)	10 (40.00%)

^a: Some of the Lyudao records were obtained from interviews with elderly residents. ^b: Nonnative species.

Resident interviews

We interviewed 25 elderly residents on Lyudao during 2009-2010. Each of them reported having seen flying foxes in the past. Locals referred to flying foxes as “*panichi*” but could not explain the term’s exact meaning. A few interviewees also referred to flying foxes as “*tò-tiàu tsiáu*” in Taiwanese (literally “upside-down bird”). Most interviewees reported that flying foxes used to be very common (84.00%) and could be seen year-round (64.00%, Table 4). The height at which the flying foxes roosted during the daytime varied among seasons and was higher in summer than in winter. A few interviewees claimed that they had seen flying foxes flying over the open ocean, heading to Lyudao at night.

Nearly half of the Lyudao interviewees (48.00%) reported capturing flying foxes for consumption in the past. Captures often occurred during the winter slack farming season when residents could not go fishing. Long bamboo sticks with ends sharpened or mounted with iron wires, nails or darts were used to stab or strike bats off trees. Fallen bats could not take off from the ground. Some residents used homemade dip nets (mesh nets with long bamboo handles) to scoop up bats on trees. From the 1970s to the mid-1980s, flying foxes were harvested commercially with bird netting installed on crest lines between valleys in the major flight paths, which was a more efficient

approach for capture. The price for each bat at that time was NT\$ 500-700 (US\$ c. 14–20; the per capita income of Taiwan was US\$ 2,139 in 1980). Flying foxes captured for commercial purposes were transported to Taiwan's main island and traded in markets. No regulations were imposed on the capture and trading of flying foxes prior to the implementation of the Wildlife Conservation Act in 1989. More than half of the interviewees had eaten flying foxes in the past (56.00%). They cooked flying foxes in several ways: mostly simmering them with local peanut crops, stir-frying chunks of flying fox meat with soy sauce and sesame sauce seasonings, or sometimes stewing them with dried vegetables. The capture and consumption of flying foxes tended to be more prevalent in villages close to mountain areas.

Table 4. Interviewee responses regarding experience with *Pteropus dasymallus* on Lyudao in 2009–2010 and 2021

Questions	Interviewee responses	Percentage reported (%)	
		2009–2010 (n = 25)	2021 (n = 16)
Population abundance in the past	Often seen	84.00%	
	Occasionally	16.00%	
Seasonal variation	Year-round	64.00%	
	Mainly in summer	8.00%	
	Mainly in winter	8.00%	
	Not sure	20.00%	
Hunting experience	Yes	48.00%	
	No	52.00%	
Consumption experience	Yes	56.00%	
	No	44.00%	
Causes for population declines	Overhunting	56.00%	
	Plantation	16.00%	
	Typhoons	12.00%	
	Not sure	20.00%	
Last observation	> 30 years ago	32.00%	37.50%
	21-30 years ago	24.00%	12.50%
	11-20 years ago	12.00%	0.00%
	≤ 10 years	12.00%	25.00%
	Not sure/no response	20.00%	25.00%
Population status	Rare	36.00%	37.50%
	Extirpated	48.00%	25.00%
	Not sure	16.00%	37.50%

Nearly half of the interviewees believed no individuals remained on Lyudao (48.00%). A total of 36.00% of the interviewees claimed that the flying fox was still present or likely present, and 16.00% were uncertain about its presence. However, only a few (12.00%) witnessed flying foxes in the last ten years (1999–2009). Most of them had not seen flying foxes for more than 20 years (*i.e.*, flying foxes were last seen before 1989; 56.00%). Overhunting was considered the main cause of population decline (56.00%), followed by habitat degradation due to extensive plantations of the alien Australian pine (*Casuarina equisetifolia* L.) and damage from typhoons (Tables 4, 5).

A more recent interview of 16 Lyudao residents in 2021 showed that more interviewees recently encountered flying foxes (2011-2021, 25.00%). Fewer (25.00%) reported that the flying

fox was extirpated. Of the interviewees, 37.50% claimed that the flying fox was present on the island; another 37.50% of the interviewees were uncertain that it was present.

Table 5. Examples of interviewee responses regarding the occurrence and ecology of *Pteropus dasymallus* on Lyudao

Previous sightings
<i>"I saw it every day when going to the mountains to collect firewood."</i> (G13)
<i>"Everywhere in the mountains."</i> (G14)
Ecology of the flying fox
<i>"Normally one or two bats (hanging on trees)."</i> (W15)
<i>"As many as 30-40 bats hanging on a fig tree in the Big Valley."</i> (N02)
<i>"They hung on trees and hid within vines."</i> (G09)
<i>"Particularly more bats in cool shaded valleys."</i> (DW42)
<i>"A group of five or six bats, sometimes three or four, were on a screw pine, biting each other and scrambling for the fruits."</i> (DW40)
<i>"While fishing on the coast, we saw a group of panichi flying over the open ocean, heading over to Lyudao."</i> (DW42)
Capturing the flying fox for local consumption
<i>"We could not go fishing during winter so no harvest at all. We went to the mountains to find some food."</i> (DW06)
<i>"Use a long bamboo stick with a sharp-pointed metal hook to stab bats. Then, pull the bats off the trees."</i> (G6)
<i>"We needed to hide downwind. Bats could escape if we approached from an upwind direction."</i> (G05)
Capturing the flying fox for the commercial market
<i>"Purchasers from Taiwan's main island come to buy bats. Since then, hunters used nets to catch bats, which drove the bats extinct."</i> (N02)
<i>"He (the hunter) caught bats every day for years."</i> (C03)
Consumption of the flying fox
<i>"Boil it in hot water to remove the hair. Then, chop into small pieces. Simmer with peanuts or fry with sesame oil and shredded ginger."</i> (DW49)
Remaining population
<i>"Few, less than five or six."</i> (A12)
<i>"It is gone. Most likely, will not see it again."</i> (DW11)
Conservation of the flying fox
<i>"The Formosan flying fox is so unique, only on Lyudao. We did not know that until now. We want to preserve it, but the population has gone."</i> (C04)

We interviewed 15 elderly residents who inhabited Gueishan Island until 1977. All claimed that they had never encountered, or heard about, flying foxes when living there. We interviewed 16 indigenous Tao elders on Lanyu. None of them had ever seen a flying fox. Locals called bats “*peypeynet*.” Five interviewees (31.25%) learned the term “*panichi*” from earlier generations to refer to bats. However, they interpreted the meaning differently as follows: (1) The two terms are indistinguishable, both referring to bats. In Tao, objects are commonly identified by more than one term. (2) The two terms denote different species inhabiting different habitats. Some interviewees mentioned that *panichi* was larger than *peypeynet* and was caught for food by earlier generations. Some described *panichi* as present on Lanyu in the past but currently absent.

Historical records

All occurrences of *P. dasymallus* were in eastern, northeastern or northern Taiwan based on the literature and interviews of observers (Fig. 1, Table 1). The only exception was the record of Kaohsiung in southwestern Taiwan, which was likely the locality of the donor rather than where the animals were collected (Kuroda 1920, Selater 1873). This record was therefore excluded from the analysis of sporadic records. Islands with records of sightings included Lyudao, Lanyu, Gueishan Island, Pengjia Islet and Taiwan's main island. Lyudao was the only locality with resident *P. dasymallus* until 2004, when a new resident population was found on Gueishan Island. No resident population was recorded on Taiwan's main island until 2009, when one was reported in Hualien. Most of the sporadic recorded sightings on Taiwan's main island occurred in the east (Hualien and Taitung). Few were in the northeast (Yilan) or north (Taipei). There was one historical record from Lanyu in 1933 (Kuroda 1938) and a recent record in 2017. To date, there was only a single record on Pengjia Islet in 2015. No flying fox fossils have been found.

The number of sporadic individuals found ranged from one to six. When more than one individual was recorded, they were often found at the same time (*e.g.*, six individuals in Luodong in 1995–1996 and three in Hualien City in 1995) or within a few days of each other (*e.g.*, two in Gongliao in 2015). Of the verified events, 68.18% occurred in September and October. Males (60.00%) slightly outnumbered females (40.00%). Only two individuals were examined for age, and both were subadult. Most localities were close to the coast, with a median linear distance of 587 m for observations with precise coordinates (mean = 2.62 km, standard deviation = 4.10 km, $n = 22$).

DISCUSSION

The population of *P. dasymallus* in Taiwan is currently growing after a long period of few sightings. It is in a state of ongoing oceanic dispersal and colonization. In addition to remaining in its historic habitat on Lyudao, *P. dasymallus* has expanded its geographic range across islands in recent decades and has become a resident on Gueishan Island and in Hualien (Hualien City, Ji'an and Shoufeng) on Taiwan's main island. No seasonal migration or movement among areas was detected; it inhabits these three areas year-round and was observed breeding.

Our study estimated that approximately 240 individuals were in Taiwan, with the majority on Gueishan Island, representing 73.64% of the entire population. Based on a more detailed examination of Gueishan Island, the population increased by 54.39% over 9 years. This high growth

rate implies that the population was productive. Based on the estimated intrinsic rate of natural increase, the female population will potentially increase at a constant exponential rate, leading to an approximate doubling time of 11.9 years. However, in nature, the intrinsic rate of natural increase is not constant and varies in response to intrinsic and environmental factors (Fox et al. 2008; McIlwee and Martin 2002). Nevertheless, it still serves as a feasible model to monitor population trends and develop conservation measures.

Genetic techniques have considerably increased our ability to identify individuals and effectively estimate population size. We were thus able to assess the sex ratio, an important population parameter. On Gueishan Island, the sex ratio was significantly skewed toward males (1.96:1). Since the samples were collected from various locations and sources (capture, feces, pellets and food remains) across seasons and years, the sex ratios likely reflected the authentic sex ratio of the population rather than bias introduced by sexual differences in foraging sites or the ability to avoid nets. On the other hand, no statistically significant difference was found in Hualien City (3.5:1), possibly due to the small sample size. Different *Pteropus* species may show variable extents of bias, even varying by locality (Clark et al. 1997; Divljan et al. 2011). Diet also influences the determination of embryo sex (Parry-Jones 2011). We could not verify whether the skewed sex ratio in our study was local bias since no information for the same species was available for comparison. However, given that the populations on Gueishan Island and in Hualien City were recently established, the skewed sex ratio might have resulted from sex-biased dispersal or unstable population structure (Chen et al. 2021; Meade et al. 2021; Olival et al. 2020).

A sex ratio strongly biased toward males in small populations implies that the genetically effective population size is likely much smaller than the census population size (Charlesworth 2009). Small flying fox populations might have suffered from founder and bottleneck effects. Demographic and environmental stochasticity, loss of genetic variation, and the density-dependent Allee effect substantially influence small populations (Newman and Pilson 1997, Stephens and Sutherland 1999). Further investigation is needed to monitor the long-term effect of a disproportionately small number of adult females on population dynamics and structure.

Based on previous literature and information collected in the present study, flying foxes have been found sporadically along Taiwan's east, northeast and north coasts, including outlying islands (Table 1). However, resident populations were established only recently on Gueishan Island and in Hualien. The dispersal of individuals to new habitats was occasional, nonrandom and irregular, but seemed highly centralized in 1995, 2006–2010, and after 2015. A single dispersing individual cannot establish a new colony without residing in the new habitat for an extended period and successfully recruiting others to the colony. Given the long lifespan and high mobility of flying foxes, if multiple individuals disperse together or reach the same uninhabited habitat at similar

times, these dispersers might be able to assemble and eventually form a successful colony. The hypothesis of several dispersal events from adjacent islands over time was supported by the high genetic diversity of *P. dasymallus* on Gueishan Island, which is considered to result from multiple ancestral origins (Chen et al. 2021).

The observed dispersal was possibly promoted by many different extrinsic and intrinsic factors, as well as interactions among these factors. Food availability is an important potential determinant of dispersal. Seasonal typhoons and the northeast monsoon often bring heavy rains and strong winds, which may cause food deficiency, threaten survival and further promote active dispersal (McConkey et al. 2004; Pierson et al. 1996). The influential northeast monsoon, spanning September to April, possibly drove seasonal oceanic dispersal. This idea was supported by the sporadic records of flying foxes, which mainly occurred during September and October. In addition, most reported locations were close to the coast in eastern and northeastern Taiwan, which could represent the first arrival of other subspecies if the neighboring eastern *P. d. yayeyamae* (on the southern Ryukyu Islands) or southern Philippine populations (on the Batanes and Babuyan Islands) dispersed westward or northward, respectively.

Extreme weather with increased frequency and intensity may affect the timing, direction and rate of wildlife dispersal, further changing population dynamics and species distributions (Knutson et al. 2010; Kuussaari et al. 2016; Lea et al. 2009). Gueishan Island is an important stopover point on the seasonal route of migratory birds along the western edge of the Pacific Ocean. We observed thousands of transient and vagrant birds during our winter surveys on the island, many of which showed signs of starvation or were even dead, particularly during harsh weather. Extreme weather may also impact flying foxes' survival and trigger their dispersal.

Population increases could expand the distribution. The neighboring eastern *P. d. yayeyamae* and southern Philippine populations are large and stable (Heaney et al. 1998; Saitoh et al. 2015). The success of oceanic dispersal and colonization of the Miyako Islands by the former subspecies has been recorded; individuals traveled 45 km to colonize a new island, even though the activity range of *P. dasymallus* is generally limited (Nakamoto et al. 2011; Nakamoto et al. 2012).

Movement among adjacent islands has also been evidenced by direct population censuses and indirect genetic studies (Chen et al. 2021; Nakamoto et al. 2011; Taki et al. 2021). In our study, a subadult male was rescued on a fishing boat in the open ocean in September 2006, approximately 40 km and 70 km away from the nearest lands of Taiwan and the Ryukyu Islands, respectively (Fig. 1, no. 13). A few residents on Lyudao claimed to have witnessed flying bats heading over to Lyudao from the open ocean. Given that insular *P. dasymallus* has a wide distribution across regions and countries, monitoring its dynamic changes in biogeography is critical for its management and conservation on a larger spatial scale (Nakamoto 2017).

Our study revealed that *P. dasymallus* altered its roosting and foraging behavior in urban areas. Flying foxes on Gueishan Island returned to dense forests before sunrise. Elderly residents on Lyudao spotted flying foxes roosting in forests. However, in Hualien City, flying foxes roosted in trees on campuses and parks close to construction sites and areas of other human activity. The diet of flying foxes in this area also included more introduced agricultural and horticultural plants. An increasing number of *Pteropus* species have been reported to successfully adapt to urban environments ((Parry-Jones and Augee 2001; Tait et al. 2014). Greater availability and stability of food resources are considered the drivers of urbanization (Meade et al. 2021). The distribution, abundance and ecology of flying foxes would be markedly altered by increased urbanization (Williams et al. 2006).

Through resident interviews, we were able to examine the past abundance, ecology and population decline of the flying fox in its historic Lyudao habitat. Community perception of the flying fox's status as an endangered species changed over time. A previous study revealed that 39% of interviewees considered the flying fox extirpated in 1994 (Lin and Pei 1999). Our study showed that the percentage slightly increased to 48% in 2009 and decreased to 25% in 2021. From 1994–2009, it appeared to be more difficult to sight flying foxes. In contrast, in 2009–2021, more residents learned that the flying fox was not extirpated through its rediscovery and related press reports. However, a higher percentage of residents were unaware of the existence of the flying fox, probably due to its lack of relevance to their daily lives. Most of the last observations occurred before or during the 1980s, when hunters intensively trapped bats to sell in markets.

One interesting finding of this study was that elderly residents on Lyudao (Han Chinese) commonly referred to flying foxes as *panichi* but could not clarify the term's origin. *Panichi* (or *paniki*) is a Malayo-Polynesian term widely used in insular Southeast Asia to refer to bats or specifically denote flying foxes (Blust 2002; Forth 2021; Kano 1941). According to our interviews, few indigenous Tao on Lanyu learned this term from earlier generations; however, their descriptions were discrepant. It is unusual for the Han in Taiwan to denote local wildlife with an indigenous or foreign term. We presumed that Lyudao residents denoted flying foxes as *panichi* following the Tao.

The Tao have a strong cultural and linguistic affiliation with the northern Philippines Batanes (Bellwood and Dizon 2013; de Beauclair 1969). A group of Tao inhabited Lyudao, the only historic habitat of *P. dasymallus* in Taiwan, until the Han arrived and settled approximately 200 years ago (Liu et al. 1995). Therefore, the Tao likely had continuous contact with flying foxes up to 200 years ago. The history of the Tao on Lyudao is a plausible explanation for the maintenance of the term *panichi* for generations. Sporadic occurrences, although very rare, could be helpful in collecting relevant knowledge and experience with this species. The interaction between the Tao and the new

Han immigrants on Lyudao possibly facilitated the introduction of this indigenous faunal term to the Han. We could not exclude the possibility that the species previously existed on Lanyu. The island's tropical rainforest habitat is considered suitable for flying foxes (Chao et al. 2010; Kano 1929). However, to date, there has been no solid evidence to support this from oral histories or sighting records.

Conservation implications

The Formosan flying fox was previously widespread on Lyudao and had long been used as a supplementary food source to supply protein. Past hunting for local consumption did not threaten the population. Subsequent commercial hunting that occurred since the flying fox became a valuable commodity drove the depletion of the population within less than two decades. The rapid population collapse of the flying fox highlights the vulnerability of an insular species in the Anthropocene.

The primary threats to the population should be carefully reviewed and eliminated. Illegal hunting still exists in Taiwan and threatens wildlife. One of our recorded flying foxes was caught by bird netting used to catch songbirds for markets. Netting installed next to orchards and fishponds sometimes traps flying foxes. Although flying foxes are not the targets of the hunters or farmers, bycatch does occur and cause avoidable deaths and injuries. We also found cases in which captured individuals were improperly treated due to hunters' insufficient understanding of flying foxes. Preventing hunting by enforcing conservation laws and improving public awareness about wildlife conservation is crucial.

A sound natural habitat is preserved on the uninhabited Gueishan Island. Although the island is bustling with tourists during the day, tourists can only access a small part of the island. Therefore, tourist activity does not seem to negatively impact these nocturnal bats.

The main concern for the sustainability of the flying fox on Lyudao is an insufficient number of individuals to maintain a viable population. In addition, the quality of the habitat on Lyudao needs to be further evaluated. Lyudao is largely covered by mixed alien Australian pine and native hardwood. The habitat has improved since native species have gradually replaced the plantation of Australian pine through succession (Chung and Lu 2006). However, a substantial number of Australian pine seedlings continuously invade primary forests via natural regeneration (Chen 2006), which has significantly reduced the area of primary forests. We also observed that the Pallas's squirrel (*Callosciurus erythraeus*) may impact the activities and survival of *P. dasymallus* on Lyudao. The squirrel was introduced in the 1990s and spread quickly over the entire island (Lin 2009). Several biological and ecological features (*e.g.*, high vagility, fecundity, and behavioral

plasticity as well as low predation pressure) enable squirrels to be successful invaders and strong resource competitors on islands (Palmer et al. 2007). The Pallas's squirrel, which consumes a wide range of food items and nests and lives in trees, potentially competes with flying foxes for food and space. Diurnal, abundant and arboreal squirrels may also severely disturb roosting flying foxes. During our survey, we observed squirrels disturbing one flying fox, causing it to screech and fly away from its day roost. Last, wildlife on Lyudao continues to be threatened by hunting. Active efforts to restore the habitat, control invasive species and combat hunting are needed.

In Hualien City, the flying fox lives in close proximity to local communities. Local parks and schools with a higher availability of food resources are important for flying foxes living in urban areas. Specific roosting and foraging habitats and trees should be identified and maintained so that overpruning or removal can be prevented. The presence of endangered wildlife in cities has received considerable attention. However, issues of the growing population, associated crop damage, fear of strange animals, concerns about disease, and potential noise, smell and mess might result in conflict between communities and wildlife, which should be carefully assessed. The attitude of the community will affect future mitigation strategies (Currey et al. 2018). Stakeholders and surrounding communities need to be encouraged to change their perceptions of flying foxes and increase their willingness to include wildlife in communities.

Local ecological knowledge and personal accounts of the flying fox based on recall were used to reconstruct the historic changes in the flying fox populations, since our ability to determine the original baseline numbers is limited by the lack of past studies. Preserving local knowledge and experiences with *panichi* is becoming more challenging in present-day communities since the flying fox has been absent or rare in the local vicinity for an extended period. The disappearance of a rare species might change community members' perception of the species, causing them to overlook the importance of its conservation (Turvey et al. 2010). By transferring the community memory of flying foxes to younger generations, environmental changes could be tracked over time, and additionally, a new, more positive relationship between residents and wildlife could be established.

CONCLUSIONS

We surveyed the historical range, newly recorded locations and potential habitat of *P. dasymallus* and determined its current distribution and population size in Taiwan. The flying fox is currently present year-round on Lyudao and Gueishan Island and in Hualien. The population is estimated to be 240 individuals, with the majority residing on Gueishan Island, representing 73.64% of the entire population. A strongly male-biased sex ratio was observed. Small populations might

suffer from demographic and environmental stochasticity, loss of genetic variation, and density-dependent impacts. Maintaining a sufficient population size with adequate genetic variability is fundamental to the population's long-term survival. The occurrence and distribution range of *P. dasymallus* in Taiwan have obviously increased in recent years, particularly in urban Hualien. Thus, monitoring the interaction between the flying fox and local communities and the local ecology in urban areas is becoming increasingly important. In the historic habitat on Lyudao, the interviews revealed that commercial hunting was the leading cause of the population decline. We also found that the experience and awareness of the flying fox in the local community tended to drop with the disappearance of the species. Preventing illegal hunting and bycatch, restoring foraging and roosting habitat, controlling invasive species and increasing public awareness about wildlife conservation are crucial for the recovery and sustainability of the flying fox population in Taiwan.

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