







# Exploring Human-Flying Fox Interactions in Sabah Malaysia Borneo: Observations, Cultural-Utilitarian Practices, Conflicting Interactions and Trade

Lawrence Alan Bansa<sup>1</sup> , Rayzigerson Rodney<sup>1,2</sup> , Marcela Pimid<sup>1</sup> , Liesbeth Frias<sup>3</sup> ,  
Sergio Guerrero-Sánchez<sup>4</sup>  and Noor Haliza Hasan<sup>1\*</sup> 

## ABSTRACT

Studying human-flying fox interactions is crucial for conservation planning, yet they remain understudied in Sabah and across the region. This study examines cultural and utilitarian practices, hunting, fruit-raiding conflicts, and trade across three of Sabah's five administrative divisions, Sandakan (SND), Interior (IRD), and West Coast (WCD). The study used a multi-mode survey design with 100 semi-structured questionnaires, market observations, and 839 Sabah Wildlife Market Logbook records (2015–2019) covering 16 of Sabah's 27 main districts. Data were analysed using descriptive statistics in R and thematic analysis for qualitative insights. Twenty-three percent of participants consumed flying foxes for food (26.1%), traditional medicine (30.4%) or both (43.5%). Over the past five years, participants observed reduced flying fox sightings and meat availability, suggesting a population decline. Hunting was reported among Kadazandusun (72.7%), Sungai (18.2%), and Murut (9%) participants, which was driven by meat consumption (53.3%), protection of fruiting trees (33.3%), selling meat (6.7%), and medicinal purposes (6.7%). Fruit-raiding conflicts affected 48% of participants, with seasonal crops such as duku-langsats (34.3%) and rambutan (24.1%) being the most impacted. Among those affected by fruit raiding, 71.4% of participants tolerated flying foxes, 28.6% employed lethal control methods, including nets and *rawai*. Market logbooks recorded 23 flying foxes (0.18% of total trade) indicating both low prevalence and likely underreporting. This study highlights the need for context-specific conservation efforts that integrate local ecological knowledge, address food security and alternative protein/livelihood options, promote sustainable, non-lethal conflict mitigation strategies and strengthen wildlife trade monitoring.

**Keywords:** Flying fox consumption, flying fox hunting, fruit raiding, local ecological knowledge, wildlife logbooks, *Pteropus*.

1 Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, UMS Road, 88400, Kota Kinabalu, Sabah, Malaysia.

2 Danau Girang Field Centre, c/o Sabah Wildlife Department, Wisma MUIS, Block B 5th Floor, 88100, Kota Kinabalu, Sabah, Malaysia.

3 Department of Infectious Diseases and Public Health, Jockey Club College of Veterinary Medicine and Life Sciences, 1A-501, Block 1, To Yuen Building, 31 To Yuen Street, City University of Hong Kong, Tat Chee Avenue, Kowloon, Hong Kong SAR.

4 Centre for Applied One Health Research and Policy Advice, City University of Hong Kong, 83 Tat Chee Avenue, Kowloon Tong, Kowloon, Hong Kong SAR.

\* Corresponding author ✉. E-mail address: LAB ([bansalawrence@gmail.com](mailto:bansalawrence@gmail.com)), NHH ([hhaliza@ums.edu.my](mailto:hhaliza@ums.edu.my)).

---

## SIGNIFICANCE STATEMENT

This manuscript offers a novel, multidisciplinary analysis of human–flying fox interactions in Sabah, Malaysian Borneo, an ecologically significant yet understudied aspect of the region’s biodiversity research. Employing a multi-methods design that integrates semi-structured surveys, ethnographic market observations, and analysis of 839 Wildlife Market Logbook entries (2015–2019), the study elucidates cultural-utilitarian practices, hunting motivations, fruit-raiding conflicts, and informal wildlife trade. Key findings include evidence of declining population visibility, underreported trade activity, and ethnically-influenced consumptive behaviours. The study also links these interactions to food security and protein access, suggesting alternative food or livelihood options to reduce hunting. Notably, it documents community-led lethal and non-lethal responses to fruit-raiding conflicts and underscores the role of local ecological knowledge (LEK) in conservation outcomes. By combining quantitative and qualitative evidence, this study provides essential baseline data to guide culturally grounded conservation strategies and inform regional policy to address threats to flying foxes in Sabah.

## INTRODUCTION

Flying foxes (*Pteropus* spp.) are keystone species primarily associated with tropical and subtropical ecosystems, where they play critical roles in pollination and seed dispersal, contributing to forest regeneration (Chen *et al.* 2017; Oleksy *et al.* 2017; Kingston *et al.* 2023). Flying foxes inhabit diverse environments, ranging from tropical rainforests and mangroves to urban areas with abundant fruiting trees (Mildenstein *et al.* 2016; Yabsley *et al.* 2022), where they interact with humans in long-term coexistence. However, these interactions have intensified in recent decades due to rapid urbanisation, habitat fragmentation, and land-use changes (Florens *et al.* 2017; Meade *et al.* 2021) that further increase their vulnerability to threats (Florens and Baider 2019; Kingston *et al.* 2023). On the other hand, cultural associations with flying foxes can foster stewardship and conservation efforts, while localised strategies integrating community perspectives have been shown to enhance conservation outcomes and promote human-flying fox coexistence (Currey *et al.* 2018; Mo and Demers 2020; Paz and Gonzalez 2021).

Building on these cultural and ecological dynamics, the complex relationship between humans and flying foxes in the Asia-Pacific is shaped by cultural beliefs, utilitarian practices, and increasing human-wildlife conflicts. In many Southeast Asian communities, flying foxes symbolise prosperity, fertility, and protection, while some ethnic groups, such as the Thai Dum (Thailand), Han Chinese, and Iban (Malaysia), use their body parts in traditional medicine, despite the lack of scientific evidence supporting their healing properties (Suwannarong *et al.* 2020; Low *et al.* 2021; Mardiasuti *et al.* 2021; Tackett *et al.* 2022). Additionally, flying fox meat is consumed and traded, contributing to overhunting and population declines (Low *et al.* 2021; Rocha *et al.* 2021; Kingston *et al.* 2023). Habitat destruction and agricultural expansion have further intensified conflicts, as flying foxes raid fruit crops, leading to economic losses for farmers (Oleksy

*et al.* 2021; Charentantanakul *et al.* 2023; Kingston *et al.* 2023). In response, various mitigation strategies have been implemented, ranging from invasive methods like culling to more sustainable approaches such as flying fox-friendly tree netting (Florens and Baider 2019; Shapiro *et al.* 2020; Charentantanakul *et al.* 2023; Kingston *et al.* 2023).

Human-wildlife interactions shape conservation awareness and influence conservation policies and management strategies (Stevens *et al.* 2024; Ahmad and Bhat 2025). Interactions between humans and flying foxes have been documented in various regions but remain understudied in Borneo, with outdated or geographically limited research. In many Pacific islands and Australia, studies have shown that conflict over crop raiding, hunting for food, and disease concerns can directly influence conservation outcomes and public attitudes (Mildenstein *et al.* 2016; Tait *et al.* 2020). For example, lethal control and negative perceptions in Australia have challenged flying fox protection, while community-based education and alternative livelihood options in Pacific Island nations have been linked to improved conservation awareness (Breed *et al.* 2010; Kingston *et al.* 2023). While unsustainable hunting and trade have been reported in Kalimantan, often linked to bushmeat markets and perceptions of disease risk (Harrison *et al.* 2011), updated systematic data are lacking. In Sarawak, more recent studies show that hunting continues, with detailed accounts of meat preparation practices, cultural use, small trade and community perceptions (Mohd-Azlan *et al.* 2022a,b). By contrast, equivalent information from Sabah is sparse, and cultural significance and traditional practices remain largely undocumented.

In Sabah, the protection of flying foxes falls under the Wildlife Conservation Enactment (SWCE) 1997, which regulates wildlife hunting and trade through the Sabah Wildlife Department (SWD) enforcement. The SWD issues three types of hunting licenses: sporting (game), commercial (trade), and "animal kampung" (local consumption) (SWCE 1997). The Wildlife Mar-

ket Logbooks (WML) system was introduced in 2015, requiring traders to record license details, market locations, species, meat weight, and sales to enhance monitoring of the legal wildlife meat trade. Although implemented across all districts, its effectiveness in regulating the flying fox trade remains largely unexamined, underscoring the need for further research and assessment.

This study aims to investigate human-flying fox interactions in Sabah by (1) exploring their cultural and utilitarian significance and describing population trends inferred from participant surveys, market observations, and analysis of Sabah WML and (2) examining anthropogenic threats affecting flying foxes in the region. Understanding human-flying fox interactions provides insights into Sabah's conservation context, supporting the design of sustainable measures that conserve populations, address anthropogenic pressures, and sustain local livelihoods. Recognising their cultural significance further ensures strategies remain grounded in community practices and values, enhancing relevance and support.

## MATERIAL AND METHODS

### Ethical statement

Ethical approval and the Sabah Biodiversity Access License were obtained before data collection (Reference number: JKM/MBS.1000-2/2 JLD.10 (25)). Before applying for the license, permission was sought from the Regional Sabah District Offices and village heads to access the study areas. Access to the Wildlife Market Logbooks (WML) was granted by the Sabah Wildlife Department (SWD) under the reference letter JHL.10-7/27.

### Study Area

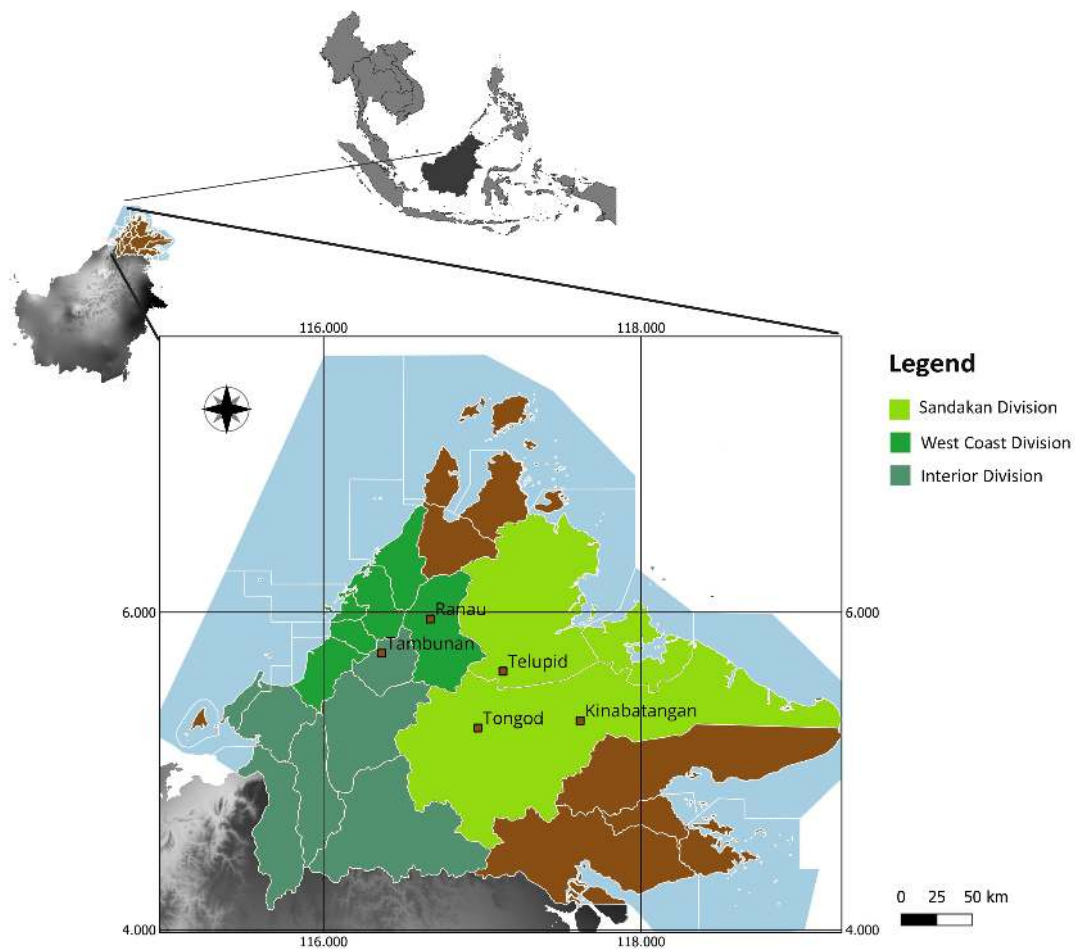
This study was conducted in Sabah, East Malaysia, Borneo, focusing on three administrative divisions: West Coast Division (WCD), Interior Division (IRD), and Sandakan Division (SND) (Figure 1). The questionnaire survey was conducted in five districts (Tambunan, Ranau, Telupid, Tongod, and Kinabatangan) within the WCD and IDN, which were selected based on known flying fox activity and accessibility (Bansa unpublished). These locations were prioritised as participants were more likely to have direct experience with the IUCN Red List 'Endangered' *Pteropus vampyrus* (Mildenstein *et al.* 2022), the focal species of this study. To achieve this, purposive and snowball sampling were employed, with initial contacts established through local leaders and markets, and subsequent participants recommended by those already interviewed. The village head was first consulted within

each district, and only villages where community consent was granted were included. Data was also collected in four local markets located in Tambunan, Ranau, Telupid, and Tongod. Additionally, WMLs from markets in WCD and IRD (2016–2019) were analysed to examine trends in the flying fox trade. Although WMLs may not capture all transactions, they constitute the only official records available for this period and thus provide a valuable minimum baseline of temporal patterns in local market activity in Sabah. Field surveys were conducted between September 2021 and September 2023, while the questionnaire surveys were carried out in September 2021.

### Questionnaire Design, Data Validation and Bias Mitigation

The questionnaire, adapted from Aziz *et al.* (2017), was structured into five main sections to ensure consistency in responses while allowing for open-ended insights (Kabir 2016). The questionnaire was designed and administered in *Bahasa Melayu* using simple, non-technical phrasing. Where necessary, clarification was provided in local languages such as *Dusun* and *Sungai* with assistance from bilingual community members. The *Bahasa Melayu* version of the questionnaire is included in the Additional Files 1. The first section gathered socio-demographic information, including participants' residence, age, gender, ethnicity, highest education level, and occupation. The second section focused on species recognition, where participants were shown two images of flying foxes (*Pteropus* spp.) to ensure better subject recognition. They were then asked to distinguish flying foxes from other bats or animals and describe them. This section also recorded participants' perceptions of disease risks associated with flying foxes, providing a baseline for assessing their awareness regarding zoonotic diseases from flying foxes.

The third section explored cultural and utilitarian practices, documenting local names, traditional beliefs, folklore, and symbolic representations associated with flying foxes. The utilitarian aspects examined the motivations for eating flying foxes, frequency of consumption, access to meat source, preparation and culinary practices, and perceived medicinal benefits and practices. The fourth section asked participants about flying fox observations in the past five years, including sighting locations, districts, and frequency of encounters. The final section examined adverse human-flying fox interactions, focusing on hunting and fruit raiding. For hunting, participants provided information on their motivations, tools used, and trends in hunting activities. This fruit raiding section examined raid frequency, locations, affected crops, and farmers' responses or control measures to reduce losses.



**Figure 1.** Survey locations in Sabah, Malaysia, covering Sandakan (SND), Interior (IRD), and West Coast (WCD) Divisions. Kudat and Tawau Divisions (brown) were not surveyed; IRD and WCD included Wildlife Market Logbooks. Inset map showing the location of Borneo within Southeast Asia.

A pilot study was conducted with ten participants before full implementation to ensure clarity and consistency. This process allowed for refinement of questionnaire wording to prevent ambiguity and enhance participant understanding. Control questions (labelled in Additional File 1) were integrated across sections of the questionnaire to cross-verify participants' self-reported experiences with flying foxes and enhance data reliability. This strategy, consistent with methodological guidance from Adam and Cox (2008) and Taherdoost (2022), was employed to minimise response bias and improve the validity of findings. Additionally, reported flying fox sightings were cross-validated against established ecological and behavioural patterns to enhance data reliability.

Next, sensitive questions covered 'harmful behaviours,' which in this study refers to consuming flying foxes, hunting, capturing, harming flying foxes during fruit raiding and trade. These behaviours are con-

sidered harmful both legally, since they often occur without licenses, and from a public health perspective, due to the zoonotic disease risks associated with handling and consumption. Given the sensitive nature of questions related to harmful behaviours, measures such as ensuring anonymity, emphasising voluntary participation, and reassuring participants about data confidentiality were implemented to reduce social desirability bias and encourage honest reporting. During data collection, follow-up inquiries were made during self-administered surveys to clarify vague, missing, or ambiguous responses, ensuring data accuracy.

### Data Collection: Survey Design and Administration

Participants were recruited using a combination of purposive and snowball sampling, a method well-suited for accessing individuals with direct experience



despite its non-random nature (Atkinson and Flint 2001; Palinkas *et al.* 2015). Initial recruitment was facilitated by village heads and local committees, who coordinated participation at the community level. In markets, participants were approached randomly from among sellers and buyers. This ensured that individuals with various experiences, including farmers, hunters, and consumers, were included in the study. Surveys were conducted in public (local markets) and private settings (participants' homes), depending on participant preference.

The surveys were primarily self-administered and took about 15–20 minutes to complete. Trained surveyors remained present throughout to provide clarification or assistance, particularly for participants with limited literacy, and to conduct follow-up checks. While most sections used fixed-choice questions for quantitative analysis, selected sections (e.g., utilitarian practices and hunting experience) included open-ended items facilitated by surveyors through short qualitative interviews, with responses recorded directly on the forms. This multi survey–interview approach reflects established social and conservation research practices, enabling standardised data collection while allowing qualitative probing to capture depth, context, and culturally sensitive topics (Creswell and Hirose 2019; Roemer *et al.* 2025). Completed forms were subsequently entered into Microsoft Excel for coding and analysis, with a subset of entries cross-checked against originals to ensure accuracy.

## Data Collection: Flying Fox Trade

In addition to questionnaire surveys, field observations were conducted at local markets in Tambunan and Ranau in September and October 2021, and again in January, October, and November 2022. In Telupid and Tongod, observations were made in September and October 2021, in January, October, and November 2022, and in August and September 2023. These visits coincided with fruiting seasons, when rambutans and langsat are abundant and flying foxes typically forage in the region. The objective was to assess whether flying foxes were openly sold with other wildlife meats and whether restaurants advertised them on menus. While this approach allowed targeted monitoring during peak selling periods, the visits were limited in number and restricted to certain months, which may have excluded off-season or discreet trade activities. During each survey, key information recorded included the date, location, number of flying foxes sold, specific body parts traded, and the availability of flying fox dishes on restaurant menus. These observations provided independent validation of market trade activity, complementing data from the WMLs spanning 2016 to 2019.

This study analysed WMLs spanning 2016 to 2019, focusing on flying fox sales recorded in markets within WCD and IRD. The WML records key information, including vendors' names, commercial license numbers, market addresses, hunted and traded wildlife species, and the corresponding meat weights (in kilograms). Additionally, receipts for game meat purchases document the price per kilogram, the animal parts sold, and details of the hunter or supplier, including their name and license number (Additional File 2). Due to missing or incomplete entries in the logbooks, only the locations of markets and the number of animals per species were used.

## Data Analysis

This multi-method approach integrated both quantitative and qualitative insights. Responses were systematically screened for consistency. Screening for consistency meant checking participants' answers across control questions (e.g., Q2a, Q2e, Q4a). If responses contradicted each other or were illogical, surveyor notes were consulted; unresolved cases were omitted from analysis. Data from multiple participants were compared to identify shared patterns (e.g., fruit species raided, hunting reasons), and not to remove responses. Comparisons with existing literature and conservation reports were made after coding and quantifying responses, at the interpretation stage, to contextualise findings without influencing initial categorisation. This triangulation process ensured the robustness of the findings and enhanced their reliability by validating them against existing literature and local conservation reports (Heale and Forbes 2013; Busetto *et al.* 2020).

Descriptive statistics, including frequency distributions and cross-tabulations, were computed using R software version 4.3.1 (R Core Team 2024). Associations between fruit raiding frequency and response type (non-lethal vs. lethal) were tested using a chi-square test for the overall 4×2 contingency table. Focused pairwise comparisons were examined using Fisher's exact test implemented, which also generated odds ratios and 95% confidence intervals for 2×2 contrasts.

Open-ended responses on cultural significance, observations, hunting, and fruit-raiding were analysed using manual thematic coding. Responses were entered into a spreadsheet, read repeatedly for familiarity, and inductively coded with short labels to capture common ideas. Codes were then grouped into broader categories and themes (Braun and Clarke 2006; Buchholtz *et al.* 2023). Multiple themes could apply to a single response, and because participants often gave more than one answer, the number of responses exceeded the number of participants. Themes and fre-

quencies were then summarised for interpretation, consistent with recent conservation applications (Buchholtz *et al.* 2023; Murphy *et al.* 2025).

Wildlife Market Logbooks (2015–2019) were reviewed to extract information on market distribution by division and district, number of recorded entries, and species composition. Records were entered into a spreadsheet, and descriptive statistics were used to calculate the number of active markets, frequency of entries, and relative proportions of species traded. Records of flying foxes were examined by year and location to assess their representation in the trade. As license and receipt details were often incomplete, analysis focused on presence–absence, counts, and relative species frequencies.

## RESULTS

### Demographic Profile

A total of 100 participants (53 males, 47 females) were surveyed, with most participants aged 45–54 years (31%). The majority had a secondary education (62%) and were self-employed (43%). Geographically, most participants were from Kinabatangan (29%), Ranau (23%), Tambunan (22%), and Tongod (15%), regions with known flying fox activity. Kadazandusun (52%) and Sungai (33%) were the most represented ethnic groups (details in Table 1, Additional File 3). Demographic information for registered logbook owners was more limited. A total of 490 registered commercial hunting licence holders were identified, with 18.6% ( $n=91$ ) residing in WCD and 81.4% (399) in IRD.

### Cultural and Utilitarian Perspectives

Participants reported varying local names for flying foxes across different regions and ethnic groups in Sabah. Among the Kadazandusun in western Sabah, they are commonly called *gawir* (ga-wir), except in Papar and Beaufort, where *mangkalau* (mang-ka-lau) is used. The Kadazan in Penampang refer to them as *gavi* (ga-vi), while the Dusun in central and eastern Sabah use *mangkawot* (mang-ka-wot). Similarly, the Sungai ethnic group also uses *mangkawot*, with some variations such as *ngkawot* (ng-ka-wot). In Kinabatangan (Sukau, Bukit Garam region: East), certain Sungai communities use the term *keboi* (ke-boi). The Murut commonly call flying foxes *bengkawot* (beng-ka-wot) or *bangkawot* (bang-ka-wat), while the Bajau in Kota Belud use *bangkuet* (bang-ku-et).

Participants did not report any traditional belief and folklore. Two Murut participants linked flying foxes to a local Tongod motif called *vinangkawot*. This motif, commonly represented in woven crafts, sym-

bolises the elegance of flying foxes in flight and reflects their significance in traditional artistic expressions. The Sungai in Kinabatangan reported a taboo: they must avoid flying fox urine, as contact was believed to cause baldness ( $n=3$ ).

Overall, 23% of participants reported consuming flying foxes across the study area, with the highest consumption recorded in the IRD (34.8%) and SDN (34.7%). Most consumers belonged to the Kadazandusun (73.9%) and Sungai (21.7%) ethnic groups, with consumption most prevalent among adults aged 35 and above (82.6%). The primary reasons for consuming flying foxes were food (26.1%), traditional medicine (30.4%) or both (43.5%). Additionally, most consumers reported consuming flying foxes only once every several years (60.9%) (details in Table 2, Additional File 3). Furthermore, 18 consumer participants reported that flying fox meat has become scarce and increasingly difficult to obtain.

Flying fox dishes were primarily served during social events, particularly for guests when the meat was available (see Text Box 1 for details). Among consumer participants, 43.5% ( $n=10$ ) reported learning to prepare and serve flying fox dishes from family and friends. Of these, ten individuals (9 females, one male) had direct experience in cooking flying foxes. The preparation of flying fox meat involved several steps, which were consistently reported by these participants (see Text Box 2 for details). In terms of hygiene, all participants stated that they practiced basic cleanliness; however, none were aware of the risks associated with zoonotic disease transmission. Additionally, the most (78.3%,  $n=18$ ) preferred to removing the internal organs before cooking.

#### Box 1:

The most common foods made of flying foxes are porridge, stew, and dry fried soy sauce. The participants mentioned that these dishes eat as meals or as accompaniments or "finger foods" (known as *pusas* among Kadazandusun) often paired with alcoholic drinks like beer and traditional Kadazandusun liquors such as *lihing* and *montoku* and rice wines such as *tumpang* and *tapai*.

#### Box 2:

The preparation of the meat involves several stages: singeing the fur, removing the internal organs, boiling for up to two hours, and cooking with herbs such as onions, garlic, and ginger. The process begins by burning off the fur over an open flame. The flying fox is then butchered into smaller pieces, washed, and boiled for at least an hour or until tender. Once cooked, the meat is used in various dishes, including porridge and stew.

Local participants noted that consuming flying foxes is believed to offer various medicinal benefits,

primarily for asthma (65.2%), as well as for joint pain (4.3%) and high blood pressure (4.3%). Additionally, 39.1% (n=9) of participants reported variations in consumption methods for medicinal purposes. The most common practice was eating the meat (n=6), followed by drinking fresh blood (n=1), consuming liver soup with herbs (n=1), and drinking *montoku* infused with flying fox (n=1) (details in Table 2 and Image 1, Additional File 3).

## Flying Fox Observations and Population Trends

Based on observations of flying foxes, 77% of participants reported having observed these animals firsthand. Most participants (59.7%) reported encountering fewer than ten individuals per sighting. Regarding sighting frequency, 37.6% stated that their last observation occurred more than five years ago, while only 15.6% reported frequent sightings. The primary locations of sightings included orchards (37.6%), open skies (23.4%), and forests (21.4%). The most reported sighting locations included Kinabatangan (36%), Ranau (22.1%), Tambunan (17.4%), and Tongod (16.3%) (details in Table 3, Additional Files 3).

## Flying Fox Hunting

Of the eleven hunters, most were male (81.8%), with different ethnic groups (Kadazadusun (72.7%), Sungai (18.2%), and Murut (9%)) participating in this survey; only one male hunter reported holding a hunting licence from the Sabah Wildlife Department. The main reasons for hunting were meat (53.3%), protection of fruiting trees (33.3%), selling (6.7%), and medicinal purposes (6.7%) (details in Table 4). All eleven hunters expressed that they were unaware of the risks associated with zoonotic transmission from flying foxes.

Based on their responses, hunters were categorised into two groups based on their primary hunting location: on-site hunters (36.4%) and orchard hunters (63.7%). Two on-site hunters reported that they opportunistically hunt flying foxes at foraging sites, particularly during the fruiting season, but they experience greater success at roosting sites. All four on-site hunters acknowledge that hunting in roosting sites presents several challenges such as accessibility and forced translocation of the population after the hunting event, and a reduction in the population size in the following season. All four on-site hunters indicated that their primary hunting grounds were mangroves and remote forested areas near water bodies. Shotguns are the primary hunting tool, and at roosting sites, hunters typically harvest between 10 and 100 individuals in a single night. Two participants reported

that mother flying foxes are killed, leading to the capture of their pups, which are either taken as pets or used for consumption.

For orchard hunting, they usually hunt flying foxes during fruiting seasons and durian flower blooming periods. As for hunting methods, they listed common tools they use to hunt flying foxes: nets (26.7%), *rawai* (26.7%), slingshot (13.3%) and shotgun (6.7%) (details in Table 4, Additional File 3). Based on the orchard hunters (n=3), they usually get from 1 to 15 flying foxes in one trapping event.

## Flying Fox Fruit Raiding

Out of 100 participants, 48% reported experiencing flying foxes raiding their fruit trees. Among these 48 participants, there were 79 reported instances of fruit raiding across various locations, with the highest occurrences in Kinabatangan (38.0%), Ranau (22.8%), Tambunan (19.0%), and Tongod-Pinangah (17.7%). Percentages reflect the districts where participants reported experiencing fruit raiding, which may or may not coincide with their residential district or interview location. Regarding the frequency of fruit raiding, 34.6% of participants experienced crop raiding at least once, more than five years ago, while 30.8% reported annual raids. Additionally, 17.3% experienced raids 1–2 times in the past five years, and another 17.3% reported 3–4 incidents within the same period. (see Table 5, Additional File 3 for details).

Regarding resolving fruit raiding conflicts, most participants preferred non-lethal responses (71.4%), with 45.8% allowing flying foxes to feed and 18.8% allowing feed and chase. Consistent with this, deterrents were mainly non-lethal (70.3%), including lamps (37.8%), sound devices (13.5%), customised poles with sacs (13.5%), and other manual techniques (5.4%). Lethal methods (29.7%) included *rawai* (10.8%), nets (10.8%), slingshots (5.4%), and shotguns (2.7%) (see Figure 2 for more details on the use of customised poles with sacs and *rawai*). For net catching, all four participants indicated they would kill any flying fox caught in the nets rather than release it.

Across all four raiding frequency categories, non-lethal responses predominated. Among participants who experienced annual fruit raiding, chasing flying foxes was the most common reaction (16.7%), while lethal methods accounted for 8.3%. However, the proportion of lethal responses increased overall with more frequent raiding (from 4.7% in >5 years ago to 8.3% in annual raiding). Although a chi-square test did not detect a statistically significant association between raiding frequency and response type ( $\chi^2 = 5.4$ ,  $df = 3$ ,  $p = 0.10$ ), the observed trend suggests that repeated crop losses may reduce tolerance and raise the likelihood of lethal responses. Participants with

annual fruit-raiding were nearly four times more likely to adopt lethal responses than those raided >5 years ago. However, this difference was not statistically significant (Fisher's exact test, OR = 3.9, 95% CI = 0.5–48.0,  $p = 0.2$ ).

Participants reported only seasonal fruit tree species, totalling 187 mentions, as several individuals listed more than one species. They identified nine commercially important fruit trees frequently visited or eaten by flying foxes, including dukulangsat (*Lansium domesticum*) (34.3%,  $n=64$ ), rambutan (*Nephelium lappaceum*) (24.1%,  $n=45$ ), durian (*Durio zibethinus*) (15.0%,  $n=28$ ), mango (*Mangifera indica*) (9.1%,  $n=17$ ), rose apple (*Syzygium jambos*) (8.0%,  $n=15$ ), longan or *mata kucing* (*Dimocarpus longan*) (5.4%,  $n=10$ ), and tarap fruit (*Artocarpus odoratissimus*) (4.3%,  $n=8$ ). Ten participants reported earning additional income by selling these fruits during the fruiting season, while five mentioned that fruits were primarily for their own consumption. Two participants noted that flying foxes are attracted to durian flowers at night and believed they damage the flowers and reduce fruiting.

## Flying Fox Trade

During the survey in September 2021 at the towns and main local markets in Ranau, Telupid and Tambunan, the meat of flying foxes was not seen in local markets nor sold in restaurants or roadside stalls. However, three hunters, one of whom was a seller (interviewed in local markets) indicated that flying fox meat was discreetly available, mainly through personal contacts, and discreetly sold in local markets. Five consumers reported that interdistrict trade was used to meet the demand in other districts. The price of flying fox meat ranged from MYR 25 to MYR 40 (approximately USD 4 to USD 9) per bat.

A review of the WMLs from 2015 to 2019 revealed 839 records: 706 from the IRD and 133 from the WCD, contributing to a total of 15,631 wildlife records. Based on the logbooks, 455 markets were identified, 365 in IRD and 90 in WCD. Six wildlife species were recorded in the logbooks: bearded pig (*Sus barbatus*,  $n=13,179$ , 85.8%), sambar deer (*Rusa unicolor*,  $n=1,851$ , 11.8%), barking deer (*Muntiacus* spp.,  $n=518$ , 3.3%), saltwater crocodile (*Crocodylus porosus*  $n=37$ , 0.2%), mousedeer (*Tragulus* spp.,  $n=23$ , 0.1%), and flying foxes (*Pteropus* spp.  $n=23$ , 0.1%). For flying foxes, the records were that in 2019, only two markets in Keningau and Tambunan District (IRD) sold flying foxes, accounting for just 0.2% ( $n=23$ ) of the total wildlife species recorded in the IRD ( $n=13,132$ ). The logbooks did not specify the exact number of flying foxes sold, as they typically lacked hunting licenses or transaction receipts.

## DISCUSSION

### Cultural, Utilitarian Values and Zoonotic Risks

Findings from this study indicate that terminology affects species recognition, influencing survey responses. While the Malay term *keluang* was used, many participants ( $n=23$ ) were unfamiliar with it, identifying flying foxes only after seeing pictures and hearing local names. Some also misidentified them as common bats ( $n=15$ ), underscoring the importance of region-specific terminology for accurate data collection. This study suggests using the term *gawir* (WCD) and *mangkawot* (IRD and SND) for clearer species distinction.

Flying foxes hold cultural and utilitarian importance among participants from the Kadazandusun, Sungai, and Murut ethnic groups. These findings in Sabah align with the predominantly positive representations of flying foxes across Southeast Asia. For instance, among the Iban in Sarawak, they feature in children's rhymes and warrior tattoos; in Malaysia and Indonesia, they appear in *songket* textile motifs; and in the Philippines, they are regarded as guardians of fishing grounds (Low *et al.* 2021). Such examples indicate that, despite occasional taboos such as beliefs in Myanmar that flying foxes can foretell storms (Low *et al.* 2021) or among the Sungai community in Sabah that their urine causes baldness, flying foxes are also regarded as positive symbols. Recognising this broader pattern of positive cultural values strengthens the case for conservation strategies that draw upon existing traditions, reinforcing stewardship and coexistence (Low *et al.* 2021; Kingston *et al.* 2023).

Flying fox meat is considered a delicacy, typically stewed, fried, or made into porridge, often served at social gatherings, a tradition seen across Southeast Asia (Sheherazade and Tsang 2015; Mildenstein *et al.* 2016; Mohd-Azlan *et al.* 2022a). Recipes have been passed down through generations, reinforcing their cultural significance. Notably, locals cook flying fox meat multiple times, a practice also observed in Sarawak to reduce odour (Mohd-Azlan *et al.* 2022a). Beyond food, flying foxes are used in traditional medicine, believed to treat asthma, joint pain, and high blood pressure, though these claims lack scientific evidence. Similar medicinal practices occur in Indonesia, Thailand, and India, where flying fox meat and blood are consumed for perceived health benefits (Mardiastuti *et al.* 2021; Mohd-Azlan *et al.* 2022a; Tackett *et al.* 2022).

While respondents possess cultural significance and local ecological knowledge (LEK) about flying foxes, the majority have little to no knowledge of zoonotic risk. The contact with flying fox fluids poses zoonotic risks, particularly from Nipah virus (Chua *et al.* 2002;





**Figure 2.** In Tongod, bamboo (a1) or pipe poles (a2) with white sacs move with the wind to deter flying foxes from rambutans. In Sandakan, *rawai* fishing lines (b1) with hooks spaced approximately 50 cm apart are used lethally to hook flying fox (b2, b3) or rupture the wing membrane, causing it to fall to the ground and eventually facilitating capture. Source: L. Bansa, Overs N.

Sendow *et al.* 2013). Consuming raw blood for traditional ailment reported in this study is risky and dangerous, as flying foxes are known disease reser-

voirs (Wacharapluesadee *et al.* 2006; Sendow *et al.* 2013). While thorough cooking reduces pathogen viability, zoonotic risks remain (Tumelty *et al.* 2023). In

addition, hunting and trade increase human–animal contact, raising the risk of zoonotic disease transmission (Choo *et al.* 2024). To mitigate public health risks, awareness efforts should target high-risk groups such as hunters, consumers, and traders (Keatts *et al.* 2021).

## Observations on flying foxes

This study suggests that human-flying fox interactions inform local flying fox observations, providing valuable insights into habitat use and potential population trends. Most of participants reported having seen fewer than ten individuals (59.7%), with many indicating that their last sighting occurred more than five years ago (37.6%), suggesting a potential population decline. Additionally, consumer and hunter participants noted a reduced availability of flying fox meat and presence in recent years, further supporting this observation. Comparable observations have been documented in Kalimantan and Sarawak (Harrison *et al.* 2011; Mohd-Azlan *et al.* 2022a). Participants identified key roosting and feeding locations, with frequent sightings in Kinabatangan, Ranau, and Tongod, areas crucial for endangered species like the large flying fox (*P. vampyrus*) (Phillipps and Phillipps 2018; Mildenstein *et al.* 2022). Additional reports from Papar, Tambunan, Lahad Datu, and Paitan highlight other important habitats in various districts of Sabah requiring protection and monitoring.

It remains uncertain whether these patterns reflect an actual population decline or a shift in distribution driven by habitat changes and hunting pressure. Nonetheless, this anecdotal observation is consistent with the latest population trend for flying foxes especially the IUCN-listed endangered species *P. vampyrus* reported across its distribution range (Tsang 2018; Mildenstein *et al.* 2022). To address this uncertainty a state-wide survey integrating local knowledge, such as identifying roosting sites, with scientific methods like citizen science, population monitoring, and satellite tracking is essential (Biddle *et al.* 2021; Zulian *et al.* 2021; Mohd-Azlan *et al.* 2022b). This interdisciplinary approach is crucial for data-driven conservation, particularly in regions lacking formal monitoring.

## Flying Fox Hunting in Sabah

Hunting of flying foxes (*Pteropus* spp.) in Sabah occurs at both roosting and foraging sites, driven by LEK developed through long-term human-flying fox interactions. Hunters rely on generational knowledge of habitats, seasonal movements, and fruiting cycles, paralleling the Local Ecological Calendar (LEC) used by indigenous communities in Indonesia (Tukuboya *et al.* 2024). While this deep ecological understanding

aids traditional hunting, it also increases hunting efficiency, raising conservation concerns. This efficiency is further reinforced by modern technologies such as shotguns and motorised boats, which make hunting faster and more accessible to remote roosting sites. Based on the participants, hunting peaks during the fruiting seasons, when flying foxes congregate around rambutan, *duku-langsar*, and longan trees, as well as during the flowering season of durian. This seasonal pattern has been documented in several studies, which report that hunting pressure closely coincides with major fruiting periods (Fujita and Tuttle 1991; Struebig *et al.* 2007; Harrison *et al.* 2011; Aziz *et al.* 2019). As flying foxes become more visible near orchards and residential areas, they are easier to target (Aziz *et al.* 2017). In addition, frequent hunting disrupts roosting behaviour, forcing flying foxes to abandon traditional sites and relocate to remote areas.

Despite their familiarity with flying fox habitats, hunters report that active roosting sites are harder to find due to hunting-induced displacement. Similar patterns have already been documented by Fujita and Tuttle (1991). This is especially evident in *P. vampyrus*, which seeks isolated locations to avoid disturbance (Aziz *et al.* 2019; Mohd-Azlan *et al.* 2022a). Most flying fox captures in this study occurred in Nipah mangroves and remote forests in interior districts, while coastal and island populations of *P. hypomelanus* were less targeted due to logistical challenges and protected island area restrictions. Tanalgo *et al.* (2023) emphasise that in many low-income regions, hunting intensity is driven not only by cultural practices but also by economic and geographic accessibility, which mirrors the Sabah context where modern tools and mobility expand access to once-remote roosts.

Shotgun hunting at roosting sites increases hunting efficiency and raises serious conservation concerns (Kingston *et al.* 2023). The widespread use of shotguns allows hunters to harvest large numbers of bats in a single night, far exceeding what could be achieved with traditional nets or hook lines. Traditional hunting methods include kites, hook lines, and nets, also contribute to overharvesting, particularly on small islands where populations are naturally low (Kingston *et al.* 2023). Given their low reproductive rate (one pup per year) and long generation time (6–8 years) (Mildenstein *et al.* 2016), intensified hunting pressure could lead to unsustainable population declines. Such vulnerability of island-dwelling has also been highlighted globally, with island endemics identified as particularly exposed to overhunting pressures (Tanalgo *et al.* 2023).

Hunting practices in Sabah today, such as the use of *rawai*, nets, and occasional shooting, are generally small-scale and tied to household consumption or crop protection. However, historical evidence suggests in-

tensive culling once occurred in plantation settings (Fujita and Tuttle 1991). For example, a large-scale shooting took place at the Sabah Softwoods plantation in 1983, where thousands of large flying foxes feeding on *Eucalyptus deglupta* were killed for sport (Fujita and Tuttle 1991). Thousands of bats were reportedly killed annually in 1983–1984, but by 1985 their numbers had collapsed (Fujita and Tuttle 1991). Other than shotguns, the use of large fine-mesh nets, such as those used by the Iban in Sarawak and Kalimantan, could capture hundreds of bats in a single evening for the bushmeat trade (Fujita and Tuttle 1991; Struëbig *et al.* 2007; Harrison *et al.* 2011). These illustrate that sport and commercial hunting across Borneo drove sharp local declines, highlighting the need for regional conservation strategies.

While LEK from long-term human–flying fox interactions helps hunters develop efficient tracking and hunting techniques, it also increases conservation risks. Disruptions to roosting behaviour, forced relocations, and intensified hunting methods highlight the urgent need for conservation interventions. However, such knowledge can also be harnessed for conservation purposes. For instance, hunters in New Caledonia provide vital knowledge of roost sites and seasonal patterns, and their willingness to adjust hunting practices positions them as key partners in monitoring and policy-based conservation (Oedin *et al.* 2021). Similarly, in Sabah, adopting such approaches could transform hunters' knowledge into a conservation asset by involving them in roost monitoring, community education, and awareness on hunting regulations, providing alternative livelihoods and strengthening community-based management.

## Flying Fox Fruit Raiding in Sabah

Half of the surveyed participants (48%) reported experiencing flying foxes raiding seasonal fruit crops, a localised and seasonal issue that elicited mixed responses. Responses among participants highlight a divide: some participants accepted fruit losses as part of coexistence, while others, particularly orchard hunters, favoured lethal measures. Letting flying foxes be was the most common reaction, especially when fruit raiding was infrequent. Chasing was the second most frequent response and increased with more frequent raiding. Non-lethal responses outweighed lethal ones by about 8:1 among participants who had not experienced raiding in five years, but only 2:1 among those with annual raids. This suggests that more frequent fruit raiding may be associated with an increase in lethal responses. The trend resembles conflict escalation documented in other human–wildlife interactions (Nattrass and Conradie 2018; Sharma *et al.* 2020) and is consistent with findings from flying fox stud-

ies, where growers experiencing higher levels of crop raiding were more likely to support or employ lethal measures (Aziz *et al.* 2017). Although the relationship in this study was not statistically significant, likely due to the small sample size, the similarity underscores the need for further research with larger datasets.

Participants' tolerance of fruit raiding appeared to be shaped by fruit abundance, the seasonal and short-term nature of economic losses, and the fact that some participants gained secondary income from fruit sales (Win and Mya 2015; Aziz *et al.* 2017). In areas where fruit farming is a primary livelihood, and where some individuals may also sell flying fox meat, tolerance may be lower, and retaliatory killings could pose a greater conservation risk (Harrison *et al.* 2011; Sheherazade and Tsang 2015; Aziz *et al.* 2017; Oleksy *et al.* 2021). A minority of individuals may also sell flying fox meat for additional income; however, flying fox meat is typically consumed as a seasonal delicacy rather than a staple protein in Sabah. While it does not play a major role in food security, its supplementary value and associated economic incentives could undermine long-term coexistence, particularly if conflicts increase; further studies are needed to understand these dynamics better.

Using of non-lethal strategies among local farmers presents an opportunity for scalable, sustainable solutions. Such strategies were already reported in the early 1990s, when farmers used bright lamps or small fires beneath fruiting trees to deter flying foxes (Fujita and Tuttle 1991). In addition to traditional local methods, other effective deterrents, such as safely netting individual trees, planting decoy crops, and using repellents with unpleasant smells or tastes, have been reported and can be further promoted (Berthius *et al.* 2022). While local conservation efforts emphasise non-lethal approaches, global examples highlight the risks of lethal measures. In Mauritius, government-supported culling of flying foxes led to unintended ecological consequences and may have exacerbated long-term crop losses (Oleksy *et al.* 2017; Florens and Baider 2018). Similarly, traditional netting and hook-line hunting in the Philippines have driven unsustainable population declines (Mildenstein *et al.* 2016; Kingston *et al.* 2023). These cases serve as cautionary lessons for Sabah, where lethal control methods could threaten both biodiversity and agricultural sustainability.

Human–flying fox interactions related to fruit raiding demonstrate varying degrees of tolerance and persecution, shaping conservation outcomes. Addressing this conflict through effective, non-lethal strategies is essential to balancing conservation and agricultural needs. Conservation efforts can enhance coexistence between human and flying foxes in Sabah by improving community awareness, promoting sustainable mit-



igation techniques, and preventing retaliatory killings. In practical terms, this could complement existing wildlife regulations with community-based initiatives that promote awareness, alternative livelihoods, and incentives for non-lethal management. Such a dual approach combines policy frameworks with local engagement, ensuring conservation measures are effective, inclusive, and sustainable.

## Flying Fox Trade and Sabah Wildlife Trade Logbooks

The trade of flying foxes (*Pteropus* spp.) in Sabah remains local, informal, and vastly underreported, reflecting broader challenges in monitoring and regulating wildlife markets. While market surveys found no evidence of open sales in dining shops or *tamu* (open-air local markets) (Pugh-Kitingan 2014), flying foxes are still sold seasonally in certain local markets. Much of the trade, however, occurs privately and informally, leading to significant gaps in official records. Similar biases have been noted globally, where wildlife trade records tend to overrepresent larger and charismatic species, while failing to capture the full diversity and extent of traded taxa (Soares *et al.* 2025).

From 2015 to 2019, WMLs recorded flying foxes as only 0.18% of total wildlife sales, primarily in Keningau and Tambunan. However, data collection inconsistencies, such as the use of digital logbooks in the ID and physical records in the WCD, increase the risk of data loss and reporting errors. Establishing a centralised digital database and conducting regular audits would improve monitoring, transparency, and enforcement (Hinsley *et al.* 2024).

Although this study documented only two markets and 23 records of flying fox sales, the accurate scale of trade is likely higher. Several participants emphasised that flying foxes are often sold discreetly through personal contacts rather than openly in markets, partly to avoid licensing requirements and enforcement scrutiny. This pattern of underreporting is consistent with findings elsewhere in Southeast Asia, where wildlife deemed sensitive or restricted is commonly traded outside formal market structures (Mickleburgh *et al.* 2009; Nijman 2010; Sheherazade and Tsang 2015). As such, the available figures should be interpreted as conservative estimates. Recognising this hidden trade is essential for conservation planning, as this unregulated trade poses a hidden threat to flying fox populations and may increase the risk of viral spillover (Roe and Booker 2019). Addressing the informal wildlife trade is therefore critical for biodiversity conservation and public health.

While Sabah's flying fox trade remains small and localised, it is not isolated from the broader regional wildlife trade network. Neighbouring Indonesia

records high trade volumes, particularly in Sulawesi and Kalimantan (Mildenstein *et al.* 2016; Sheherazade and Tsang 2018). Cross-border trafficking of flying foxes from Sabah has been documented often alongside pangolins (*Manis javanicus*) and sun bear (*Helarctos malayanus*) paws (Ladjana and Raimi 2019). This suggests Sabah serves as both a source and transit point in the illegal wildlife trade.

Both flying fox species in Sabah (*P. vampyrus* and *P. hypomelanus*) are listed under CITES Appendix II, requiring strict monitoring and regulation to prevent overexploitation (CITES 2024). Evidence shows that threatened and CITES-listed species are often traded for a greater number of parts and uses, as their rarity increases both demand and market value (Soares *et al.* 2025). Without stronger enforcement, continued trade could push these species toward a higher-risk conservation category. With this, strengthening trade regulations, enforcement mechanisms, and public awareness is essential to curbing illegal trade and ensuring the long-term survival of Sabah's flying fox populations.

Market prices for flying foxes have ranged from less than USD 1 in some locations (Mildenstein *et al.* 2016) to nearly USD 10 in Jakarta in the early 1990s (Fujita and Tuttle 1991; Mickleburgh *et al.* 2009). Intermediate values were reported at USD 2.50–3.30 in Kuching (early 1990s) (Fujita and Tuttle 1991), USD 0.36–3.63 in Sulawesi (Sheherazade and Tsang 2018), and about USD 3.60 in Luzon, Philippines (Scheffers *et al.* 2012). More recently, in Sabah and Sarawak, bats were sold for MYR 10–40 (USD 2.50–9) per bat, considerably higher than chicken (MYR 8.50/kg, USD 2/kg) (Mohd-Azlan *et al.* 2022a). These patterns suggest flying foxes are valued across Southeast Asia as delicacies or specialty foods tied to cultural utilitarian practices and medicinal use, rather than as staple protein.

These trade patterns highlight the need for conservation strategies that go beyond blanket hunting bans. Targeted interventions could include strengthening enforcement in high-demand local markets, promoting culturally appropriate awareness campaigns that emphasise the ecological role of flying foxes, and developing community-based alternatives in hunting areas. Cross-border collaboration is also crucial, given the regional nature of trade networks across Borneo and the wider Southeast Asian region.

## Limitations and Future Studies

This study encountered several limitations, mainly due to restricted access to villages and challenges in participant recruitment during the post-COVID-19 period and associated movement restrictions. Consequently, the sample size was modest, which may have affected the representativeness of the findings. De-



scriptive statistics (frequencies and percentages) were used to analyse survey and logbook data, yielding valuable insights. A larger sample size and the application of advanced statistical analyses, might further enhance the robustness and generalisability of the overall results.

In addition, the market survey and logbook components may have underestimated the accurate scale of the flying fox trade. Market observations were periodic and limited to specific months, while trade in protected species is often concealed. Similarly, logbooks frequently lacked details such as quantities sold or license numbers. As a result, the trade findings should be interpreted as conservative estimates. Future research should incorporate more frequent, year-round monitoring and complementary approaches such as vendor interviews, triangulation with enforcement data, and adoption of indirect questioning techniques to minimise underreporting.

Collecting information on sensitive topics such as hunting and trade required a careful ethical approach. In this study, surveyors reassured participants of strict confidentiality before the survey began to encourage honest responses. Nevertheless, a potential limitation of this approach is that, despite assurances, some participants may still have underreported or concealed behaviours they perceived as incriminating. This could affect the completeness and accuracy of the data. To strengthen future research, indirect questioning techniques such as the Unmatched Count Technique (UCT) or Randomised Response Technique (RRT) are recognised as valuable tools, as they allow sensitive data to be captured while protecting participant confidentiality (Hinsley *et al.* 2019; Ibbett *et al.* 2021).

The surveyed participants were predominantly from Kadazandusun-majority districts such as Tambunan and Ranau. At the same time communities in Telupid, Tongod, and Kinabatangan represented the Orang Sungai, Murut, and Kadazandusun ethnic groups (Department of Statistics Malaysia 2024). Although the study captured perspectives from Sabah's major indigenous communities, it did not fully reflect the broader demographic diversity, particularly in urban areas. Broadening future studies to include additional regions and ethnic groups may help minimise sampling bias and improve inclusivity.

Moreover, interactions with human-flying fox populations contribute to shaping conservation awareness among participants in Sabah, yet current understanding remains incomplete. Further investigation into key stakeholders' knowledge, attitudes, and perceptions including hunters, consumers, buyers, and those affected by fruit-raiding conflicts, could provide deeper insights. Addressing these gaps strengthen conservation efforts and guide evidence-based policy decisions for flying foxes in Sabah. Recommendations for future

research include:

1. Expanding geographical coverage (e.g., Tawau and Kudat Divisions) and increasing the sample size.
2. Utilising anonymous survey methods (e.g., the Randomised Response Technique) for sensitive topics like hunting.
3. Examining local attitudes and perceptions of flying foxes.
4. Enhancing wildlife trade data by interviewing enforcement agencies.
5. Evaluating the economic impacts of crop-raiding to inform cost-effective mitigation strategies.
6. Exploring the role of flying foxes in disease ecology to inform public health policies better.

## CONCLUSION

This study investigated human–flying fox interactions in Sabah, focusing on cultural and utilitarian practices, population visibility, and anthropogenic pressures. Flying foxes were valued for food, medicine, and symbolism; however, participants noted reduced sightings and meat availability, consistent with population declines across their range. Hunting, fruit-raiding, and informal trade were evident, with ecological knowledge and modern tools enhancing hunting efficiency, while tolerance toward fruit-raiding decreased under repeated losses. Collectively, these findings highlight continuous threats to *P. vampyrus*, an IUCN-listed endangered species in Sabah. The results emphasise that conservation strategies should extend beyond regulation alone. Hidden trade, underreporting in WMLs, and reliance on lethal crop protection underscore the need for stronger monitoring, targeted enforcement, and promotion of non-lethal conflict mitigation. At the same time, the persistence of cultural values and local ecological knowledge offers important opportunities for conservation, particularly through community-based roost monitoring, culturally appropriate awareness initiatives, and stewardship practices.

## ACKNOWLEDGMENTS

We are grateful to various individuals and organizations for supporting this research. We acknowledge financial support from the Nagao Natural Environment Foundation (2019.07.09), the Rufford Foundation (38367-1), and the Fundamental Research Scheme Grant (FRGS) of the Malaysian Ministry of Higher Education (Ref. no:

FRGS/1/2022/WAB11/UMS/02/2). Thanks to participants and volunteers (Afif Mustaqim Basran, Arlsene Bryan Ajis Madaun, Nurain Musi) for their efforts and assistance in data collection. The support of agencies and committees, including the Sabah Biodiversity Centre, District Officers, head and village management committees, the Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, and the University College Sabah Foundation, is also appreciated. Additionally, we thank Sheema Abd. Aziz and Christian Vincenot for guidance, consultation, and valuable comments on the draft; Benoit Goossens, Liew Thor Seng, and Tuan Soffian Abu Bakar for their insights throughout the research process, and the anonymous reviewers for their valuable feedback.

## DATA AVAILABILITY

The data used to support the findings of this study are available from the corresponding author upon reasonable request.

## CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

## CONTRIBUTION STATEMENT

LAB and RR conceived the study and, with NHH, provided research resources. LAB and RR collected the data. Data analysis was performed by LAB, RR, MP, LF, SGS, and NHH. LAB and RR wrote the first draft, and all authors (LAB, RR, MP, LF, SGS, and NHH) reviewed and finalised the manuscript. MP, LF, SGS, and NHH supervised the work.

## DISCLOSURE OF AI USE

The authors used ChatGPT to support language refinement, literature searches and references formatting checking. All content was subsequently reviewed and edited by the authors to ensure accuracy and appropriateness.

## REFERENCES

Adams A, Cox AL (2008) **Questionnaires, In-depth Interviews and Focus Groups**. In: Cairns P, Cox AL (eds.) *Research Methods for Human Computer Interaction*. 1st ed. Cambridge University Press, Cambridge, pp. 17–34.

Ahmad K, Bhat A (2025) **Wildlife Management**. In: Mandal AK, Nicodemus A (eds.) *Textbook of For-*

*est Science*. 1st ed. Springer Nature, Singapore, pp. 333–360. doi: [10.1007/978-981-97-8289-5\\_15](https://doi.org/10.1007/978-981-97-8289-5_15).

Atkinson R, Flint, J (2001) **Accessing Hidden and Hard-to-Reach Populations: Snowball Research Strategies**. *Social Research Update* 33: 1–4.

Aziz SA, Clements GR, Giam X, Forget PM, Campos-Arceiz A (2017) **Coexistence and Conflict Between the Island Flying Fox (*Pteropus Hypomelanus*) And Humans on Tioman Island, Peninsular Malaysia**. *Human Ecology* 45(3): 377–389. doi: [10.1007/s10745-017-9905-6](https://doi.org/10.1007/s10745-017-9905-6)

Aziz SA, Low MR, Clements GR (2019) **A Conservation Roadmap for Flying Foxes *Pteropus* spp. in Peninsular Malaysia**. Kuala Lumpur: Rimba.

Berthinussen A, Richardson OC, Altringham JD (2021) **Bat Conservation: Global Evidence for the Effects of Interventions**. Cambridge: University of Cambridge.

Biddle R, Solis-Ponce I, Jones M, Marsden S, Pilgrim M, Devenish C (2021) **The Value of Local Community Knowledge in Species Distribution Modelling for a Threatened Neotropical Parrot**. *Biodiversity and Conservation* 30(6): 1803–1823. doi: [10.1007/s10531-021-02169-9](https://doi.org/10.1007/s10531-021-02169-9)

Braun V, Clarke V (2006) **Using Thematic Analysis in Psychology**. *Qualitative Research in Psychology* 3(2): 77–101.

Breed AC, Field HE, Smith CS, Edmonston J, Meers J (2010) **Bats Without Borders: Long-Distance Movements and Implications for Disease Risk Management**. *EcoHealth*, 7(2): 204–212. doi: [10.1007/s10393-010-0332-z](https://doi.org/10.1007/s10393-010-0332-z)

Buchholtz EK, McDaniels M, McCulloch G, Songhurst A, Stronza A (2023). **A Mixed-methods Assessment of Human-elephant Conflict in the Western Okavango Panhandle, Botswana**. *People and Nature* 5(2): 557–571. doi: [10.1002/pan3.10443](https://doi.org/10.1002/pan3.10443).

Busetto L, Wick W, Gumbinger C (2020) **How to Use and Assess Qualitative Research Methods**. *Neurological Research and Practice* 2: 14. doi: [10.1186/s42466-020-00059-z](https://doi.org/10.1186/s42466-020-00059-z)

Charentantanakul W, Shibata S, Vincenot CE (2023) **Amidst Nets and Typhoons: Conservation Implications of Bat–Farmer Conflicts on Okinawa Island**. *Oryx* 57(4): 467–475. doi: [10.1017/S0030605322000631](https://doi.org/10.1017/S0030605322000631).

Chen SF, Shen TJ, Lee HC, Wu HW, Zeng WT, Lu DJ, Lin HC (2017) **Preference of an Insular Flying Fox for Seed Figs Enhances Seed Dispersal of a Dioecious Species**. *Biotropica* 49(4): 511–520. doi: [10.1111/btp.12449](https://doi.org/10.1111/btp.12449).

- Choo J, Le TPN, Serene Chng, Carrasco LR, Benítez-López A (2024). **Hotspots of Zoonotic Disease Risk from Wildlife Hunting and Trade in The Tropics.** *Integrative Conservation* 2(4). doi: [10.1002/inc3.3410](https://doi.org/10.1002/inc3.3410). [10.1002/inc3.3410](https://doi.org/10.1002/inc3.3410). [10.1002/inc3.3410](https://doi.org/10.1002/inc3.3410).
- Chua KB, Lek Koh C, Hooi PS, Wee KF, Khong JH, Chua BH, Chan YP, Lim ME, Lam SK (2002) **Isolation of Nipah Virus from Malaysian Island flying-foxes.** *Microbes and Infection* 4(2): 145–151. doi: [10.1016/s1286-4579\(01\)01522-2](https://doi.org/10.1016/s1286-4579(01)01522-2).
- Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). 2024. **Appendices I, II and III.** [<https://cites.org/eng/app>] Accessed 13 December 2024. .
- Creswell JW, Hirose M (2019) **Mixed Methods and Survey Research in Family Medicine and Community Health.** *Family Medicine and Community Health* 7(2). doi: [10.1136/fmch-2018-000086](https://doi.org/10.1136/fmch-2018-000086).
- Currey K, Kendal D, van der Ree R, Lentini P (2018) **Land Manager Perspectives on Conflict Mitigation Strategies for Urban Flying-Fox Camps.** *Diversity* 10(2). doi: [10.3390/d10020039](https://doi.org/10.3390/d10020039).
- Department of Statistics Malaysia (2024) **Population Statistics by District (2020–2024).** OpenDOSM. [[https://open.dosm.gov.my/data-catalogue/population\\_district](https://open.dosm.gov.my/data-catalogue/population_district)] Accessed 4 February, 2025.
- Florens FBV, Baider C (2019) **Mass-culling of a Threatened Island Flying Fox Species Failed to Increase Fruit Growers’ Profits and Revealed Gaps to Be Addressed for Effective Conservation.** *Journal for Nature Conservation* 47: 58–64. doi: [10.1016/j.jnc.2018.11.008](https://doi.org/10.1016/j.jnc.2018.11.008).
- Fujita MS, Tuttle MD (1991) **Flying Foxes Threatened Animals of Key Economic Importance.** *Conservation Biology* 5: 455-463. .
- Harrison ME, Cheyne SM, Darma F, Ribowo DA, Limin SH, Struebig MJ (2011) **Hunting of Flying Foxes and Perception of Disease Risk in Indonesian Borneo.** *Biological Conservation* 144(10): 2441–2449. doi: [10.1016/j.biocon.2011.06.021](https://doi.org/10.1016/j.biocon.2011.06.021).
- Heale R, Forbes D (2013) **Understanding Triangulation in Research.** *Evidence-Based Nursing*, 16(4): 98.
- Hinsley A, Hughes A, Margulies J (2024) **Creating a More Inclusive Approach to Wildlife Trade Management.** *Conservation Biology* 38(5). doi: [10.1111/cobi.14360](https://doi.org/10.1111/cobi.14360).
- Hinsley A, Keane A, St. John FAV, Ibbett H, Nuno A (2019) **Asking Sensitive Questions Using the Unmatched Count Technique: Applications and Guidelines for Conservation.** *Methods in Ecology and Evolution* 10(3): 308–319. doi: [10.1111/2041-210x.13137](https://doi.org/10.1111/2041-210x.13137).
- Ibbett H, Jones JPG, St John FAV (2021) **Asking sensitive questions in conservation using Randomised Response Techniques.** *Biological Conservation* 260: 109191. doi: [10.1016/j.biocon.2021.109191](https://doi.org/10.1016/j.biocon.2021.109191).
- Kabir SMS (2016) **Methods of Data Collection.** In: Kabir SMS (eds.) *Basic Guidelines for Research: An Introductory Approach for All Disciplines.* 1st ed. Book Zone Publication, Bangladesh, pp. 201-275.
- Keatts LO, Robards M, Olson SH, Hueffer K, Insley SJ, Joly DO, Kutz S, Lee DS, Chetkiewicz CLB, Lair S, Preston ND, Pruvot M, Ray JC, Reid D, Sleeman JM, Stimmelmayer R, Stephen C, Walzer C (2021). **Implications of Zoonoses from Hunting Use of Wildlife in North American Arctic and Boreal Biomes: Pandemic Potential, Monitoring, and Mitigation.** *Frontiers in Public Health* 9. doi: [10.3389/fpubh.2021.627654](https://doi.org/10.3389/fpubh.2021.627654).
- Kingston T, Florens FBV, Vincenot CE (2023) **Large Old World Fruit Bats on the Brink of Extinction: Causes and Consequences.** *Annual Review of Ecology, Evolution, and Systematics* 54(1): 237–257. doi: [10.1146/annurev-ecolsys-110321-055122](https://doi.org/10.1146/annurev-ecolsys-110321-055122).
- Ladjana J, Raimi R (2019) **Local Pangolin Smuggling Syndicate Busted.** New Straits Times [<https://www.nst.com.my/news/crime-courts/2019/02/458608/local-pangolin-smuggling-syndicate-busted-nsttv>.] Accessed 25 February 2025.
- Low MR, Hoong WZ, Shen Z, Murugavel B, Mariner N, Paguntalan LM, Tanalgo K, Aung MM, Sheherazade, Bansa LA, Sritongchuay T, Preble JH, Aziz SA (2021) **Bane or Blessing? Reviewing Cultural Values of Bats across the Asia-Pacific Region.** *Journal of Ethnobiology* 41(1). doi: [10.2993/0278-0771-41.1.18](https://doi.org/10.2993/0278-0771-41.1.18).
- Mardiastuti A, Masy’ud B, Ginoga LN, Sastranegara H, Sutopo (2021) **Short Communication: Wildlife Species Used as Traditional Medicine by Local People in Indonesia.** *Biodiversitas* 22: 329-337. .
- Meade J, Martin JM, Welbergen JA (2021) **Fast Food in The City? Nomadic Flying-Foxes Commute Less and Hang Around for Longer in Urban Areas.** *Behavioral Ecology* 32(6): 1151–1162. doi: [10.1093/beheco/arab078](https://doi.org/10.1093/beheco/arab078).
- Mickleburgh S, Waylen K, Racey P (2009) **Bats as Bushmeat: A Global Review.** *Oryx* 43(02): 217-234. doi: [10.1017/s0030605308000938](https://doi.org/10.1017/s0030605308000938).
- Mildenstein T, Abdul Aziz S, Paguntalan L,

- Jakosalem PG, Mohd-Azlan J, Tagtag A, Bansa L, Reintar AR, Struebig M, Fredriksson G, Lee B, Thong VD, Sheherazade (2022) *Pteropus vampyrus*. (In: IUCN Red List of Threatened Species 2025). IUCN. [[10.2305/IUCN.UK.2022-2.RLTS.T18766A22088824.en](https://doi.org/10.2305/IUCN.UK.2022-2.RLTS.T18766A22088824.en).] Accessed 29 January 2025.
- Mildenstein T, Tanshi I, Racey PA (2016) **Exploitation of Bats for Bushmeat and Medicine**. In Voigt CC, Kingston T(eds.) *Bats in the Anthropocene: Conservation of Bats in a Changing World*. 1st ed. Springer, Switzerland, pp. 325-375.
- Mo M, Roache M, Demers MCA (2020) **Reducing Human-Wildlife Conflict Through Subsidizing Mitigation Equipment and Services: Helping Communities Living with The Gray-Headed Flying-Fox**. *Human Dimensions of Wildlife* 25(4): 1–11. doi: [10.1080/10871209.2020.1735580](https://doi.org/10.1080/10871209.2020.1735580).
- Mohd-Azlan J, Yong JY, Hazzrol NNM, Pengiran P, Atong A, Aziz SA (2022a) **Local Hunting Practices and Perceptions Regarding the Distribution and Ecological Role of the Large Flying Fox (Chiroptera: Pteropodidae: *Pteropus vampyrus*) in Western Sarawak, Malaysian Borneo**. *Journal of Threatened Taxa* 14(1): 20387-20399. doi:
- Mohd-Azlan J, Kaicheen SS, Lok L (2022b) **The Distribution and Community's Perception of Flying Fox, *Pteropus vampyrus* in Limbang, a Transboundary Area in Sarawak**. *Tropical Life Sciences Research* 33(3): 195–225. doi: [10.21315/tlsr2022.33.3.11](https://doi.org/10.21315/tlsr2022.33.3.11).
- Murphy KJ, Kenny U, Ciuti S, Byrne AW (2025) **Understanding Deer Management Dilemmas: A Mixed Methods Approach to Understand Diverse Stakeholder Values in Human-Wildlife Conflicts**. *European Journal of Wildlife Research* 71: 78. doi: [10.1007/s10344-025-01954-z](https://doi.org/10.1007/s10344-025-01954-z).
- Nattrass N, Conradie B (2018). **Predators, Livestock Losses and Poison in the South African Karoo**. *Journal of Cleaner Production* 194: 777–785. doi: [10.1016/j.jclepro.2018.05.169](https://doi.org/10.1016/j.jclepro.2018.05.169).
- Nijman V (2010) **An Overview of International Wildlife Trade from Southeast Asia**. *Biodivers Conserv* 19: 1101–1114. doi: [10.1007/s10531-009-9758-4](https://doi.org/10.1007/s10531-009-9758-4).
- Oedin M, Brescia F, Vidal E, Millon A (2021) **Make Flying-Fox Hunting Sustainable Again: Comparing Expected Demographic Effectiveness and Hunters' Acceptance of More Restrictive Regulations**. *Ambio* 51(4): 1078–1089. doi: [10.1007/s13280-021-01630-x](https://doi.org/10.1007/s13280-021-01630-x).ang.
- Oleksy RZ, Ayady CL, Tatayah V, Jones C, Froidevaux JSP, Racey PA, Jones G (2021) **The Impact of The Endangered Mauritian Flying Fox *Pteropus Niger* on Commercial Fruit Farms and The Efficacy of Mitigation**. *Oryx* 55(1): 114–121. doi: [10.1017/S0030605318001138](https://doi.org/10.1017/S0030605318001138).
- Oleksy RZ, Giuggioli L, McKetterick TJ, Racey PA, Jones G (2017) **Flying Foxes Create Extensive Seed Shadows and Enhance Germination Success of Pioneer Plant Species in Deforested Madagascan Landscapes**. *PLOS ONE* 12(9). e0184023. doi: [10.1371/journal.pone.0184023](https://doi.org/10.1371/journal.pone.0184023).
- Palinkas LA, Horwitz SM, Green CA, Wisdom JP, Duan N, Hoagwood K (2015) **Purposeful Sampling for Qualitative Data Collection and Analysis in Mixed Method Implementation Research**. *Administration and Policy in Mental Health and Mental Health Services Research* 42(5): 533–544. doi: [10.1007/s10488-013-0528-y](https://doi.org/10.1007/s10488-013-0528-y).
- Paz SL, Gonzalez JCT (2021) **Understanding Human-Flying Fox Interactions in The Agusan Marsh Wildlife Sanctuary as Basis for Conservation Policy Interventions**. *Journal of Threatened Taxa* 13(11): 19431–19447. doi: [jott.7466.13.11.19431-19447](https://doi.org/jott.7466.13.11.19431-19447).
- Phillipps Q, Phillipps K (2018) **Phillipps' Field Guide to the Mammals of Borneo and their Ecology: Sabah, Sarawak, Brunei and Kalimantan**. 2nd Ed. Kota Kinabalu, Malaysia: Natural History Publications (Borneo).
- Pugh-Kitingan J (2014) **Cultural and Religious Diversity in Sabah and Relationships with Surrounding Areas**. In M Toyota, DK Okamoto, N Ishikawa (eds.) *Cultural and Religious Diversity in Southeast Asia*. 1st ed. Kyoto University Press, Kyoto, pp. 273–290. .
- R Core Team (2024) **R: A Language and Environment for Statistical Computing**. R Foundation for Statistical Computing. [<https://www.R-project.org>].
- Rocha R, López-Baucells A, Fernández-Llamazares Á (2021) **Ethnobiology of Bats: Exploring Human-Bat Inter-Relationships in A Rapidly Changing World**. *Journal of Ethnobiology* 41(1). doi: [10.2993/0278-0771-41.1.3](https://doi.org/10.2993/0278-0771-41.1.3).
- Roe D, Booker F (2019) **Engaging Local Communities in Tackling Illegal Wildlife Trade: A Synthesis of Approaches and Lessons for Best Practice**. *Conservation Science and Practice* 1(5). e26. doi: [10.1111/csp2.26](https://doi.org/10.1111/csp2.26).
- Roemer C, Fromont C, Barot S, Couvet D, Danet



- A, Martin J-L, Navas M-L, Matutini F, Monnet A-C (2025) **Pressured Researchers in Ecology and Conservation Demand Support to Guarantee Fair Interactions with Stakeholders.** *Biological Conservation* 310: 111324–111324. doi: 10.1016/j.biocon.2025.111324.
- Sabah Wildlife Conservation Enactment 1997 (1997) [<https://sagc.sabah.gov.my/sites/default/files/law/WildlifeConservationEnactment1997.pdf>]. Accessed 25 February 2025.
- Scheffers BR, Corlett RT, Diesmos A, Laurance WF (2012) **Local Demand Drives a Bushmeat Industry in a Philippine Forest Preserve.** *Tropical Conservation Science* 5(2): 133–141. doi: 10.1177/194008291200500203.
- Sendow I, Ratnawati A, Taylor T, Adjid RMA, Saepuloh M, Barr J, Wong F, Daniels P, Field H (2013) **Nipah Virus in the Fruit Bat *Pteropus vampyrus* in Sumatera, Indonesia.** *PLoS ONE* 8(7): e69544. doi: 10.1371/journal.pone.0069544.
- Shapiro H, Willcox A, Tate M, Willcox E, (2020) **Can Farmers and Bats Co-Exist? Farmer Attitudes, Knowledge, And Experiences with Bats in Belize.** *Human–Wildlife Interactions* 14(1). doi: 10.26077/5wwp-sp53.
- Sharma P, Chettri N, Wangchuk K (2021) **Human–Wildlife Conflict in the Roof of The World: Understanding Multidimensional Perspectives Through a Systematic Review.** *Ecology and Evolution* 11(17): 11569–11586. doi: 10.1002/ece3.7980.
- Sheherazade, Tsang SM (2015) **Quantifying the Bat Bushmeat Trade in North Sulawesi, Indonesia, with Suggestions for Conservation Action.** *Global Ecology and Conservation* 3: 324–330. doi: 10.1016/j.gecco.2015.01.003.
- Sheherazade, Tsang SM (2018) **Roost of Gray Flying Foxes (*Pteropus griseus*) in Indonesia and Records of a New Hunting Threat.** *Diversity*, 10(3): 102. doi: 10.3390/d10030102.
- Soares HK de L, Barboza RRD, Feijó A, Provete DB, Romeu RRN (2025) **Worldwide Patterns of Wild Mammal Trade Are Driven by Species Ecology, Evolutionary Relatedness, And Socio-Political Variables: Inferences from the TRAFFIC Bulletin.** *Ethnobiology and Conservation* 14(25): 1–27. doi: 10.15451/ec2025-07-14.25-1-17.
- Stevens M, Rawat S, Satterfield T (2024) **Care, Conflict, and Coexistence: Human–Wildlife Relations in Community Forests.** *People and Nature*. doi: 10.1002/pan3.10760.
- Struebig MJ, Harrison ME, Cheyne SM, Limin SH (2007) **Intensive Hunting of large Flying Foxes *Pteropus vampyrus natunae* in Central Kalimantan, Indonesian Borneo.** *Oryx*, 41(3), 390–393. doi: 10.1017/s0030605307000310.
- Suwannarong K, Balthip K, Kanthawee P, Suwannarong K, Khiewkhern S, Lantican C, Ponlap T, Bupha N, Amonsin A (2020) **Bats and Belief: A Sequential Qualitative Study in Thailand.** *Heliyon* 6(6). e04208. doi: 10.1016/j.heliyon.2020.e04208.
- Tackett ES, Kingston T, Sadeghmoghaddam N, Rutrough AL (2022) **Global Medicinal Use of Bats: A Systematic Literature and Social Media Review.** *Diversity* 14(3): 179. doi: 10.3390/d14030179.
- Taherdoost H (2022) **Designing A Questionnaire for A Research Paper: A Comprehensive Guide to Design and Develop an Effective Questionnaire.** *Asian Journal of Managerial Science* 11(1): 8–16.
- Tait J, Perotto-Baldivieso HL, McKeown A, Westcott DA (2014) **Are Flying-Foxes Coming to Town? Urbanisation of the Spectacled Flying-Fox (*Pteropus conspicillatus*) in Australia.** *PLoS ONE* 9(10). e109810. doi: 10.1371/journal.pone.0109810.
- Tanalgo KC, Sritongchuay T, Agduma AR, Dela Cruz KC, Hughes AC (2023) **Are We Hunting Bats to Extinction? Worldwide Patterns of Hunting Risk in Bats Are Driven by Species Ecology and Regional Economics.** *Biological Conservation* 279:109944. doi: 10.1016/j.biocon.2023.109944.
- Tsang S (2018) *Pteropus hypomelanus* (In: IUCN Red List of Threatened Species 2025). IUCN [<https://www.iucnredlist.org/species/18729/22081642>] Accessed 29 January 2025.
- Tukuboya F, Mizuno K, Herdiansyah H, Frimawaty E (2024) **Togutil Tribe’s Ecological Hunting Calendar on Halmahera Island, Indonesia.** *Global Ecology and Conservation* 55. e03244. doi: 10.1016/j.gecco.2024.e03244.
- Tumelty L, Fa JE, Coad L, Friant S, Mbane J, Cedric TK, Caleb YT, Ickowitz A (2023) **A Systematic Mapping Review of Links Between Handling Wild Meat and Zoonotic Diseases.** *One Health* 17. 100637–100637. doi: 10.1016/j.onehlt.2023.100637.
- Wacharapluesadee S, Boongird K, Wanghongsas S, Phumesin P, Hemachudha T (2006) **Drinking Bat Blood May Be Hazardous to Your Health.** *Clinical Infectious Diseases* 43(2): 269–269. doi: 10.1086/505311.

Win SS, Mya KM (2015) **The Diet of the Indian Flying Fox *Pteropus giganteus* (Brünnich, 1782) (Chiroptera: Pteropodidae) in Myanmar - Conflicts with Local People?** *Journal of Threatened Taxa* 7(9): 7568–7572. doi: [10.11609/jott.o4178.7568-72](https://doi.org/10.11609/jott.o4178.7568-72).

Yabsley SH, Meade J, Hibburt TD, Martin JM, Boardman WSJ, Nicolle D, Walker MJ, Turbill C, Welbergen JA (2022) **Variety Is the Spice of Life: Flying-Foxes Exploit a Variety of Native and Exotic Food Plants in An Urban Landscape Mosaic.** *Frontiers in Ecology and Evolution* 10. doi: [10.3389/fevo.2022.907966](https://doi.org/10.3389/fevo.2022.907966).

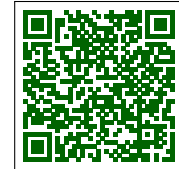
Zulian V, Miller DAW, Ferraz G (2021) **Integrating Citizen-Science and Planned-Survey Data Improves Species Distribution Estimates.** *Diversity and Distributions* 27(12): 2498–2509. doi: [10.1111/ddi.13416](https://doi.org/10.1111/ddi.13416).

**Received:** 30 March 2025

**Accepted:** 01 October 2025

**Published:** 10 October 2025

**Editor:** Anna Karolina Borges



## Additional Files

**Add File 1**

## Sample of Questionnaire Form Used in This Study

### Section 1: Demographic Information *Maklumat demografi*

Latest residential area (district): \_\_\_\_\_

*daerah kediaman terkini*

Age (y/o- years old) *umur:*

<input type="checkbox"/>	24 y/o and below <i>tahun ke bawah</i>
<input type="checkbox"/>	25 – 34 y/o <i>tahun</i>
<input type="checkbox"/>	35 – 44 y/o <i>tahun</i>
<input type="checkbox"/>	45 – 54 y/o <i>tahun</i>
<input type="checkbox"/>	55 y/o and above <i>tahun ke atas</i>

Gender *jantina:*

<input type="checkbox"/>	Male <i>lelaki</i>
<input type="checkbox"/>	Female <i>wanita</i>

Ethnicity *etnik:*

<input type="checkbox"/>	Kadazandusun	<input type="checkbox"/>	Murut
<input type="checkbox"/>	Rungus	<input type="checkbox"/>	Bugis
<input type="checkbox"/>	Bajau	<input type="checkbox"/>	Banjar
<input type="checkbox"/>	Cina	<input type="checkbox"/>	Idahan
<input type="checkbox"/>	Melayu	<input type="checkbox"/>	Iban
<input type="checkbox"/>	Sungai	<input type="checkbox"/>	Jawa
<input type="checkbox"/>	Others: _____		

Highest education level  
*taraf pendidikan tertinggi:*

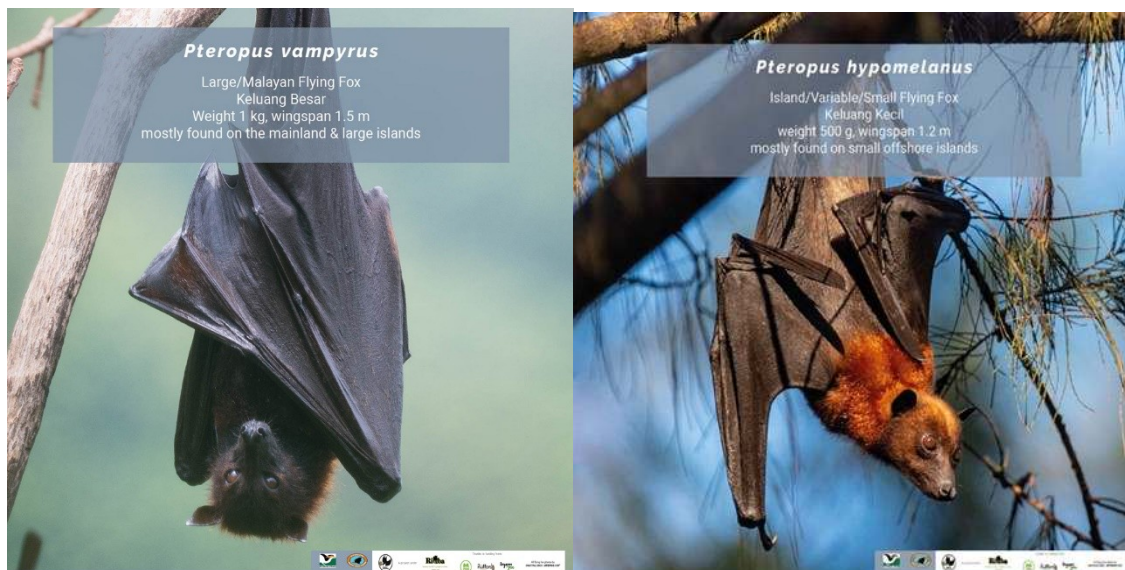
<input type="checkbox"/>	No formal education/ quit school <i>Tidak bersekolah/ Tamat sekolah awal</i>
<input type="checkbox"/>	SRP/PMR/PT3
<input type="checkbox"/>	SPM
<input type="checkbox"/>	STPM/Diploma/ Certificate
<input type="checkbox"/>	Bachelor degree <i>Sarjana muda</i>
<input type="checkbox"/>	Postgraduate <i>pascasiswazah</i>

Occupation *pekerjaan:*

<input type="checkbox"/>	Self-employed <i>bekerja sendiri</i> (State here, <i>Sila nyatakan</i> ): _____
<input type="checkbox"/>	Government workers <i>penjawat awam</i> (State here): _____
<input type="checkbox"/>	Private sectors <i>swasta</i> (State here): _____
<input type="checkbox"/>	Others <i>lain-lain</i> (State here): _____

### Section 2: Introduction to Flying fox

Please refer to the following figure, *sila rujuk gambar di bawah:*





2a. Based on the figure, had you seen flying fox? *Berdasarkan gambar yang diberikan adakah anda pernah melihat keuang?* \*Control question

Yes ya / No tidak

2b. If your answer is yes, which flying fox that you had seen? *Jika jawapan anda 'ya', keuang yang manakah pernah lihat?*

	Big flying fox <i>keluang besar</i>
	Small flying fox <i>keluang kecil</i>
	Not sure which one, please describe <i>tidak pasti, sila huraikan:</i> <hr/> <hr/> <hr/>

2c. Based on the figures, these are flying foxes. Can you differentiate it from other animals, especially bats and birds? *Berdasarkan gambar yang diberikan, ini ialah keuang. Bolehkah anda membezakan keuang daripada haiwan lain?* \*Control question

Yes ya / No tidak

2d. Do you think flying foxes can transmit diseases? *Adakah keuang boleh membawa penyakit?*

Yes ya / Unsure *tidak pasti* / No tidak

2e. What is your experience with flying fox? \*Control question

*adakah anda mempunyai pengalaman berdepan dengan keuang?*

	Eating <i>makan keuang</i>
	Hunting/ hurting <i>memburu/mencederakan keuang</i>
	Observe flying fox flying nearby <i>melihat keuang terbang berdekatan</i>
	Flying fox raid on fruiting trees <i>Keluang menyerang buah yang ditanam</i>
	Roost near house <i>bersarang berdekatan kawasan kediaman</i>
	None <i>tiada</i>
	Others, please describe <i>lain-lain sila nyatakan:</i> <hr/> <hr/>

### Section 3: Flying Fox Cultural Utilitarian significance

3a. What is local name for flying foxes? *Apakah nama tempatan bagi keluang?*

---

3b. Are there any cultural motifs, folklore, taboos or traditional beliefs related to flying foxes?

*adakah keluang terdapat di dalam budaya kaum anda? (cerita rakyat, motif budaya, tatu, kepercayaan dan ritual?*

---

---

3c. Do you consume flying foxes? *adakah anda pernah memakan keluang?* \*Control question

Yes ya / No tidak

3d. If your answer is 'yes', what is/are the reason/s of consuming flying foxes? *sekiranya jawapan*

*anda 'Ya' apakah sebab anda memakan keluang?*

---

---

3e. If your answer is 'yes', what is the frequency of you consuming the flying foxes? *sekiranya*

*jawapan anda 'Ya', apakah kekerapan anda memakan keluang?*

	Often: A few times in a year <i>kerap: lebih daripada sekali dalam setahun</i>
	Frequent: Subject to availability/once a year <i>kadang-kadang: mengikut musim/sekali setahun</i>
	Sometimes: Once in several years <i>Jarang-jarang: sekali dalam beberapa tahun</i>
	Rare: Last ten years ago <i>Sangat jarang: lebih daripada sepuluh tahun lalu</i>

3f. Do you know any unique recipes, preparation methods and ways of serving flying fox dishes?

*adakah anda tahu mengenai resipi unik, cara penyediaan dan penyajian lauk keluang?*

---

---

---

---

---

---

---

3g. What illness or health conditions do you believe can be treated or cured by consuming flying foxes?

*apakah penyakit atau masalah kesihatan yang anda percaya boleh dirawat atau diubati dengan memakan keluang?*

---

---

---

---

3h. Explain how you utilise flying foxes for medicinal purposes or to treat ailments.

*Terangkan bagaimana anda menggunakan keluang sebagai ubat atau merawat kesakitan.*

---

---

---

---

#### **Section 4: Flying Fox and Population Sightings *Pemerhatian populasi keluang***

4a. Based on your experience, have you seen flying foxes? \*Control question

*berdasarkan pengalaman anda, pernahkah anda melihat keluang?*

Yes ya / No tidak

4b. If your answer is 'yes', how estimated many numbers of flying fox observed in one colony?

*Sekiranya jawapan anda 'Ya', Berapakah anggaran individu dalam satu kawanan/koloni keluang yang anda pernah lihat?*

	Less than 10 <i>Kurang dari sepuluh ekor</i>
	Between 10 to 20 <i>Dalam 10-20 ekor</i>
	More than 20

	<i>Lebih daripada 20 ekor</i>
--	-------------------------------

4c. If your answer is 'yes', how often do you see flying foxes within the past five years?

*Sekiranya jawapan anda 'Ya', berapakah kekerapan anda melihat keluang dalam tempoh lima tahun yang lalu?*

	Frequent: more than five times within five years or seen every year <i>Kerap: lebih daripada lima kali dalam lima tahun atau setiap tahun</i>
	Often: three to five observations within five years <i>Kadang-kadang: tiga ke lima kali dalam lima tahun</i>
	Sometimes: one to two times within five years <i>Jarang-jarang: satu ke dua kali dalam lima tahun</i>
	Rare: More than five years ago <i>Sangat jarang: lebih daripada lima tahun dahulu</i>
	Never <i>tidak pernah melihat</i>

4d. If your answer is 'yes', where do you usually see them? (You can choose more than one answer)

*sekiranya jawapan anda 'Ya', di manakah tempat kebiasaan anda menjumpai keluang?*

*(Jawapan boleh lebih daripada satu)*

	Flying in the sky <i>terbang di langit</i>
	Orchard <i>kebun</i>
	Forest <i>hutan</i>
	Others <i>lain-lain</i> (State here <i>sila nyatakan</i> ):

4e. If your answer is 'yes', can you name the district/s where you see the flying foxes based on your experience?

*sekiranya jawapan anda 'Ya', di manakah daerah/daerah-daerah anda menjumpai keluang?*

---



---

### **Section 5: Human- flying fox interactions *Interaksi Manusia-keluang***

5a. Based on your experience, have you hunt flying foxes? *berdasarkan pengalaman anda, pernahkah anda memburu keluang?* (Control question)



Yes ya / No tidak

5b. If your answer is 'yes', what is/are the reason/s of hunting flying foxes? *sekiranya jawapan anda 'Ya', apakah sebab anda memburu keluang?*

---

---

5c. If your answer is 'yes', where do you usually hunt flying foxes? (For example: forest, mangrove) *sekiranya jawapan anda 'Ya', di manakah anda biasanya memburu keluang? (contoh: hutan, hutan paya)*

---

5d. If your answer is 'yes', what do you use for flying fox hunting? *sekiranya jawapan anda 'Ya', apakah yang anda gunakan untuk memburu keluang?*

---

5e. If your answer is 'yes', can you explain your hunting experience? *sekiranya jawapan anda 'Ya', bolehkah anda terangkan pengalaman anda memburu?*

---

---

---

---

---

5f. Do you experience flying fox raiding your fruiting trees? \*Control question *adakah keluang pernah menyerang pokok buah-buahan anda?*

Yes ya / No tidak

5g. Where is/are district/s that you experience this fruit raiding by flying fox? *sekiranya jawapan anda 'Ya', di daerah manakah anda mengalami serangan pokok buah oleh keluang?*

---

---

5h. What is the estimated frequency of fruit raiding that you have experienced within the last five years?

sekiranya jawapan anda 'Ya', berapakah kekerapan anda mengalami serangan pokok buah oleh keluang dalam tempoh lima tahun lalu?

	Every year <i>setiap tahun</i>
	3-4 times within five years ago <i>3-4 kali dalam tempoh lima tahun lalu</i>
	1-2 times within five years ago <i>1-2 kali dalam tempoh lima tahun lalu</i>
	At least once > 5 years ago <i>sekurang-kurangnya sekali dalam tempoh lebih lima tahun lalu</i>
	Never <i>tidak pernah mengalami</i>

5i. What do you do when flying fox raid your fruiting trees? (Can choose more than one answers).

sekiranya jawapan anda 'Ya', anda yang anda lakukan apabila mengalami serangan pokok buah oleh keluang? (pilihan jawapan boleh lebih daripada 1)

	Let the flying fox (allow feeding) <i>membiarkan keluang makan</i>
	Chase <i>menghalau</i> Please state how do you chase <i>sila nyatakan:</i> _____
	Catch <i>menangkap</i> Please state how do you catch <i>sila nyatakan:</i> _____
	Kill <i>membunuh</i>
	Others <i>lain-lain</i> Please state your response here <i>sila nyatakan:</i> _____

5j. List the name of your fruiting trees affected by the flying fox fruit raiding. *Senaraikan pokok buah-anda yang mengalami serangan oleh keluang?*

---



---

**Add File 2**

FORM 3  
(Reg. 23(b))  
STATE OF SABAH  
WILDLIFE CONSERVATION ENACTMENT 1997  
COMMERCIAL LICENCE  
(Not transferable)

Licence Number .....

Name of licensee in full .....

Address in country of residence .....

Names of persons authorised to hunt under this licence

.....  
.....  
.....

The above-named persons are authorised to hunt animals of the species below in the area and number stated below and subject to the above Enactment and Regulations made thereunder and the conditions endorsed on this licence.

Species	Area	Number
---------	------	--------

Fees paid:

Date of issue:

Date of expiry:

.....  
*Signature and title of officer issuing licence  
on behalf of the Director.*

Renewals

From	to	Signature .....
------	----	-----------------

From	to	Signature .....
------	----	-----------------

CONDITIONS

.....  
*Signature of issuing officer or officer  
endorsing amendment.*



**Add File 3**

### Supplementary Material 3:

Socio-demographic characteristics, consumption patterns, sightings, hunting practices, and fruit-raiding responses of participants in Sabah.

**Table 1.** Socio-demographic characteristics of participants (n=100).

Variable	Category	Frequency (n)	Percentage (%)
Gender	Female	48	48
	Male	52	52
Age	<24 years old	18	18
	>55 years old	24	24
	25-34 years old	11	11
	35-44 years old	16	16
	45-54 years old	31	31
Education	No formal/ Primary education	25	25
	Secondary education	62	62
	Tertiary education	13	13
Occupation	Self-employed	43	43
	Government sectors	26	26
	Private sectors	13	13
	Students	9	9
	Housewife	4	4
	Unemployed	4	4
	Pensioners	1	1
Ethnicity	Bajau	3	3
	Bugis	2	2
	Jawa	1	1
	Kadazandusun	52	52
	Melayu	2	2
	Murut	2	2
	Rungus	2	2
	Sino-Kadazan	2	2
	Suluk	1	1
Sungai	33	33	
Residential Area	Beluran	1	1
	Kinabatangan	29	29
	Kota Kinabalu	2	2
	Kota Marudu	1	1
	Ranau	23	23
	Sandakan	1	1
	Tambunan	22	22
	Telupid	6	6
Tongod	15	15	

**Table 2.** Overview of participants who consume flying foxes (n=23), categorised by residential area, ethnicity, age group, reasons for consumption, and frequency of consumption.

<b>Category</b>	<b>Frequency (n)</b>	<b>Percentage (%)</b>
<b>West Coast Division</b>		
Ranau	6	26.1
Kota Marudu	1	4.3
<b>Interior Division</b>		
Tambunan	8	34.8
<b>Sandakan Division</b>		
Tongod	7	30.4
Kinabatangan	1	4.3
<b>Kadazandusun</b>		
Sungai	5	21.7
Murut	1	4.3
> 35 years old	19	82.6
< 35 years old	4	17.4
<b>Consumption reasons</b>		
Food	6	26.1
Medicine	7	30.4
Food and medicine	10	43.5
<b>Traditional belief: ailments/medicine</b>		
Asthma	15	65.2
Joint pain	1	4.3
High blood	1	4.3
Others (various benefits)	1	4.3
None	5	21.7
<b>Consumption frequency</b>		
Frequent: A few times in one year	4	17.4
Sometimes: Once in several years	14	60.9
Rare: Last ten years ago	5	21.7



**Image 1.** One respondent described the various perceived benefits of *montoku* (traditional liquor) infused with flying fox pups, a remedy prepared by preserving flying fox, monkey brain, medicinal roots, and other ingredients in liquor; it is not commercially produced and is traditionally used to treat ailments such as internal bleeding, stroke, and injuries from falls. Similar practices also reported by Iban participants in Western Sarawak, used for asthma (Mohd-Azlan et al. 2022a).  
Source: Anonymou participants, villager, aged 40 years old.

**Table 3.** Information on the flying fox sighting trends covering estimated number of bats observed (n=77), sighting frequency (n=77), sighting area (n=117), and sighting districts (n=86).

Category	Frequency (n)	Percentage (%)
<b>Estimated number of bats observed (n=77)</b>		
Less than 10	46	59.7
Between 10 to 20	9	11.7
More than 20	22	28.6
<b>Sightings frequency (n=77)</b>		
Rare: > Five years ago	29	37.6
Sometimes: One to two times within five years	18	23.4
Often: three to five observations within five years	18	23.4
Frequent: > Five times within five years or seen every year	12	15.6
<b>Sighting area (n=117)</b>		
Orchard	44	37.6
Flying in the sky	31	26.5
Forest	25	21.4
Tree near house	11	9.4
Mangrove	4	3.4
Market	1	0.9
Pet	1	0.9
<b>Reported sightings districts (n=86)</b>		
<b>SDN</b>		
Kinabatangan	31	36.0
Tongod	14	16.3
Beluran	1	1.2
<b>IRD</b>		
Tambunan	15	17.4
<b>WCD</b>		
Ranau	19	22.1
Kota Marudu	2	2.3
Papar	2	2.3
<b>Other Divisions</b>		
Lahad Datu	1	1.2
Paitan	1	1.2

\*Note: The number of responses exceeds the number of reporting participants (n = 77) because some participants reported more than one sighting area or district.



**Table 4.** Types of hunters (n=11), hunting reasons (n=15) and tools (n=15) used to report by hunter participants (n=11).

<b>Variables</b>	<b>Frequency (n)</b>	<b>Percentage (%)</b>
<b>Gender</b>		
Male	9	81.8
Female	2	18.2
<b>Ethnicities</b>		
Kadazandusun	8	72.7
Sungai	2	18.2
Murut	1	9
<b>On-site hunter</b>		
On-site hunter	4	36.4
Orchard hunter	7	63.6
<b>Reason (n=15)</b>		
<b>On-site hunter</b>		
Meat	4	26.7
Protecting fruiting trees	1	6.7
Selling	1	6.7
<b>Orchard hunters</b>		
Meat	4	26.7
Protecting fruiting trees	4	26.7
Medicinal purpose	1	6.7
<b>Tools used (n=15)</b>		
<b>On-site hunter</b>		
Shotgun	4	26.7
<b>Orchard hunters</b>		
<i>Rawai</i>	4	26.7
Nets	4	26.7
Slingshots	2	13.3
Shotgun	1	6.7

\*Note: The number of responses exceeds the number of hunters (n=11) because some participants provided more than one reason and reported using multiple tools.

**Table 5.** Participants experienced fruit raiding (n=48), listed 6 districts affected by flying fox fruit raiding (n=79), estimated fruit raiding frequency (n=48), responses to fruit raiding (n=56) and methods used to resolve the conflicts reported by participants (n=37).

<b>Category</b>	<b>Frequency (n)</b>	<b>Percentage (%)</b>
<b>Districts (n=79)</b>		
Kinabatangan	30	38.0
Ranau	18	22.8
Tongod-Pinangah	14	17.7
Tambunan	15	19.0
Lahad Datu	1	1.3
Papar	1	1.3
<b>Fruit raiding Frequency (n=48)</b>		
At least once > 5 years ago	18	37.5
Every year	12	25
3-4 times within five years ago	9	18.8
1-2 times within five years ago	9	18.8
<b>Responses (n=56)</b>		
<b>Non-lethal</b>		
Allowing feed	31	55.4
Chase away	9	16.1
<b>Lethal</b>		
Catch	8	14.3
Kill	6	10.7
Hurt	2	3.6
<b>Method used (n=37)</b>		
<b>Non-lethal</b>		
Lamp	14	38.7
Sound deterrents	5	13.5
Customised pole with sacs	5	13.5
Others	2	5.4
<b>Lethal</b>		
<i>Rawai</i>	4	10.8
Nets	4	10.8
Slingshot	2	5.4
Shotgun	1	2.7

\*Note: The number of responses exceeds the number of affected participants (n=48) because some participants provided more than one respond for the districts and their responses to fruit raiding conflict. Participants also listed more than one response for method used in resolving fruit raiding.

**Table 6.** Cross-tabulation of responses (n=48) to fruit raiding and frequency of fruit raiding incidents. Participants who experience annual fruit raiding tended to chase away flying foxes rather than use lethal methods.

<b>Categorised responses</b>	<b>&gt; 5 years ago n (%)</b>	<b>1-2 times within 5 years n (%)</b>	<b>3-4 times within 5 years n (%)</b>	<b>every year n (%)</b>	<b>Total n (%)</b>
<b>Non-lethal responses</b>					
allowing feed	10 (27.8)	5 (13.9)	6 (16.7)	1 (2.8)	22 (61.1)
allowing feed + chase	3 (8.3)	0	0	6 (16.7)	9 (25)
chase	3 (8.3)	0	1 (2.8)	1 (2.8)	5 (13.9)
<b>Total</b>	<b>16 (44.4)</b>	<b>5 (13.9)</b>	<b>7 (19.5)</b>	<b>8 (22.3)</b>	<b>36 (100)</b>
<b>Lethal responses</b>					
catch	0	1 (8.3)	0	1 (25)	2 (16.7)
catch + kill	0	0	0	1 (25)	1 (8.3)
chase + catch	0	0	0	1 (25)	1 (8.3)
chase + catch + kill	1 (8.3)	0	1 (8.3)	0	2 (16.7)
allow feed + catch + kill	0	1 (8.3)	0	0	1 (8.3)
allow feed + chase + kill	0	2 (16.7)	0	0	2 (16.7)
allow feed + chase + hurt	0	0	0	1 (8.3)	1 (8.3)
allow feed + catch + hurt	0	0	1 (8.3)	0	1 (8.3)
allow feed + hurt	1 (8.3)	0	0	0	1 (8.3)
<b>Total</b>	<b>2 (16.7)</b>	<b>4 (33.3)</b>	<b>2 (16.7)</b>	<b>4 (33.3)</b>	<b>12 (100)</b>