



Nighttime behavioral study of flying foxes on the southern coast of West Java, Indonesia

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ABSTRACT. Flying foxes are important in the maintenance of forests and diversity. However, knowledge of their behavioral ecology, especially of movement and foraging patterns, which are essential for conservation and management of their populations, are not well known. Therefore, movement behavior of two individuals of *Pteropus vampyrus* were examined using an Argos telemetry system, and foraging pattern of *Pteropus* spp. was directly observed, at West Java province, Indonesia in October 2017. The maximum distance between the location at which bats were released and their furthest roost, recorded via satellite telemetry, was approximately 100 km. This reflects the long-distance flight ability of *P. vampyrus*. Daytime roosting sites and nighttime foraging places consisted of several types of habitats, such as intact forests, agricultural lands, and residential areas. This evidence indicated that there was habitat overlap between humans and bats in West Java province. According to direct observation of the behaviors of flying foxes at two locations within residential areas, various activities such as wing spreading, excretion, fighting, aggressive calls, movement, hanging relax, and hanging alert were found. The number of bat-visits to the trees varied among night hours, and had a positive correlation with the number of fruit dropping. The data obtained in this study have improved our understanding of nighttime behavior and habitat utilization of *P. vampyrus*, that can be used to support landscape management, species conservation, and disease prevention in regions of Southeast Asia.

KEY WORDS: foraging behavior, *Pteropus vampyrus*, satellite telemetry

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Southeast Asia is home to up to 30 species of flying foxes (family Pteropodidae), which play an important role in ecosystem functions of tropical forests, through pollination and seed dispersion [12, 17]. Based on high deforestation rates in this region, approximately 24% of fruit bat species in the family Pteropodidae may become extinct by the end of this century, due to habitat loss [17]. This anthropogenic disturbance is not only a major threat to flying fox species, but also impacts on humans. For instance, urban areas of eastern Australia have received a large influx of flying fox populations (*P. scapulatus*), causing a nuisance, and public health concerns for the humans living close to them [18]. In general, the movement of flying foxes depends on the distribution of food resources and roosting sites [8]. As natural food resources decline (up to 75% on the east coast of Australia), flying foxes tend to find an alternative food source in residential areas, such as fruit in orchards [22]. The abundance of food resources has attracted the flying foxes, which have set up their colonies in the east coast cities of Australia, with no migration [22]. This increases the conflicts and contacts among flying foxes, horses and humans, leading to Hendra virus (HeV) transmission across species.

The understanding of movement patterns and foraging behaviors of flying foxes is essential for developing conservation methods, as well as for minimizing the conflicts between humans and flying foxes. However, such ecological behaviors of flying foxes are not well understood. To gain this knowledge, we explored the movement pattern of *P. vampyrus*, a species listed as ‘Near Threatened’ by the international IUCN Red List, using satellite telemetry, a powerful research tool for tracking migratory animals [4], and also performed direct observation on the foraging behavior of fruit bats (*Pteropus* spp. and non-*Pteropus* spp.) in West Java, Indonesia.

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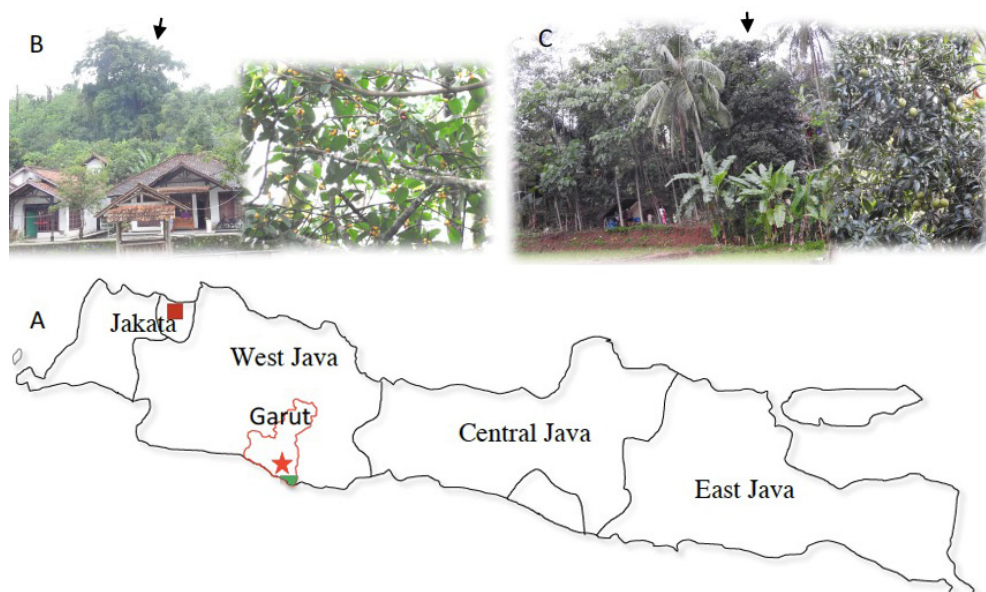


Fig. 2. *P. vampyrus* with solar-powered satellite transmitters.

Fig. 1. Map showing the location of capture sites in the Leuweung Sancang conservation area (green area, 7° 43' 45.12" S, 107° 54' 10.08" E). A: The behavioral study took place in the red star area of the Garut district, Indonesia. There were two study sites for observation. B: At a fig tree in Mekarsari village (7° 38' 28.9" S, 107° 46' 03.8" E). C: At a mango tree in Sancang village (97° 41' 44.5" S, 107° 52' 59.2" E).

MATERIALS AND METHODS

Study areas

The studies were performed in the Garut district of the West Java province, Indonesia. For the telemetry study, we captured *P. vampyrus* in roosting site at the Leuweung Sancang conservation area (7° 43' 45.12" S, 107° 54' 10.08" E), a home for more than 10,000 flying foxes [3]. For the behavioral study, we observed the foraging behavior of fruit bats at 2 locations. The first location was Mekarsari village (7° 38' 28.9" S, 107° 46' 03.8" E); the second site was in the adjacent village, Sancang village (7° 41' 44.5" S, 107° 52' 59.2" E) (Fig. 1).

Data collection

For the telemetry study, we captured 3 adult males of *P. vampyrus*, for tracking from roosting site in the Leuweung Sancang conservation area, using a mist net between 1600 and 1730 hr on October 4, 2017. We kept the captured bats in cloth bags until they were anesthetized, using a ketamine and xylazine combination, to reduce stress during handling, following Heard *et al.* (1996) [15]; these processes were approved by Bogor Agricultural University Ethical Committee, as permitted by the Indonesian government. Body mass and forearm length of all bats were recorded. The bats were fitted with tracking collars with a solar-powered satellite Platform Terminal Transmitter (9.5 g Solar PTT-100, Microwave Telemetry, Columbia, MD, U.S.A.) (Fig. 2). The mass of the collar with the PTT was 0.8% of the average body mass of a bat (1.31 ± 0.11 kg); this equates to less than 5% of the animal's body weight, as recommended [1]. To reduce stress, all bats were hand-fed with banana before releasing. Each bat was identified by platform ID (164317, 164318 and 164319). The transmitters were programmed to have 10 hr on and 48 hr off. This enabled the gadgets to save battery, and provided the location data for day and night times. Data were obtained via global satellite-based location, and Data Collection System (DCS). The geolocation data included latitude, longitude, local time, and estimated location errors, which allowed the researcher to estimate the accuracy of locations. We explored the 3 accessible sites where flying fox ID 164319 visited, with an estimated error of <200 m. The habitat types, fruit trees, and animal species within a 200 m radius of observed points were noted. The data from the first night of tracking were excluded from the analysis, because handling may affect the behavior of flying foxes.

For nighttime behavioral observation, we directly observed flying foxes, *Pteropus* spp. by night vision CCTV camera (EAH-S750VP, ELMO LTD., Nagoya, Japan), from October 5 to 17, 2017. The observation took place at 2 locations, where local people reported that bats had visited. The first point was at a fig tree (*Ficus stupenda*), located on a small hill behind Mekarsari village (Fig. 1B). The second point was at a mango tree (*Mangifera indica*), located at Sancang village (Fig. 1C). There were other fruit trees such as banana (*Musa* spp.), Sapodilla plum (*Achras sapota*), coconut (*Cocos nucifera*) and soursop (*Annona muricata*) trees around these two locations. Small fruit bats always visited these trees; this allowed us, on occasion, to observe the foraging behavior of non-*Pteropus* bats. Observations were made from 1700 to 0600 hr, which ranged from before sunset and sunrise times. The observation point was set at 20 m away from the selected trees, so as not to disturb the behavior of the bats. The observers

Table 1. Data summary of characteristic, distance moved, the number of roosting sites over 14-days of tracking period in *P. vampyrus*

Bat ID	Capture site	Weight (kg)/ Forearm length (cm)	Night roosts	Day roosts	Max displacement (km)	Cumulative distance (km)	% of re-visited night roosts	Home range (ha)
164317	Leuweung Sancang	1.45/74	22	24	100.0	25.5 ± 9.2	22.00	136,773
164319	Leuweung Sancang	1.25/72	26	18	15.6	8.7 ± 2.3	11.50	6,505

noted; (1) the number of bat-visits, defined as the number of flying foxes that landed in or around the tree, which may include re-visited individuals, (2) the duration of bats on the trees, (3) the number of fruit dropping onto the ground, and (4) the behavior of bats during foraging. The behavior of bats was characterized according to the classification by Hengjian *et al.* (2017) [16].

Analysis

Satellite telemetry study. Day roosts were identified as the recorded locations during sunrise to sunset periods; night roosts were defined as the recorded locations during sunset to sunrise periods. Four values were calculated for each tracked bat: 1) the maximum displacement, which was the distance in km between the day roost at which the bat was captured and the furthest recorded roost; 2) cumulative distance, which was determined as the summation of all distances between consecutive roosts within a 1-day period; 3) the home range, which was specified as the area covering all recorded day/night roosts of the tracked individual; 4) percentage of revisited feeding roosts, which were calculated using:

$$\% \text{ of re-visited feeding roosts} = f / T \times 100$$

f = the number of night roosts which the bat had visited more than once throughout the tracking period

T = the total number of recorded night roosts during the tracking period.

Night time behavioral study. We calculated the average number of bat-visits, the average duration that the bat stayed on the tree, and the average number of fruit dropping for each location. We also analyzed the difference in number of bat-visits at different times of night, using the Kruskal-Wallis test. The relationship between the number of bat-visits and the number of fruits dropping at different times were analyzed by Spearman correlation. Significant correlations and differences for all tests were determined at a probability of $P < 0.05$ (IBM SPSS 18, IBM Corporation, New York, NY, U.S.A.).

RESULTS

We downloaded 14 days' data from three satellite-tracked males (ID number: 164317, 164318 and 164319). Unfortunately, the data from bat ID 164318 was lost by unknown reason. The bat might be died, and the body fallen down to ground wherein satellites could not detect the signal from transmitter. For bat ID 164317, we obtained a total of 22 location points for night roosts, and 24 location points for day roosts. Daytime roosting sites were in various habitat types, such as forest protected areas, agricultural areas, and mountainous ranges. The nighttime roosts consisted of forest protected areas, agricultural land, and small wooded plantations in residential areas. The maximum displacement was about 100 km, with the furthest roost being located outside the Garut district, but still in the West Java province. The cumulative travelling distance for a day was 25.5 ± 9.2 km on average ($n=5$) (Table 1). The home range, which encompassed all recorded roosts, was 136,773 ha (Fig. 3). Site fidelity of day roosts was low for this individual bat. Three to four day-roost shifts were seen in a single day. For the foraging sites, 22% of all nighttime roosts were repeatedly visited at least twice during the tracking period.

For bat ID 164319, we collected a total of 26 locations for night roosts, and 18 geolocations of day roosts. The day roosts were found in forest protected areas, agricultural landscapes, and mountain ranges, as for the former bat; the night roosts considered as feeding sites were located in forest protected areas, agricultural areas, mountain ranges, and residential areas. The maximum displacement was approximately 15.6 km, with the furthest roost located within the Garut district. The cumulative displacement for a 1-day period was 8.7 ± 2.3 km on average ($n=5$). The home range of this bat covered 6,505 ha of Garut city, a much smaller area than the former individual (Fig. 4). Roost fidelity was also low for this bat. This flying fox switched day roosts around 3–6 times in a single day. However, 11.5% of all feeding sites were repeatedly visited during the tracking period (Table 1). To estimate the risk of disease transmission, we performed a walking survey at 3 feeding sites of this bat. The first location was agricultural land, 0.9 km away from the nearest village; the food plants were soursop (*Annona muricata*), jackfruit (*Artocarpus heterophyllus*), banana (*Musa* spp.), and fig trees (*Pittosporum moluccanum*). The second foraging place was located in a small village in which domestic animals such as dogs, goats, and chicken were free-living; the fruit trees found in this location were banana (*Musa* spp.), fig trees (*Ficus* spp.), and rambutan (*Nephelium lappaceum*). The third point was located in an *Albizia chinensis* garden, where fruit trees such as *Bridelia tomentosa*, *Musa* spp., and *Carica papaya* (papaya) were planted. Therefore, these locations were considered to be contact zones for flying foxes, humans, and domestic animals.

Nighttime behavior

Study site 1: Fig tree. During 4 nights of direct observation, the number of bat-visits (which may including re-visiting by the same individuals) was an average of 121.0 ± 30.4 per night. At least 39.1% of visiting bats landed on the tree, with 60.9% of bats flying around, or passing by, the tree. Most of the observed bats (83.5%) performed solitary foraging, while 16.5% foraged in a group containing 2–5 individuals. The average duration for a bat to search and consume fruit on the tree was 12.0 ± 1.7 min

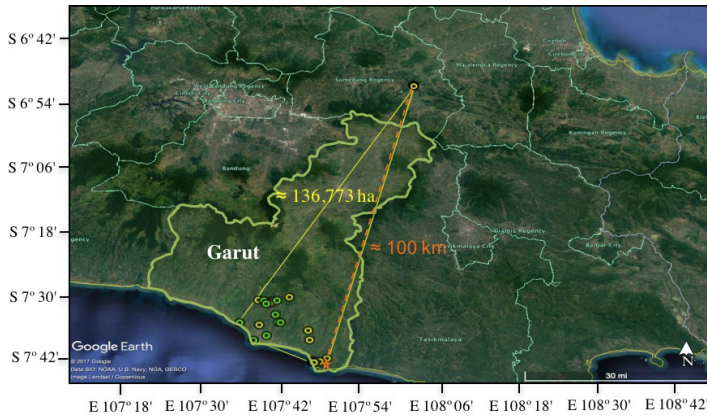


Fig. 3. The minimum home range of *P. vampyrus* (ID 164317) is represented in the yellow polygon. Green dots represent day roost locations, while yellow dots represent night roost locations. The maximum distance from the release point (orange star) to the furthest roost is shown as a dashed line.

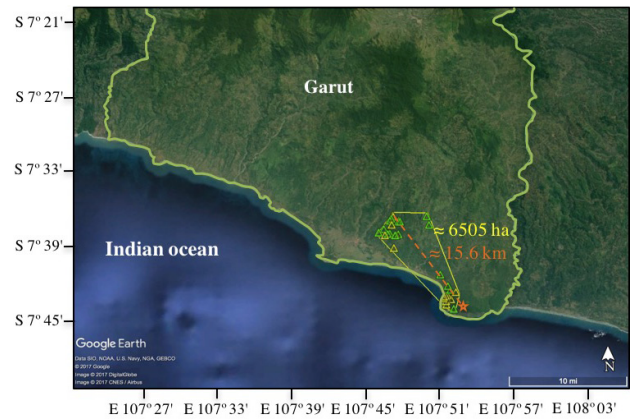


Fig. 4. The minimum home range of *P. vampyrus* (ID 164319) is represented in the yellow polygon. Green triangles represent day roost locations, while yellow triangles represent night roost locations. The maximum distance from the release point (orange star) to the furthest roost is shown as a dashed line.

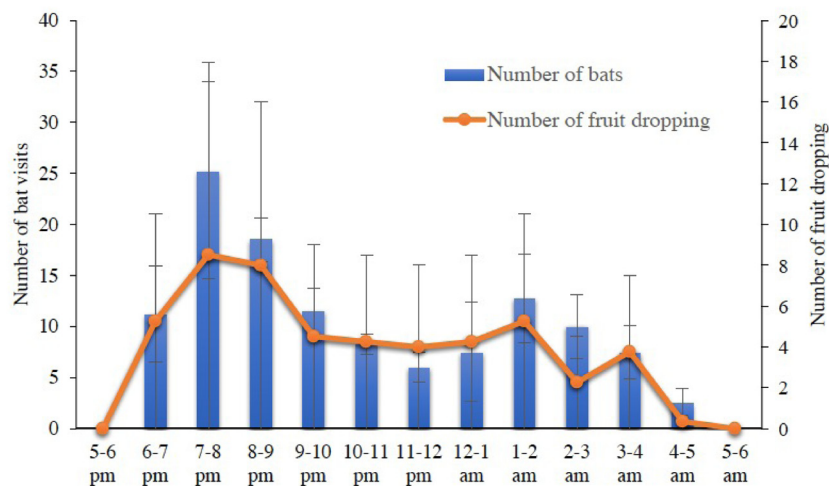


Fig. 5. The number of bat-visits and dropping fruits observed at different times of night at the fig tree study site.

(maximum=67 min, minimum=1 min). Behaviors observed during foraging were wing spreading, excretion, fighting, aggressive calls, movement, hanging relax, and hanging alert. The flying foxes visited the fig tree from 1800 to 0500 hr, which was around 30 min after sunset and 30 min before sunrise. The number of bat visits was significantly different during the night hours (Kruskal-Wallis test, $\chi^2=27.18$, $d.f.=11$, $P=0.004$). The number of bat visits was highest from 1900 to 2100 hr, and lowest from 2300 to 0000 hr, and 0400 to 0500 hr. We found a positive correlation between the number of bat-visits and the number of fruits dropping (Spearman correlation, $r=0.379$, $P=0.008$) (Fig. 5). Also, the observers occasionally found domestic animals such as dog, cat, goat, and chicken, searching for food under the observed tree during daytime.

Study site 2: Mango tree. During 4 nights of investigation, the number of bat-visits was an average of 5.7 ± 2.3 per night. 60% of the total number of bats landed on the tree, while 40% just flew around or passed by the tree. All bats visiting the mango tree came alone (solitary foraging). No foraging groups were observed. The average duration for a bat to occupy the tree was 25.0 ± 6.4 min (maximum=40 min, minimum=10 min). Behaviors observed during foraging were wing spreading, movement, hanging relax, and hanging alert. As for study site 1, the flying foxes visited the mango tree from 1800 to 0500 hr. The number of bats visiting was not significantly different between the night hours (Kruskal-Wallis test, $\chi^2=15.2$, $d.f.=11$, $P=0.14$). However, the highest number of bat-visits was found from 0000 to 0100 hr. A positive relationship was detected between the number of bat-visits and the number of fruits dropping (Spearman correlation, $r=0.430$, $P=0.002$) (Fig. 6).

Differences in the foraging behavior of *Pteropus* and non-*Pteropus* species

Pteropus and non-*Pteropus* bats have some differences in their foraging behaviors. Flying fox species usually accessed the

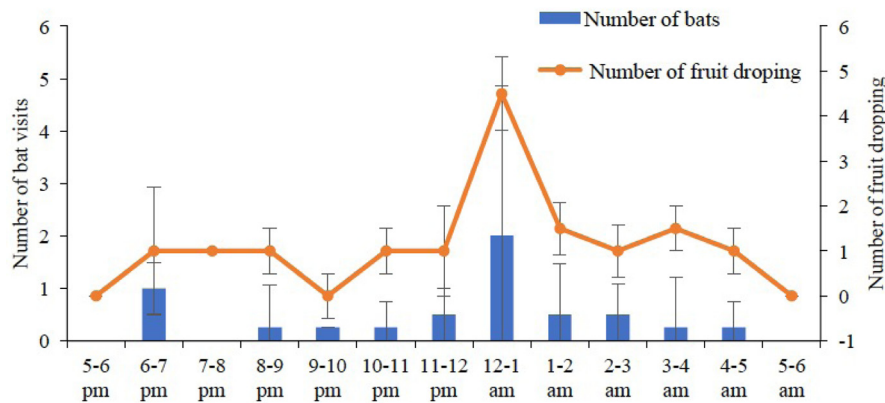


Fig. 6. The number of bat visits and dropping fruits observed at different times of night at the mango tree study site.

tree by landing at the top or middle of the canopy. On occasions where the fruit tree was near to people's homes, the flying foxes carefully accessed the fruit tree by landing on the adjacent tree firstly, and looking around for up to 20 min; after that, they jumped to the feeding tree, and started searching for food. Small fruit bats (non-*Pteropus* spp.) usually flew around, or hovered near, the targeted tree many times before approaching it. After approaching, they spent short bouts (<10 sec) eating the chosen fruit, with rest periods in an adjacent tree (<8 m away from the fruit tree) between bouts. In cases where the fruit or food was smaller than their body size, they would take the food, and move to another tree to eat it.

DISCUSSION

The telemetry study

Most flying fox species (genus *Pteropus*) are highly mobile mammals which commonly forage across wide areas [20]. However, their day/night movements are not well understood. In this study, we provided semi-quantitative data of movement patterns and foraging behavior in *P. vampyrus*, which is recognized as a host of Nipah virus (NiV) that cause a severe encephalitis disease in human [6, 9]. Our study found that: (i) The tracked bats tended to shift day roosts frequently (a maximum of 6 times) in a day. Based on Hengjan *et al.* (2017) [16], *P. vampyrus* living in Leuweung Sancang conservation area faced with the disturbances by non-human primates frequently during daytime. This should be the main cause of day roost shifts of the flying foxes. A previous study in Borneo [13] also supported that *P. vampyrus* occupied multiple day roosts. It was suggested that the benefits of frequent movement between daytime roosts were the avoidance of disturbance by humans, minimization of commuting distance to feeding areas, reduction of predation, and escape from high population densities of ectoparasites. (ii) The tracked males of *P. vampyrus* are nomadic animals, and the distance moved was unpredictable and varied between bat individuals. For example, the tracked bat ID 164319 exhibited nomadic movement, with 15.6 km of maximum displacement between releasing point to furthest recorded roost (Fig. 4). Bat ID 164317 showed a longer nomadic movement, with almost 100 km of maximum displacement (Fig. 3). The movement of all species of *Pteropus* bats is greatly dependent on food plants. Since they do not hibernate, they need to consume food all year. To find seasonal food resources, they have developed the capacity for migration or nomadic movement [14]. The southern coast area of the Garut district is covered by evergreen forest and fruit plantations, that can provide food for the flying foxes year-round. Therefore, flying foxes do not need to migrate to other regions far from Garut. Local peoples also mentioned that flying foxes are present in this area all year round. However, by our short-study period, we could not determine if the flying foxes are migratory. Therefore, long-term study on the movement behaviors of *P. vampyrus* is required. (iii) The home range of *P. vampyrus* covered diverse habitat types. The bats spent time roosting and foraging within or outside Leuweung Sancang conservation area, where was consider as riparian zone. According to the study of Milddenstein *et al.* (2005) [19], *P. vampyrus* and *A. jubatus* showed the strong preference for riparian area. From these results, we suggest that the effective management on riparian areas is important for the conservation of flying fox populations. Not only the natural conservation areas, the flying foxes also used the disturbed areas, such as forest plantations, agricultural land, and residential areas. *P. vampyrus* showed some degree of foraging site fidelity, by visiting the same feeding locations repeatedly. This result is not surprising because returning to predictable food sites allows bats to save time and energy [25]. However, larger samples including different sexes and reproductive conditions are required, to provide a comprehensive understanding of their movement ecology.

The walking surveys allowed us to identify the species of food plant, which can be consumed by humans and flying foxes. The most common fruit in the observed locations was banana. This fruit has also been recorded as the most frequently consumed plant species for *P. lylei* in Thailand [26]. Eby (1991) mentioned that fruit bats forage on cultivated fruits when natural food resources become insufficient, making them become an agricultural pest [8]. This conflict between bats and humans causes illegal hunting of flying foxes in several countries of Southeast Asia [10]. The adaptation for foraging in human areas leads to overlap zones between flying foxes, humans, and domestic animals; this factor may drive the spread of infectious disease from bats to humans and domestic animals in this region.

Foraging behavior

During our observations, we found that numerous flying foxes visited the observed trees, especially the fig tree. According to dietary study of the Philippine flying foxes [24], seeds from *Ficus spp.* were predominant in fecal samples of *P. vampyrus* and *A. jubatus*. And more than 30 species of fig tree have been recorded in the diet of pteropid bats in Asia, Australia and Africa [5]. This highlights the importance of fig trees to flying foxes. Flying foxes foraged both in groups and alone. This behavior was also observed on *P. giganteus* in India [23]. Group foraging is beneficial for sharing information about feeding locations, that improves foraging efficiency and reduces risk of predation [2, 27]. Feeding behavior of bats varied among bat species and food size. This study found that small fruit bats or non-*Pteropus spp.* performed *ex situ* feeding behavior (carrying fruit to another tree for feeding) when the fruit was smaller than them; they also exhibited *in situ* feeding patterns (feeding on fruit on the same tree), when the fruit was bigger than them. The *Pteropus* bats only showed *in situ* feeding behavior; this result is consistent with a previous study on fruit bats, *Cynopterus sphinx* and *P. giganteus* [21]. To save time and energy, flying foxes not only perform *in situ* feeding, but they also stay on the fruit tree for some period after eating [2186]. This enhances the risk of predation and intraspecific interference. In contrast, *ex situ* feeding behavior is considered a foraging strategy that reduces intraspecific competition and predation risks [7]. This reflects trade-offs between predation risks and energy gains, that vary between individuals and species. During feeding, bats dropped partially eaten fruits on the ground. The advantage of this event is to facilitate seed dispersion, but on the other hand, it increases virus-contaminated areas along the feeding route of bats.

During foraging, the observed flying foxes displayed various activities such as wing spreading, excretion, fighting, aggressive calls, movement, hanging relax, and hanging alert. Some of these activities probably lead to the transmission of pathogens from flying foxes to other animals. In 1994, chimpanzees fed on a fig tree alongside fruit bats before developing Ebola hemorrhagic fever [11]. This incident supported the idea that a feeding tree for fruit bats, being a meeting point for different animals, might be an origin for disease transmission. Fighting between bat individuals facilitates physical contact and bodily fluid exchanges among bats, and thus may cause the viral spillover at feeding sites [16]. This study found variation in the number of bat visits at different times of night. Bats started to visit the observed trees around 1800 (30 min after sunset time), leading to the possibility that bats remembered the location of the fruit. The frequency of bat visits at different hours was significantly correlated with the number of fruits dropping. This indicated that the number of fruits dropping might be used as an indicator of bat activity levels during foraging.

In conclusion, our findings have improved the knowledge of the ecological movement and foraging behavior of *P. vampyrus*, and thus will be very useful for developing an alternative method to conserve flying fox populations, as well as managing the conflict between humans and bats in Indonesia.

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