



Diurnal behavior and activity budget of the golden-crowned flying fox (*Acerodon jubatus*) in the Subic bay forest reserve area, the Philippines

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ABSTRACT. *Acerodon jubatus* (the Golden-Crowned flying fox) is an endemic species in the Philippines, which was suspected to be a host of the Reston strain of the Ebola virus. As nocturnal animals, the flying foxes spend daytime at the roosting site, which they use for self-maintenance and reproduction. To understand the variation in diurnal behavior and time allocation for various activities in the Golden-Crowned flying fox, we investigated their daytime behavior and activity budget using instantaneous scan sampling and all occurrence focal sampling. Data collection was performed from 07:00 to 18:00 hr during January 8–17, 2017. The most frequent activity was sleeping (76.3%). The remaining activities were wing flapping (5.0%), self-grooming (4.2%), hanging relaxation (3.4%), wing spread (2.9%), movement (2.4%), mating/courtship (2.4%), aggression (1.9%), hanging alert (1.2%), excretion (0.1%) and scent marks (0.05%). The frequency of sleeping, wing flapping, self-grooming, hanging relaxation, aggression, mating/courtship and movement behaviors changed with the time of the day. Females allocated more time for resting than males, while males spent more time on the activities that helped enhance their mating opportunities, for example, movement, sexual activity and territorial behavior.

KEY WORDS: *Acerodon jubatus*, activity budget, diurnal behavior, interspecific interaction

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With 1,240 identified species, bats constitute approximately 25% of all the mammalian species worldwide [17]. The fruit bats of the family *Pteropodidae*, especially species belonging to the genus *Pteropus*, sometimes aggregate in large populations, with around hundreds of thousands per colony [24]. Their geographical distribution ranges from tropical and subtropical to temperate regions of Asia, Australia and islands in the Indian Ocean and western Pacific Ocean [2, 26]. Pteropodid bats play a role in propagation of at least 289 plant species, which is important for the maintenance of ecosystem health [10]. However, they are suspected to be hosts of zoonotic viruses, such as filoviruses (Ebola and Marburg virus), which were a serious problem in Africa; henipaviruses (Hendra and Nipah virus), which had outbreaks in Asia and Australia; and lyssavirus (Australian bat lyssavirus), which is widespread in Australia [13]. To estimate the risk of disease emergence, it is necessary to understand the behavioral ecology of wildlife reservoirs. However, knowledge on the behavior of bats is still limited. Only about 5% of all bat studies focus on its ethology [4]. This information highlights the need of a bat behavioral study, especially in a natural condition.

In 2008–2009, filovirus infection was found in domestic pigs and pig farm workers in the Philippines [22]. The serological evidence of Ebola Reston virus infection strongly suggested that the endangered species, *Acerodon jubatus*, is a host of this virus [16]. *A. jubatus* (the golden-crowned flying fox) is a species endemic to the Philippines, with its individual body weight ranging from 0.73 to 1.00 kg [9, 31]. Its population has declined by more than 50% in the last few decades, owing to habitat loss [21]. A nocturnal behavioral study on this species supported the fact that they are nomadic animals with high flight capacity (maximum around 87.04 km per night), and their movement patterns depend on the distribution of food resources [9]. Long-distance flight ability is a key factor in virus transmission, because it enables the bats to come in contact with various animals utilizing in the same foraging area. Comparison between the day- and night-time behavioral data is important for the conservation of bats and the prediction of disease outbreak. However, there have been no studies on the diurnal behavior of the golden-crowned flying

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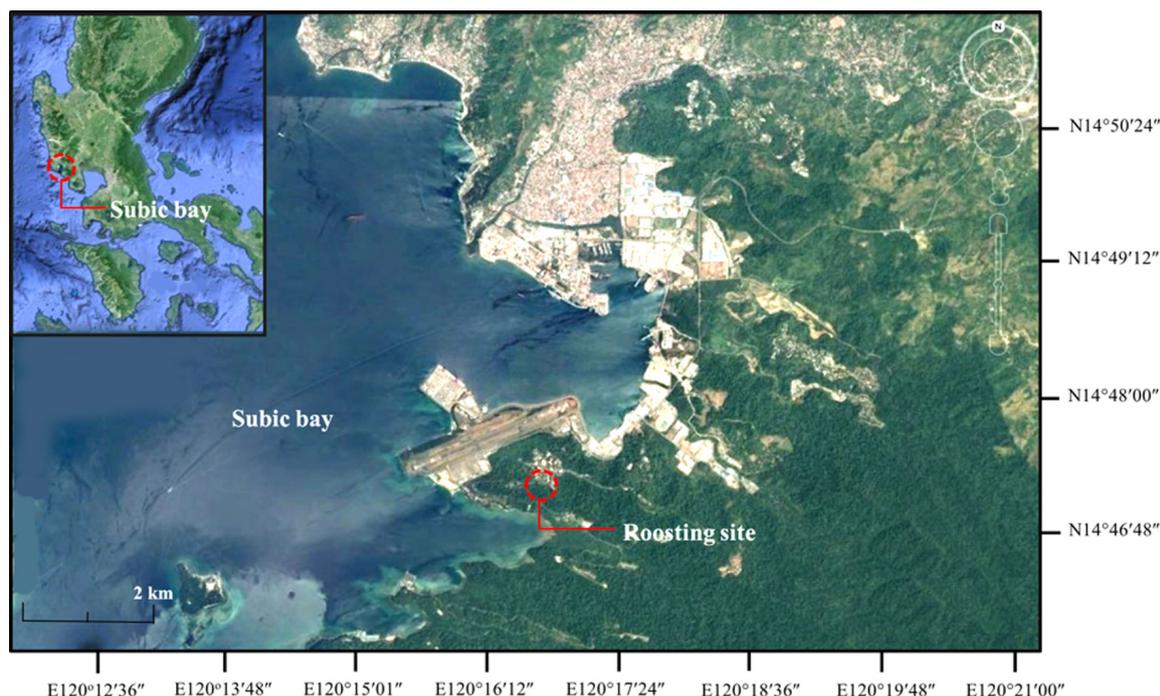


Fig. 1. Location of the study site at the Subic bay forest reserve area, the Philippines (14° 47' 13.47" N, 120° 16' 39.25" E).

fox. Therefore, the activity of *A. jubatus*, living in a mixed-species roost with *Pteropus vampyrus*, at the Subic Bay Freeport Zone, the Philippines, was investigated using instantaneous scan sampling and all-occurrence focal sampling techniques. In most animals, the activity patterns are influenced by environmental factors, such as temperature and/or light intensity [3]. Therefore, the environmental factors were measured in parallel with the behavioral observations.

MATERIALS AND METHODS

Study site

The field work was undertaken at a mixed-species roost of *A. jubatus* and *P. vampyrus* in the Subic Bay Freeport Zone, the Philippines (14° 47' 13.47" N, 120° 16' 39.25" E) (Fig. 1), under the permission of the Subic Bay Metropolitan Authority (Approval number: ECD-RPD-16-0767). The observation period was from 8 to 17 January, 2017, amid the rainy season. The population size of the two bats species was estimated by bounded count method. Estimated population size = $2n_{\max} - n_{\max-1}$, where n_{\max} is the maximum counted number and $n_{\max-1}$ is the second maximum counted number [32]. The majority of the roost was *P. vampyrus* (7,200 individuals), whereas *A. jubatus* comprised a small proportion of the mixed-species population (624 individuals).

Data collection

To examine the variation in diurnal activity of *A. jubatus*, quantitative behavioral data were collected by instantaneous scan sampling—a group scan, during which the behaviors of all individuals in the group were noted in a short period of time [1]. The presence of observer might have an influence on the behavior of the flying foxes. To minimize this, the observation point was set far away from the roosting trees, at over 20 m. We were not able to observe the whole group (containing 624 individuals) within a short time period, and therefore, we selected a subgroup containing 50 bats as the subject group for sampling. The group scans were conducted during 07:00–18:00 hr on each observation day. Each 1-hr recording session was divided into 20-min sampling intervals, yielding 3 sampling points per recording session. At each sampling point, the behavior of 50 individuals in the subject group was briskly recorded, one by one. By this technique, we got information about the activities of the scanned-group members at a particular period of time. Furthermore, the environmental data, such as ambient temperature, relative humidity, light intensity and wind speed, were measured by Light Meter (LX-2000SD, Custom Corp., Tokyo, Japan) and Hot Wire Anemometer (WS-03SD, Custom Corp.), at each sampling point of the scan sampling.

To investigate the sex differences in activity budgets, we performed all-occurrence focal sampling, which concentrates on one individual during a continuous recording period. Data collection was done during 07:00–18:00 hr, on six adult males and six adult females using binocular as a tool for observation. Sexes of the bats were identified through morphologic observation at genital area. The duration of each recording session was 1 hr, with a 30-min break between consecutive sessions, yielding 7.5 hr of observation period for each focal subject. Capturing and marking of the focal bats might alter the actual behavior of the flying fox. Therefore, we used naturally distinctive markings, such as damaged ears, scars or holes on wing membranes to distinguish the subjects from

Table 1. Ethogram used to score the instantaneous scan sampling and all occurrence focal sampling

Behavioral category	Behavioral unit	Description	Context
Sexual activities	Mating	Male grasp-restrains the female from behind, biting female's neck and inserts the penis into the vagina	Reproduction
	Courtship	Male approaches the female and licks genital area of female	Reproduction
	Masturbation	Male starts licking its penis, leading to erection, and continuously licks the erect penis for more than one min, without urination and ejaculation	Serves as masturbatory function, mostly found when male is rejected for mating by a female
Self-maintenance	Self-grooming	Licking wing membrane or occasional bouts of genital tract licking or scratching body part including head	Cleaning function or wing membrane maintenance
Thermoregulation	Wing flapping	Fanning the body with wing membrane	Reducing body temperature
Positive social behavior	Maternal care	Newborn attached to or being carried by female or juvenile grooming by female	Mostly found during lactation period, establishes social bond between the mother and offspring
	Mutual grooming	Licking one another's body, excluding the licking of juvenile by its mother or rubbing of the neck and head	Associated with group recognition, bonding within the group
	Play	Mock-biting or mock-wrestling with an absence of vocalization	Usually occurs among young males
Negative social behavior	Aggression	Aggressive vocalization, wing shaking, chasing, biting and/or fighting between individuals	Self-defense from threats or female rejecting a male
	Hang alert	Hanging bipedally or monopodally with eyes open and ear movement around	
Territorial behavior	Territory defense	Aggressive vocalization, wing shaking, chasing, biting and/or fighting towards invader	Defense of territory that is normally performed by the harem-holding male
	Scent mark	Rubbing neck or shoulder along tree branches	Marking territory
	Wing spreading	Wings widely opened and extended	Related to the defense of territory or threatening display to others, mostly performed by males
Non-categorized	Sleeping	Eyes closed and wing wrapped around the body	
	Hang relax	Hanging bipedally or monopodally with wings folded or wings opened and eyes open looking around	
	Movement	Moving along a branch or trunk without flying	
	Excretion	Turning the body upright to urinate and/or defecate	

These behavioral units were described according to the postures and were grouped into behavioral categories according to their function, following Connell *et al.* [7], Nelson [25] and Hengjan *et al.* [14].

one another. In the event of a subject going out of sight, a new focal subject was randomly chosen, immediately. This technique provided the accurate duration of behavioral data, which enables us to compare the activity budget of male and female bats. The behavioral units and categories are described in Table 1. Furthermore, the roost-switching events between *P. vampyrus* and *A. jubatus* were recorded to determine the physical inter-species interactions.

Statistical analysis

Normality of the data was examined using Kolmogorov-Smirnov Test. When the distribution of raw data was not normal, non-parametric statistics were used for the analysis of behaviors. The analysis and calculation were conducted separately for each sampling method (scan and focal sampling).

For scan sampling, Kruskal-Wallis test was performed for nine behavioral units, i.e., sleeping, self-grooming, wing spreading, movement, wing flapping, hanging relaxation, aggression, mating and courtship, to investigate how these behaviors vary with the time of the day. Pearson correlation coefficients were then used to test the possible relationships between the daily variation in daytime behaviors and the environmental factors. The results are presented as average percentage of the number of bats \pm standards errors (SE). To calculate the average percentage of bats for each behavioral unit, the number of bats displaying a particular behavior in a 1-hr recording session was grouped, and then, the average was calculated for each session. The average number of bats for each behavioral unit (n) was divided by the total number of observed bats at each sampling point (N=50) and converted into percentage ($n/N \times 100$).

For focal sampling, Mann-Whitney *U* Tests were performed for five behavioral categories and the non-categorized behaviors, in order to compare the activity budgets of adult males and females. Results are presented as average percentage of time \pm standards errors (SE). To calculate the average percentage of time spent for each activity, the average duration of time (in sec) that the focal bats allocated to each behavioral category (t) was divided by the total duration of observation (in sec) for one observation day

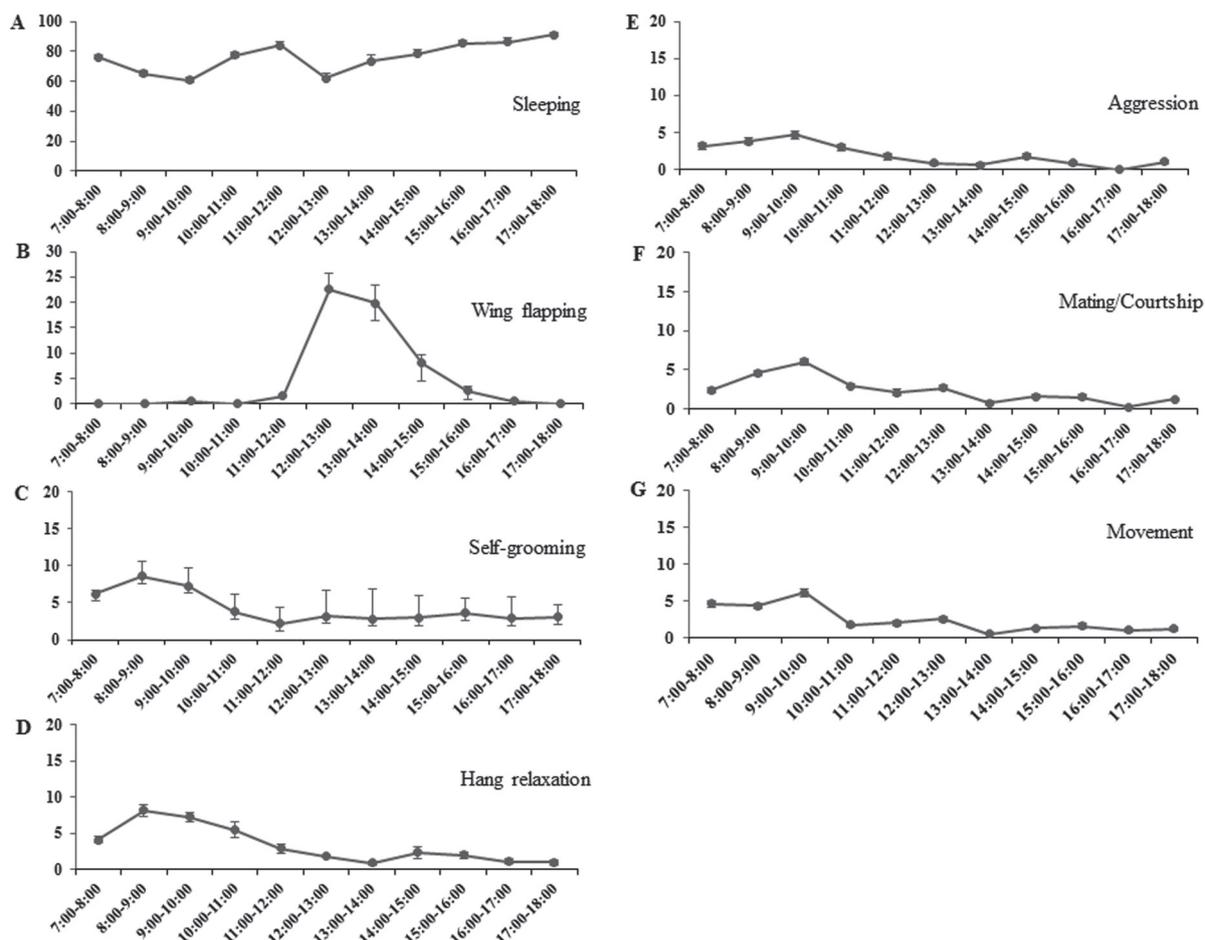


Fig. 2. The variation of sleeping (A), wing flapping (B), self-grooming (C), hang relaxation (D), mating/courtship (E), aggression (H) and movement (G) during 07:00–18:00 hr.

($T=27,000$ sec) and converted to percentage ($t/T \times 100$).

Significant correlations and differences for all tests were determined at $P < 0.05$ level (IBM SPSS 18.0).

RESULTS

Diurnal variations in behavior

The most common behavior was sleeping; on an average, $76.3 \pm 3.0\%$ of the bats exhibited sleeping behavior throughout the day, followed by wing flapping ($5.0 \pm 2.5\%$), self-grooming ($4.2 \pm 0.6\%$), hanging relaxation ($3.4 \pm 0.7\%$), wing spread ($2.9 \pm 0.4\%$), movement ($2.4 \pm 0.5\%$), mating/courtship ($2.4 \pm 0.2\%$), aggression ($1.9 \pm 0.4\%$), hanging alert ($1.2 \pm 0.6\%$), excretion ($0.1 \pm 0.03\%$) and scent marks ($0.05 \pm 0.02\%$).

The statistical analysis showed a significant effect of time on the number of bats performing the following behaviors: sleeping ($\chi^2=29.3$, $d.f.=10$, $P=0.001$), wing flapping ($\chi^2=52.2$, $d.f.=10$, $P < 0.001$), self-grooming ($\chi^2=26.2$, $d.f.=10$, $P=0.003$), hanging relaxation ($\chi^2=55.3$, $d.f.=10$, $P < 0.001$), aggression ($\chi^2=46.7$, $d.f.=10$, $P < 0.001$), mating/courtship ($\chi^2=40.0$, $d.f.=10$, $P < 0.001$) and movement ($\chi^2=49.6$, $d.f.=10$, $P < 0.001$) (Fig. 2). The highest frequency of sleeping was noted during 17:00–18:00 hr, whereas the lowest was recorded during 12:00–13:00 hr. Wing flapping was observed only in late morning and afternoon (11:00–16:00 hr), and was higher during 12:00–14:00 hr than during the rest of this period. Self-grooming and hanging relaxation showed the same trend, peaking during 08:00–10:00 hr, and then gradually decreasing towards the evening. Mating/courtship, aggression and movement behaviors showed similar temporal patterns during the daytime. The frequencies of these behaviors were the highest during 09:00–10:00 hr and tended to decrease steadily from this period until the evening (Fig. 2).

The analysis showed a significant effect of time on the number of bats exhibiting solitary behaviors ($\chi^2=60.6$, $d.f.=10$, $P < 0.001$), social behaviors with physical contact ($\chi^2=50.3$, $d.f.=10$, $P < 0.001$) and social behaviors with no physical contact ($\chi^2=50.9$, $d.f.=10$, $P < 0.001$). The flying foxes tended to perform the solitary behaviors (e.g., sleeping, self-grooming, movement, wing flap, excretion, hang relax) in the afternoon section, compared with the morning section, whereas the social behaviors with direct contact (aggressive behavior with biting and/or fighting between individuals and mating/courtship behaviors) and those without physical

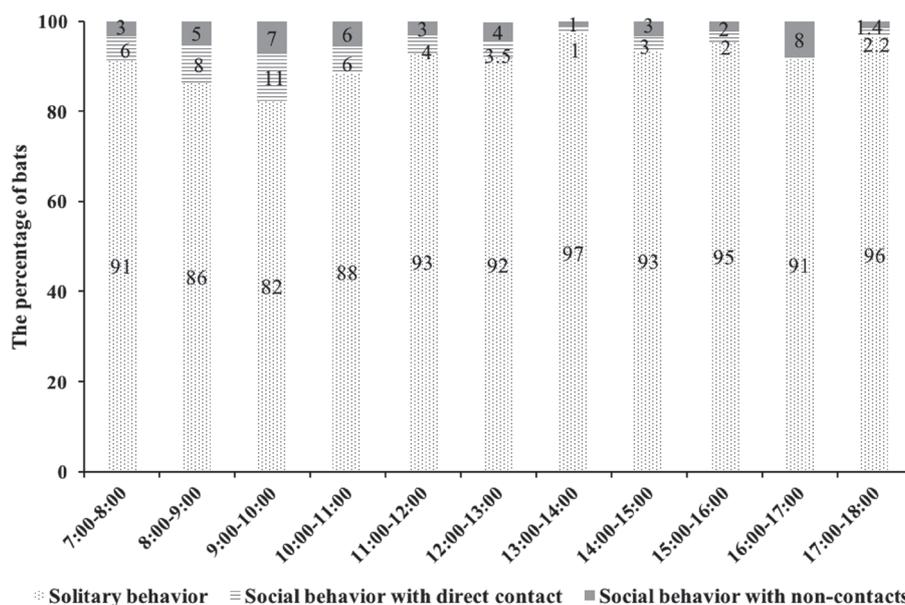


Fig. 3. The percentage of bats perform solitary behavior, social behavior with direct contact and Social behavior with non-direct contact.

contact (aggressive vocal, wing spread, hanging alert and scent marks) were more frequent during the morning, compared with the afternoon (Fig. 3).

Hanging alert is an excited behavior, which is seen when the animals were disturbed. In this study, we found that the golden-crowned flying foxes showed hanging alert behavior when they were faced with anthropogenic exposure by tourists and/or predation by aerial predators (bird in the genus *Spilornis*), but there was no disturbance by non-human primates. This is in contrast to our previous study on *P. vampyrus* in Indonesia [14], wherein the roosting site of the flying foxes was invaded by non-human primates (*Trachypithecus auratus*), an average 3.3 ± 0.5 times a day. Therefore, hanging alert was not included in the statistical analysis for behavioral variation with the time of the day. Excretion and scent masking behaviors were not analyzed due to their rare occurrence.

The effect of environmental factors on the behaviors of flying foxes

Self-grooming behavior showed a positive correlation with relative humidity ($r=0.304$; $P<0.001$). Wing flapping showed a positive correlation with the ambient temperature ($r=0.223$; $P=0.001$) and light intensity ($r=0.263$; $P<0.001$), but had a negative relationship with relative humidity ($r=-0.350$; $P<0.001$). Other correlations among the environmental factors and behaviors were not significant ($P>0.05$).

Difference in activity budget between males and females

In total, the behavioral data of six males and six females were obtained. The amount of time spent on some behavioral categories was significantly different between adult males and females. Resting state (sleeping behavior) was the most common activity for both adult males and females, with females allocating more time for rest than the males (males=83.0% and females=90.0%). Adult males spent more time in sexual activities than the females (males=1.80% and females=0%). When a male was rejected by a female, the male chased the female persistently for an average 1.1 ± 0.2 min, until the completion of copulation, which lasted for 1–2 min. Furthermore, males spent more time in thermoregulation (males=1.8% and females=0.3%), territorial behaviors (males=2.4% and females=0%) and movement (males=0.8% and females=0.1%) than the females. However, the amount of time spent on self-maintenance, negative social behaviors, hang relax and excretion was not significantly different between males and females. Positive social behavior was not found in either males or females (Table 2). The difference in the time spent on thermoregulation seemed related to the location of the observed bats on the roosting trees; males tended to perch on exposed branches (with fewer leaves) and/or on treetops, whereas the females gathered in the center of the trees where they were protected from sunlight.

*Roost switching between *P. vampyrus* and *A. jubatus**

The group of golden-crowned flying foxes seemed to select a roosting tree separate from those occupied by the group of *P. vampyrus*. In other words, there was inter-specific roost-segregation between these two bats species. However, roost-switching events were observed between these two species. On an average, 30.4 ± 4.7 bats of both species switched to the roosting trees occupied by the other species, during a day. However, the observers observed no body contact between *P. vampyrus* and *A. jubatus*.

Table 2. Average \pm standard error proportion of time spent for each activity in male and female bats, during 07:00 to 18:00 hr

Behavioral category	Behavioral unit	Male (n=5)		Female (n=5)		Z (P-value)
		Proportion of time for behavioral unit (%)	Total (%)	Proportion of time for behavioral unit (%)	Total (%)	
Sexual activities	Mating	0.16 \pm 0.10	1.80 \pm 0.29	0	0	-3.0 (0.002)
	Courtship	1.04 \pm 0.20		0		
	Masturbation	0.16 \pm 0.10		0		
Self-maintenance	Self-grooming	1.77 \pm 0.30	1.77 \pm 0.30	2.5 \pm 0.40	2.5 \pm 0.40	-1.4 (0.15)
Thermoregulation	Wing flapping	1.8 \pm 0.50	1.8 \pm 0.50	0.3 \pm 0.20	0.3 \pm 0.20	-3.5 (0.001)
Positive social behavior	Maternal care	0	0	0	0	0
	Mutual grooming	0		0		
	Play	0		0		
Negative social behavior	Aggression	0.28 \pm 0.06	1.37 \pm 0.06	0.1 \pm 0.06	1.6 \pm 0.27	-1.9 (0.055)
	Hang alert	1.09 \pm 0.14		0.5 \pm 0.20		
Territorial behavior	Territory defense	0.05 \pm 0.04	2.4 \pm 0.60	0	0	-3.0 (0.002)
	Scent mark	0.05 \pm 0.03		0		
	Wing spreading	2.3 \pm 0.60		0		
Non-categorized	Sleeping	83.0 \pm 2.49		90.0 \pm 0.90		-3.2 (0.001)
	Hang relax	6.9 \pm 1.50		5.6 \pm 0.70		-0.4 (0.631)
	Movement	0.8 \pm 0.23		0.1 \pm 0.00		-2.32 (0.02)
	Excretion	0.01 \pm 0.00		0.02 \pm 0.00		-0.6 (0.493)

Z=Mann-Whitney U Test; P<0.05 two-tailed test.

DISCUSSION

The patterns of daytime activity

In this study, we described the diurnal patterns of activity in the golden-crowned flying foxes, as well as their activity budget in a natural habitat. The most frequently observed activity in the group of flying foxes was sleeping, followed by wing flapping, self-grooming, hanging relaxation, wing spread, movement, mating/courtship, aggression, hanging alert, excretion and scent marks. Connell *et al.* [7] and Hengjian *et al.* [14], working on *Pteropus poliocephalus* and *P. vampyrus*, respectively, also found that sleeping (resting state) was the most dominant behavior, with the highest frequency in late evening, compared with the other times in a day. *A. jubatus* also showed this tendency.

Wing flapping is a common behavior in the flying fox living in tropical regions, as they are always exposed to severely high ambient temperatures during daytime. This behavior had a strongly positive correlation with the ambient temperature and light intensity, i.e., the flying foxes performed wing flapping more frequently when the ambient temperature and light intensity are higher, especially around noon and early afternoon. Flying foxes lack sweat glands for body temperature regulation [29], and wing flapping is therefore used as a thermoregulatory behavior to lower body temperature. Ochoa-Acun and Kunz [27] showed that *Pteropus hypomelanus* tended to increase the frequency of wing fanning when the ambient temperature reached 36°C, thus, exceeding the range of their thermoneutral zone. This gets further support from the fact that wing flapping was rarely observed in the flying foxes living in temperate zones [7].

Bats are known to be parasitized by mites, ticks, bugs, fleas and flies [12]. Bat flies (*Cyclopedia hirsfieldi*) are blood-sucking parasites found on the fur and wing membrane of the flying fox species living in South-East Asia [28]. These parasites have negative effects on the physical condition of their hosts, by delaying the timing of reproduction in adults and/or reducing the growth rate of the young ones [23]. In bats, self-grooming is behavioral strategy to reduce parasite loading on body, which tends to be higher during the rainy season [11, 19]. This would explain the positive correlation between the frequency of self-grooming and humidity found in this study. This behavior typically occurred early in the morning, consistent with the study of diurnal variation in self-grooming behavior of *P. vampyrus* and *P. poliocephalus* [7, 14].

There is little information available on the mating behavior of the golden-crowned flying foxes. The mating systems have been documented for only 9.2% of the total Pteropid bat species [8]. Most of flying foxes are polygynous, with mating groups that contain a single male and multiple females, also known as harems. In Australian *Pteropus* (*P. Alecto*, *P. gouldi*, *P. poliocephalus* and *P. scapulatus*), males set up their mating territory around the females, just prior to or the beginning of the breeding season, and the male reproductive success depends on the location of the territory on a roosting tree [20, 25]. To set up mating territories, males rub their neck and shoulder along tree branches, which is referred to as scent-mark behavior. This study found that male bats usually show scent-mark behavior in the late evening before the foraging fly-out. Compared with the other behaviors, the frequency of mating/courtship behavior was considerably low. However, the frequency of mating/courtship behavior seemed to vary during the day, showing the highest rate during early to middle morning, and tended to decrease gradually from noon until the evening. A similar pattern was found in aggressive and movement behaviors. Males moved towards females and then sniffed or

licked around the genital area of females. Females always repelled the males by showing aggressive behaviors, such as screaming or wing shaking towards the male and/or moving away. These behaviors normally occurred when mating/courtship behaviors were initiated by males. If a male was rejected by a female, the male chased the female persistently (an average 4.6 ± 1.1 min) until the completion of copulation. This pattern of mating/courtship behavior was also recorded in the Indian flying fox *Pteropus giganteus*; however, males of this bat species spent 20–40 min to chase the females before his copulation was completed [18].

Difference in the activity budget between males and females

Bats spend half their lives living in roosts, where they mate, bear offspring and exhibit a social life. The amount of time spent on these activities has direct effects on the energetic demands and reproductive success of the animals [33]. To balance their energy budgets, bats need to modulate their activity patterns in accordance with the environmental conditions. The golden-crowned flying foxes spend a majority of the daytime sleeping. Due to long-distance flights, the energetic demand for flight in flying foxes is 15 times higher than that of the resting state [5]. This could be the reason why bats need to save the energy for foraging at night by sleeping during the day. Compared with a previous study on *P. vampyrus* living in Leuweung Sancang conservation area, Indonesia [14], *A. jubatus* in this study site spent a greater amount of the daytime sleeping. This could be explained by lesser disturbance by other wildlife in this study area, compared with *P. vampyrus*, which were faced with high disturbance by non-human primates during daytime [14]. We also found significant differences in the activity budget for sleeping, movement, sexual activity, thermoregulation and territorial behaviors between sexes. In polygynous species, the male reproductive strategies are involved by male-male competition and/or territory defense [6]. These could be a reason why male bats allocated a greater proportion of their time for sexual activity and territorial behavior than the females. The difference in time spent for thermoregulation behavior could be explained by the roosting position of males and females. The hanging position on branch determined the amount of exposure to sunlight. Males tended to hang on the exposed branches or on treetops, whereas females roosted in more covered or central positions of the colony. Holmes suggested that the optimal roosting location would be the center of the colony and a shaded place, because it is safer from predation when flying foxes congregate in large numbers [15]. Therefore, males seemed to be exposed to a stronger sunlight and predation risk than the females.

Interspecific interactions in the mixed-species colony

Due to their small population, *A. jubatus* might need to live with the big population of *P. vampyrus*, because living in a large group enhances the protection from predators [30].

Even though the large flying foxes and the golden-crowned flying foxes occupied the same habitat areas, they showed a clear habitat segregation among trees. The roosting segregation between bat species could be a strategy to avoid interspecies breeding and competition. However, a high rate of roosting shifts between the flying fox species was observed in this study site. We could not find direct physical contacts between *P. vampyrus* and *A. jubatus*. However, parasite exchange between species is possible, given the roost shifts. For example, if a parasite detaches from the body of *P. vampyrus*, it is possible for the parasite to re-climb the tree and attach to *A. jubatus*. Moreover, *A. jubatus* must be exposed to the aerosol derived from the body fluid and/or fecal wastes of *P. vampyrus*, because of their neighboring positions after roost exchange. Therefore, there is a potential risk of the transmission of pathogens between the two bat species in Subic Bay conserved area.

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