SEASONAL VARIATION IN EMERGENCE AND ACTIVITY PATTERN AT ROOSTING SITE OF LYLE'S FLYING FOX *Pteropus lylei* Andersen, 1908 AT WAT PHO, CHACHOENGSAO PROVINCE

Miss Yupadee Hengjan

A Thesis Submitted in Partial Fulfillment of the Requirements

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ความผันแปรตามฤดูกาลของการบินออกจากที่พักและแบบรูปกิจกรรมในที่พักของค้างคาวแม่ไก่ภาคกลาง *Pteropus lylei* Andersen, 1908 ที่วัดโพธิ์ จังหวัดฉะเชิงเทรา

นางสาวยุพดี เฮงจันทร์

วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรมหาบัณฑิต
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Thesis Title	SEASONAL VARIATION IN EMERGENCE AND ACTIVITY PATTERN AT ROOSTING SITE OF LYLE'S FLYING FOX *Pteropus lylei* Andersen, 1908 AT WAT PHO, CHACHOENGSAO PROVINCE
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Field of Study	Zoology
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ยุพดี เฮงจันทร์ : ความผันแปรตามฤดูกาลของการบินออกจากที่พักและแบบรูปกิจกรรมในที่พักของค้างคาวแม่ไก่ภาคกลาง *Pteropus lylei* Andersen, 1908 ที่วัดโพธิ์ จังหวัดฉะเชิงเทรา. (SEASONAL VARIATION IN EMERGENCE AND ACTIVITY PATTERN AT ROOSTING SITE OF LYLE'S FLYING FOX *Pteropus lylei* Andersen, 1908 AT WAT PHO, CHACHOENGSAO PROVINCE) อ. ที่ปรึกษาวิทยานิพนธ์หลัก : อ.ดร. ธงชัย งามประเสริฐวงศ์, 129 หน้า.

การศึกษานี้มุ่งเน้นศึกษาอิทธิพลของปัจจัยทางกายภาพต่อความผันแปรในการบินออกจากที่พัก และพฤติกรรมตอนกลางวันของค้างคาวแม่ไก่ภาคกลาง ดังนั้นจึงทำการเก็บข้อมูลการบินออกจากที่พัก ปัจจัยทางกายภาพ และพฤติกรรมตอนกลางวันของค้างคาวแม่ไก่ภาคกลางที่วัดโพธิ์ อำเภอบางคล้า จังหวัดฉะเชิงเทรา เป็นระยะเวลา 12 เดือน ผลการศึกษาพบว่า เวลาเริ่มต้นพฤติกรรมการบินออกจากที่พักมีความสัมพันธ์กับเวลาพระอาทิตย์ตกดินและความชื้นสัมพัทธ์ ช่วงระยะเวลาที่ค้างคาวใช้สำหรับการบินออกจากที่พักมีความผันแปรตลอดปี โดยมีแนวโน้มเพิ่มสูงขึ้นในช่วงให้กำเนิดลูก และช่วงเริ่มต้นของการให้นมลูก นอกจากนี้ยังพบว่าช่วงระยะเวลาที่ใช้ในการบินออกจากที่พักมีความสัมพันธ์กับช่วงสนธยาค่อนข้างน้อย และ ข้างขึ้น-ข้างแรมไม่มีอิทธิพลต่อพฤติกรรมการบินออกจากที่พักในค้างคาวแม่ไก่ภาคกลาง

ผลการศึกษาพฤติกรรมการบินออกจากที่พักของค้างคาวแม่ไก่ภาคกลางในแต่ละเพศและสถานะทางการสืบพันธุ์โดยการบันทึกภาพวีดีโอพบว่า ค้างคาวเพศผู้ เพศเมีย และวัยอ่อนบินออกจากที่พักช้ากว่าปกติในช่วงเดือนมีนาคม และเมษายนซึ่งเป็นช่วงที่มีการให้กำเนิดลูก และช่วงเริ่มต้นของการให้นมลูก โดยในช่วงนี้ ค้างคาวเพศเมียที่อยู่ในช่วงให้นมลูกจะบินออกจากที่พักช้าที่สุด ซึ่งอาจเนื่องมาจากการแบกรับน้ำหนักเพิ่มจากการมีลูกเกาะ ส่งผลให้ศักยภาพในการบินลดน้อยลง และเพิ่มความเสี่ยงจากการถูกล่า จากผลการศึกษาสรุปได้ว่า ปัจจัยทางกายภาพ และสถานะทางการสืบพันธุ์ มีอิทธิพลต่อการบินออกจากที่พักของค้างคาวแม่ไก่ภาคกลาง

ผลการศึกษาพฤติกรรมตอนกลางวันโดยเทคนิคการสุ่มตัวแบบส่องกราด พบว่าพฤติกรรมที่ค้างคาวแสดงบ่อยที่สุดคือ พฤติกรรมการนอนหลับ การเกาและเลียบริเวณตามลำตัว และการกระพือปีก โดยรูปแบบการแสดงพฤติกรรมการนอนหลับ การเกาและเลียบริเวณตามลำตัว การกระพือปีก และการจับคู่ผสมพันธุ์และเกี้ยวพาราสีนั้นมีความแตกต่างกันอย่างชัดเจนในแต่ละช่วงเวลาของวัน และช่วงเวลาของปี นอกจากนี้ยังพบพฤติกรรมการกางปีก การเคลื่อนย้ายไปตามกิ่งไม้ และการจับคู่ผสมพันธุ์และเกี้ยวพาราสี บ่อยในค้างคาวเพศผู้ และพบพฤติกรรมการเกาและเลียบริเวณตามลำตัว และพฤติกรรมก้าวร้าวบ่อยในค้างคาวเพศเมีย ดังนั้นจากผลการศึกษาสรุปได้ว่า ช่วงเวลาของวัน ฤดูกาล และเพศ มีอิทธิพลต่อการแสดงพฤติกรรมตอนกลางวันของค้างคาวแม่ไก่ภาคกลาง

ภาควิชา ชีววิทยา ลายมือชื่อนิสิต

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YUPADEE HENGJAN : SEASONAL VARIATION IN EMERGENCE AND ACTIVITY PATTERN AT ROOSTING SITE OF LYLE'S FLYING FOX *Pteropus lylei* Andersen, 1908 AT WAT PHO, CHACHOENGSAO PROVINCE. ADVISOR: THONGCHAI NGAMPRASERTWONG, Ph.D., 129 pp.

This study addressed the question of how environmental factors influence the variation in emergence and daytime behavior of Lyle's flying fox, *Pteropus lylei*. Therefore, the colony-wide emergence, environmental factors and daytime behavior were investigated directly at roosting site of Lyle's flying fox (Wat Pho, Amphoe Bang Khla, Chachoengsao Province) for 12 months. It was found that the onset of colony-wide emergence time had significantly affected by sunset time and relative humidity. The duration of colony-wide emergence varied throughout the year, and tended to increase during parturition and early lactation periods. However, the duration was weakly correlated with seasonal change in twilight duration, and lunar phase had no influence on the colony-wide emergence of Lyle's flying fox.

The observation on individual emergence was conducted by filming. The results showed that males, female and juvenile tended to emergence later during reproductive periods, especially in parturition and early lactation. During that time, lactating females were the last to emerge. The later emergence of lactating females can be reflected from the enlargement of wing loading, which reduce flight performance and increase risk of predation. In conclusion, environmental factors and reproductive status play as crucial roles in emergence of Lyle's flying fox.

From daytime behavior observations using scan-sampling technique, the most common behaviors performing by bats were sleeping, grooming and wing flapping. Variation in sleeping, grooming, wing flapping and mating/courtship between times of day and times of the year were apparently observed. Furthermore, wing spreading, movement and mating/courtship were observed in males more frequently than in females, whereas females exhibited grooming and aggressive behaviors more frequently than males. In conclusion, time of day, season and sex have influence on daytime behavior of Lyle's flying fox.

Department : Biology Student's Signature ....

Field of Study : Zoology Advisor's Signature ....

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CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

Figure | Page

Figure Page

Figure Page

CHAPTER I
GENERAL INTRODUCTION

1.1 Rationale

Bats of genus *Pteropus* are largest fruit bats in the world. They are found in tropical and subtropical regions ranging from Madagascar, Asia and Australia (Lekagul and McNeely, 1977). In Thailand, There are four species in genus *Pteropus,* i.e. *P. lylei, P. vampyrus, P. hypomelanus* and *P. intermedius* (Bumrungsri, 2006)

Lyle's flying fox (*Pteropus lylei*), is a vulnerable species of Thailand (IUCN, 2012). It is found in Cambodia, Thailand and Vietnam (Lekagul and McNeely, 1977). It is distributed mainly on the central plain of Thailand. It has the nocturnal lifestyle like other bat species, foraging at night and returns to the colony before sunrise. As nocturnal species, the flying foxes need a roosting site where they can rest during daytime. The flying foxes do not roost in cave where providing the best natural climate control. They roosts on tree with open environment, making them exposed to environment and easy to disturb. Hence, they must adapt their behavior to survive among environmental variation

Evening emergence of bats seems to be a strategy adapted for predator avoidance. Welbergen (2008) stated emergence reflects adaptations to predation and twilight duration with the seasonal variation following season. Takahashi et al. (2001) reported that the evening emergence of bats from their roost is controlled by circadian rhythms, the rhythms that link to the light-dark cycle and have influence on their daily life.

In flying fox species, we currently don't know how the activity pattern of each individual corresponds with the behavior controlled by endogenous rhythms. In addition, there is no available information on emergence behavior as well as activity patterns in Lyle's flying foxes. Of particular interest are questions about: (1) how environmental factors such as timing of sunset, air temperature, humidity and light intensity affect the emergence time of Lyle's flying foxes? (2) how emergence time varies with an individual's social context? (3) whether daytime behaviors differed among times of day and seasons?

First, I predict that colony-wide emergence time is strongly correlated with timing of sunset and light intensity. The light level remains lower at sunset which declining in visibilities of predator and predation can be a major role shaping decisions about foraging in bats. Second, I predict that emergence time should be varied with individual's social context. Individuals with higher energy demands such as lactating females should emerge earlier than another. The young should emerge later than adult due to their limited flight capabilities. Finally, I expect hormonal behaviors (e.g. mating, aggression and nursing/maternal behavior) and thermoregulatory behaviors (e.g. grooming and wing flapping) should be varied among times of day and seasons.

In order to answer these questions, this study will observe the daytime behavior at roost by using scan sampling technique. Colony-wide emergence and individual emergence time will be investigated by filming. The knowledge gained from this study would allow us to predict the emergence behavior and activity pattern of life of Lyle's flying foxes in each stage.

1.2 Objectives

1. To study seasonal variation in colony-wide emergence of Lyle's flying foxes in relation to environmental factor.
2. To study emergence times in male, non-lactating female, lactating female and juvenile of Lyle's flying foxes.
3. To study daytime behavior of Lyle's flying foxes at roosting site.

1.3 Anticipated benefit

The information obtained from this study will provide new baseline knowledge on the ecology and behaviors of Lyle's flying foxes which is important for their conservation in Thailand. For example, what strategy that they use to adapt their emergence behavior and activity pattern to environmental variation. This knowledge is essential for bat conservation providing important information to inform habitat management and mitigate disturbance from human activity. It is hoped any results will inform further studies on the relationship between roost activity and behavior including foraging behavior and resource availability within the home range.

CHAPTER II
LITERATURE REVIEW

2.1 Classification and general description

Bats are classified in class Mammalia, order Chiroptera which is divided into two suborders, consist of the Microchiroptera and the Megachiroptera. The suborder Microchiroptera consists of 16 families, 135 genera, and 759 species. The suborder Megachiroptera consists of one family, 42 genera, and 166 species (Nowak, 1994).

Bats are distinguished from other mammals by their flight ability. They have adapted their physiology and morphology to flight, so they are well-known as flying mammals. Bats are nocturnal animal, forging at night. In daytime, bats spend most of their life living at roosting site where they are protected from diurnal predator. Bats possess a various of roosting types including caves, rock crevices, tree bark, cavities in tree and branches (Kunz and Fenton, 2003).

Most bat species have social community, so they need to develop their sensory and their behavior in order to communicate. The sensory using by bats include hearing, vision, olfactory, and touch. These do not only benefit to communication, but they also play an important role in foraging behavior. All species of Microchiroptera produce echolocation call, also called biological sonar, for navigation and prey capture at dark, but Megachiroptera bats use vision and olfactory for navigation and foraging (Kunz and Fenton, 2003).

There is only one family in the suborder Megachiroptera, Pteropodidae, distributing in Africa, Asia and Australia (Figure 2-1). These fruit-eating bats have large body size, and occupy large home ranges. Head and body length varies from 50-400 mm. This family contains the largest bats of genus *Pteropus*, having a wingspan of 1.7 m. (Nowak, 1994). They have a long life span, up to 20.4 years olds (Weigl, 2005). They have very large forward-facing eyes with highly adaptation to nocturnal vision. Well developed senses of vision and smell facilitate them to find food. They are most active at night and roost at trees by day. Radio-tracking studies on *Pteropus* species showed that these high mobility flying foxes usually emerge from their roost during twilight and travel up to 50 km a night to feed on fruit, nectar and pollen, distributing seeds in their droppings (Epstein et al., 2009; Palmer et al., 2000). This has secured their position as keystone species - animals that are disproportionately important in determining the ecological diversity, distribution and abundance of plants and other animals (Nakamoto et al., 2009).

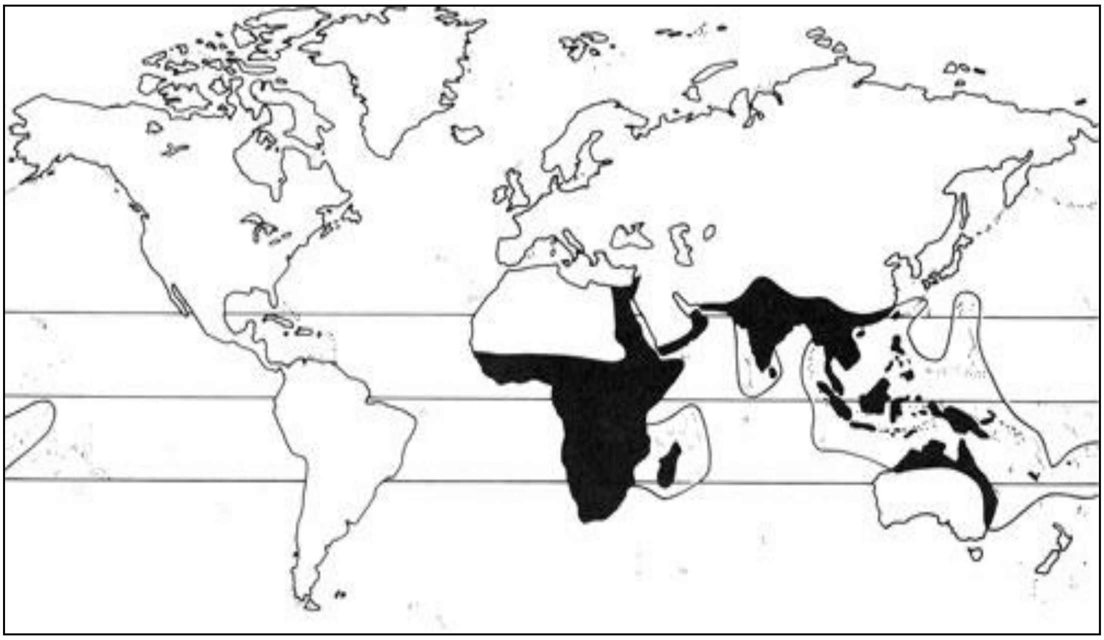

Figure 2-1 World distribution of Megachiroptera

(Modified from www.zoo.cam.ac.uk/zoostaff/be/welbergen/Megachiroptera.htm)

In Thailand, There are four species in genus *Pteropus, P. lylei, P. vampyrus, P. hypomelanus* and *P. intermedius* (Bumrungsri, 2006), but the only one species, *P. lylei,* is accused as serious pest (Lekagul and McNeely, 1977). Similar to other flying fox, Lyle's flying fox, *P. lylei*, has long pointed ears, with no tail. It has short hair with dark-brown back and wings. Their head and mantle are yellow or light-brown. Adult male is larger than adult female. In male, body weight was on average 529 g., and forearm length which measure from the outside of the elbow to the outside of the wrist was on average 156 mm. In female, body weight was on average 418 g., and the length of forearm was on average 152 mm (Boongird et al., 2006). Lyle's flying fox are highly social and vocal animals that congregate a large number of individuals. Most of them are polygynous, with males protecting their territories and harem group. The females essentially give birth to only one offspring per year. During the day, Lyle's flying fox roost on big tree used for many years and having inter-individual spacing at least about 15 cm. (Boonneung, 1997).

Roosting and feeding sites of Lyle's flying fox are found in the crucial agricultural areas of the south-eastern portion of the central plain in Thailand (Figure 2-2). This bat feeds on agricultural products. Thus this fruit-eating bat is considered to be an agricultural pest, and it is threaten by humans (Boongird et al., 2006). Consequently, the majority of known roosts of this bat species are found in temple areas where they are guarded from hunting. However, the population size of Lyle's flying foxes in Thailand continues to reduce. Although the population size reductions of this bat is not considered critical, roosting sites are declining due to habitat change by humans and effects of continual use by bats. Such a highly modified environment may impact on population size of these bats in future.

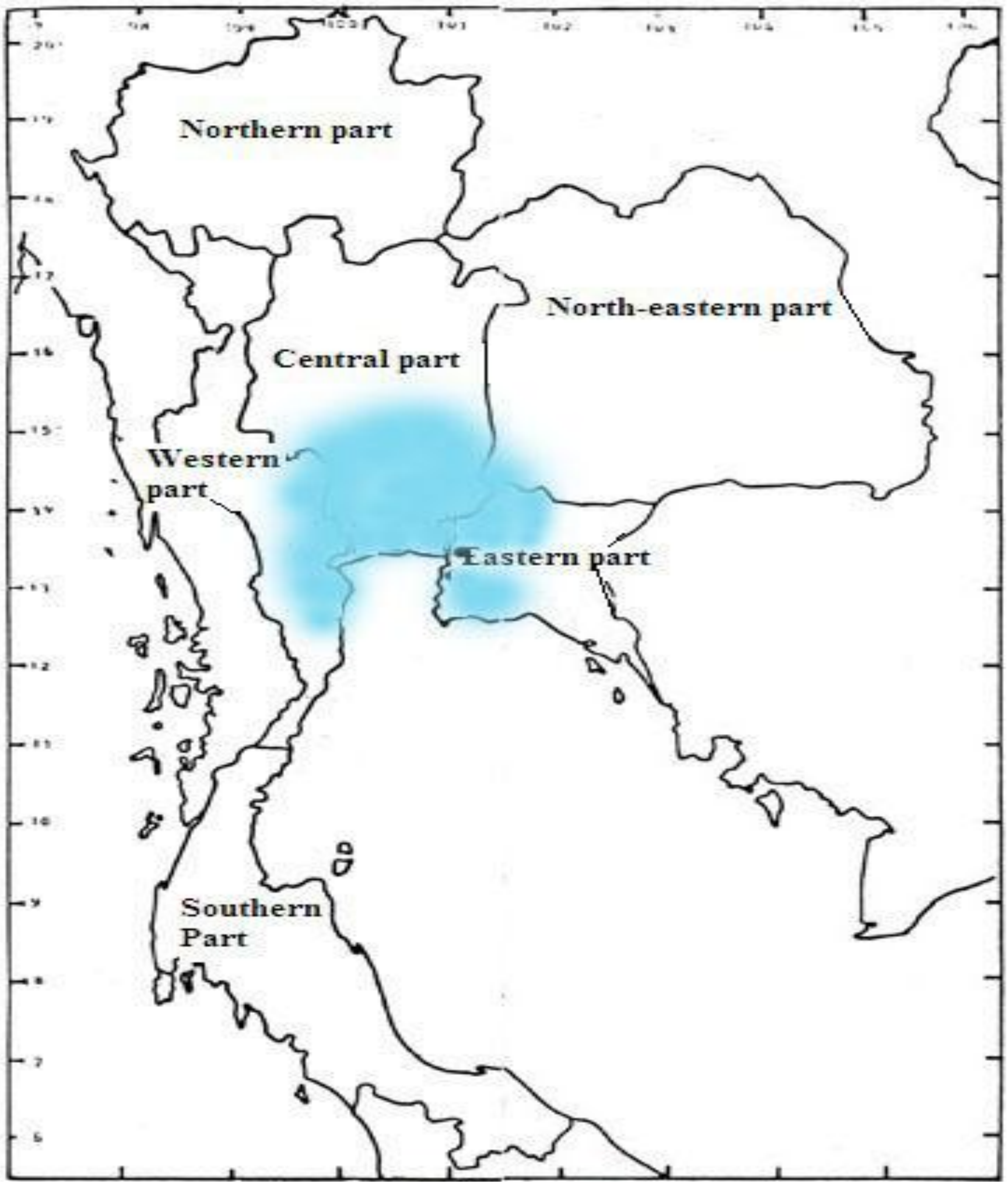

Figure 2-2 Distribution of Lyle's flying foxes in Thailand.

In 2004, Boongird and Wanghongsa reported that there are up to 37,837 Lyle's flying foxes in the central plain of Thailand. The largest colony was found in Wat Pho, where up to 10 thousands bats were counted from a single colony. Boonneung (1977) revealed that number of offspring highly increased in early rainy season and reduced in dry season which might be related to food availability. Moreover, variation in population sizes of each colony may be resulted from many reasons such as roost shift, reproductive cycle and anthropogenic factor (Boongird et al., 2004).

2.2 Emergence behavior

McNab (1976) suggested that flying foxes has low body reserve because they feed on fruits which is high in carbohydrate but low in lipids, which constitute fat storage. So they need to consume enough food to fuel up their energetic demands by foraging every night. Emergence is the starting point of foraging behavior in the flying foxes.

Boonneung (1977) observed the emergence behavior of Lyle's flying foxes. She noticed that shortly after sunset, a few individuals will awake the others by swarming and making a noise concurrently above their colony. Then other members in the colony woke up and prepared their night emergence by grooming themselves to clean their wing membranes and fur. When the number of bats swarming reach some critical density, the flying foxes began emerging, leave their camp to forage within 15 minutes later.

Hall and Richards (2000) suggested that swarming, circling and wheeling above the flying fox colony before emergence may be related to information transfer, or just warming up to flight for long distances. Moreover, Walton and Trowbridge (1983) studied the foraging behaviour of Indian flying fox, *P. giganteus.* They mentioned that a number of emerging bats occasionally spiral to gain some altitude in the sky.

For microchiropteran bats in temperate zone, the functions of swarming, flying in and around caves, were assumed to serve the purposes of hibernation site assessment, information transfer between family members about the hibernation site or mating strategy because the swarming site facilitated gene flow between populations (Fenton, 1969; Furmankiewicz and Altringham, 2007).

2.3 Factors influencing on emergence behavior

2.3.1 Environmental factors

Several studies about the factor influencing on bat emergence at dusk were carried out. For example, Takahashi et al. (2001) reported that bat emergence was controlled by circadian rhythm, endogenous timing system responding to daily light cycle. So the rhythm is crucial factor in determining the sleeping and feeding patterns of bats.

Erkert (1978) studied time of emergence in neotropical bats, genus *Molossidea* and *Vespertilionidea*. He revealed that the emergence time concorded with sunset time, and the return time was parallel with time of sunrise.

Neuweiler (2000) revealed that sun provides the timing cues for daily life in bats. They usually sleep during the day, and attempt to departure at dark. During the year, the emergence time in evening maintains a stable time correlation with the sunset time. This supports hypothesis that circadian rhythms is reset by the sun.

Welbergen (2006) studied evening emergence of *P. poliocephalus.* He showed that colony-wide emergence time of *P. poliocephalus* was strongly related with sunset time which varied with seasonal variation. Moreover, cloud cover and the presence of avian predator seemed to be factors that effect on colony-wide emergence of this bat species. Early emergence was found on the cloudy night accordingly to increased relative humidity and decreased light intensity. Delayed emergence was found on the night that diurnal avian predator was present. This can be explained by the trade-off between predation risk and foraging needs. Bats decide to emerge with falling light intensity at dark because aerial predators decline in vision with decreasing light intensity.

Welbergen (2006) revealed that precipitation have no influenced on the onset of colony-wide emergence time in *P. poliocephalus.* Thies et al. (2006) studied the effect of precipitation on the emergence of *Calollia castanea,* fruit-eating bat, and they suggested that light or moderate rain did not interrupt flight activity in *C. castanea*. However, there are several references that mentioned about the influence of precipitation on insectivorous bats emergence. Entwistle et al. (1996) found that heavy rain delayed out-flight timing of *Plecotus auritus.* Furthermore, Kunz and Anthony (1996) suggested that heavy rain prolonged emergence time and duration of colony-wide emergence in *Myotis lucifugas*, and light rain had a little impact on the onset of emergence in the bat.

Social interaction was also reported to have influences on bat emergence behavior. Marimuthu and Chandrashekaran (1981) reported that social cues such as noise of the wingbeats, active vocal signaling and specific pheromones released when they prepare to leave the roost can serve as crucial cues to emergence time in cave-dwelling bat, *Hipposideros speoris*.

A number of nocturnal animals adapt their night activity association with lunar cycle. For example, a gleaning insectivorous bat, *Lophostoma silvicolum,* adapted their night foraging to emerge earlier on full moon night than new moon night. Because of moonlight has influenced on prey activity level. During new moon night, insects were active throughout the night due to having low light level emitted by moon. The peaks of insect activity occur only at the beginning and the end of night around full moon night because these periods have the lowest light. Hence, insectivorous bats must emerge early in full moon rather than new moon night to reach foraging site at the period of highest insect activity (Lang, el at., 2006).

Furthermore, Jones and Rydell (1994) suggested that insectivorous bat species usually start their nightly emergence before sunset, which increases predation risk from diurnal avian predators, in order to take benefit of the peaks in insect activity around dusk. This is likely to be a trade-off between foraging needs and predation risk.

However, Thies et al. (2006) studied the emergence of frugivorous bats, *C. castanea*, and they reported that the emergence time and the time spent in foraging flight of the bats have not been affected by moonlight. Fruit-eating bats feed on fruit which has no impact from moonlight. They should emerge later to minimize predation risk from diurnal avian predators at dusk. In contrast, Elangovan and Marimuthu (2001), found that the flight activity of *C. sphinx* was higher during the phase of new moon compared to the phase of full moon night. The restriction of flight activity during the bright nights is commonly apprehended as an adaptation to avoid nocturnal predators.

Shirley et al. (2001) investigated the impact of a music festival at Brinkburn Priory on the emergence behavior of Daubenton's bats. They found that bat emerged significantly later during the music festival, but there was no significant difference in the number of bat emerging. So human activity within bat roost should be considered to have the harmful effects on bats behavior and the timing of such events should take this into account.

2.3.2 Sex and age class

A study on individual emergence time of three insectivorous bats, northern bats *Eptesicus nilssonii*, greater horseshoe bats *Rhinolophus ferrumequinum* and lesser horseshoe bats *R. hipposideros*, revealed individual variation in emergence time according to age, reproductive state and body condition. As expected, lactating females emerged early when they increased energy demand. This supported the hypothesis that body reserves in lactating females only buffer against short-term food shortage and higher energy demand is needed. Pregnant females emerged later due to their increase in wing loading, which affected flight capabilities, and may be lead to predation risk. Emergence time of juvenile bats was always significantly later than that of adults because of their less in flight performance. This predicable behavior reflects the trade-off between predation risk and foraging needs that depend on sex, age class and body condition (Duverge et al., 2000).

The similar pattern had been found in the study by Welbergen (2006). He observed individual emergence time of *P. poliocephalus* and suggested that adult females begin their night departure early when they had higher in energetic demands. Juvenile bats emerge later due to their undeveloped flight skill. For adult males, their emergence times were related with harem size. Bachelor males begin their emergence earlier than harem-holding males who protect their harems until the last harem member had left the roost.

2.4 Daytime behavior

Predation forced bats adapt to nocturnal lifestyles, and it also limit diurnal activity in bats. However, there are many studies that reported diurnal activity occurred in fruit-eating bats living in oceanic islands. Tidemann (1987) stated that *P. melanotus* living on Chrismas Island have high diurnal activity because they are free from predators. Furthermore, Grant et al. (1997) reported that foraging activity of *P. samoensis* and *P. tonganus,* living in Volcanic Island, occurred during the day after cyclone due to the storm destructed food resource.

Most of large fling foxes in genus *Pteropus* foraging at night, therefore they need to have a day camp where guard against diurnal predator for resting during the day. Kunz and Fenton (2003) suggested that roosts are crucial place for mating, hibernation and rearing newborn in bats. Dues to seasonal change in food resource availability and reproduction need, bats in temperate zone such as *P. poliocephalus*, needs two types of camps - summer camp and winter camps. The summer roosts are used from September to June, while the winter roosts are used from June to August. In summer camps, the offspring are born, and the flying foxes establish their territories in order to mating. Consequently, defend and aggressive behavior is highly occurred. Unlike the summer roost, winter roosts are sexually separated. Consequently little aggressive behavior is performed by bats (Nelson, 1965).

It is well-known that flying foxes are active at night as nocturnal species, but daytime is also surprisingly busy for these animals. Connell et al. (2006) had studied on daytime behaviors of grey-head flying foxes, *P. poliocephalus* in Australia, such as sleeping, grooming, wing spreading, movement, wing flapping, aggression, mating/courtship and maternal care, and suggested that these behaviors differed significantly between times of day and seasons. Active behaviors (grooming, mating/courtship and wing spreading) occurred mainly in the morning, while non-active behavior (sleeping) occurred mainly in middle of morning and late afternoon. Movement along branch, wing flapping and aggression are rare occurrence.

2.4.1 Sleeping

Funakoshi et al. (1991) studied sleeping behavior in *P. dasymallus*, and found that sleeping was negatively related with ambient temperatures. Time spent sleeping increased when ambient temperature was low. Hence, sleeping occurred more during in cold months. Zubaid et al. (2006) suggested that not only do bats hibernate, but they also enter a torpor state by reducing their activity level, body temperature and metabolic rate in order to conserve fat storage during adverse condition or during food deficiency

2.4.2 Grooming

Connell et al. (2006) reported that grooming is the second most common behavior performing by *P. poliocephalus*. This behavior varied significantly with time of the day which occurred mostly around dawn and dusk. Bats need to clean their wing membranes after return and before emergence. In addition, Nelson (1965) found that mutual grooming in bats of genus *Pteropus* can establish social relationship between group members, especially between mothers – offspring pairs.

Ter Hofstede and Fenton (2005) suggested that grooming is a behavioral strategy which bats use to eradicate ectoparasite. Linhares and Komeno (2000) found that bat grooming in rainy season were significantly higher than those in dry season because ectoparasite density peaks in wet season more than in dry seasons.

Pearce and O'Shea (2007) studied ectoparasite in big brown bat, *E. fuscus.* They reported that adult bats have more ectoparasite density than juveniles because sparsely furred in juveniles may allow parasite removal by grooming to be more effective than those in adults. Moreover, Rudnick (1960) stated that adults have experienced longer life than juveniles, which may allow adults to be more exposed to infestations rather than juveniles. Hence, adult bats with high ectoparasite density need to groom themselves more frequently than juveniles with low ectoparasite density.

2.4.3 Wing spreading

Connell et al. (2006) reported wing spreading behavior of *P. poliocephalus* varied significantly with time of the day which was highest in mid morning, and corresponded with the peak in mating activity. Hence there may be a relationship between wing spreading, mating/courtship and aggression. Moreover, they found that wing spreading was mostly observed in males rather than females. Markus (2002) studied the function of wing spreading in *P. alecto,* and he noticed that this behavior may serve as a intimidation display between territories holder and invading males.

2.4.4 Movement

Boonneung (1977) observed daytime behavior of Lyle's flying foxes, and she noticed that the climbing along branch usually occurred during daytime. The bats will move when they would like to avoid from sunlight during noon, or male bats would like to approach the female for mating. However, Connell *et al.* (2006) suggested that movement in tree was rare occurrence behavior in *P. poliocephalus,* corresponding with the suggestion by Neuweiler (2000). He stated that bats of genus *Pteropus* spent most of daytime roosting on the tree which allow them exposed to sunlight. However, they did not move to another place to avoid sunlight because they can control their body temperature efficiently. For small bats roosting on tree, they have strategy to avoid the sunlight during the day by crawling into lower branch where are shadier.

2.4.5 Wing flapping

Robinson and Morrison (1957) mentioned that flying foxes roosting on the tree at tropical zone encounter with sunlight or high ambient temperature during the day. They typically lack sweat glands to balance their body temperature and ambient temperature. Therefore, flying fox would have strategies to balance their body temperature and ambient temperature.

Boonneung (1977) suggested that Lyle' flying foxes would sleep for resting when ambient temperature was ranging between 15-20°C. If ambient temperature was over 30°C, the bats would to be cooling by mouth opening, body licking and fanning their wings.

Ochoa-Acun and Kunz (1999) investigated thermal responses *in P. hypomelanus*. They demonstrated that wing flapping is an important behavior serving as thermoregulation, the capability of animals to maintain its body temperature within thermoneutral zone, bounded by upper and lower critical temperature, when ambient temperature is very different. The range of the thermoneutral zone in large flying foxes extends between 24 °C - 35 °C (Neuweiler, 2000). The bats tended to increase the frequency of wing flapping behavior and their exposed wing surface when ambient temperature reached a maximum at about 36 °C.

Neuweiler (2000) revealed that Microchiropteran bats avoid overheating during the day through day camp selection. They select cave or cracks in rocks which provide an ideal environment, stable temperature in the certain boundaries for resting. Hence, wing flapping behavior is rare occurrence behavior which has been found in cave-dwelling bats such as *Rousettus aegyptiacus* and *Macroderma gigas* (Leitner and Nelson, 1965).

2.4.6 Aggression

Boonneung (1977) observed aggressive behavior of Lyle's flying fox, and classified this behavior as wing shaking, attempting to bite the other or making harsh sound.

Nelson, (1965) reported that male Australian flying fox always performed aggressive behavior when they began to establish their territories for mating, and they became less aggressive when the territories were learned.

Reeder et al. (2006) studied behavioral and physiological responses in *P. vampyrus and P. pumilus*. They suggested that animal behavior related with several factors, including the regulation of hormonal systems and the environment. Increasing in glucocorticoid of these two bats were considered to be a sign of the stress response which mostly found in the breeding males who attempted to compete or fight for mating success during breeding season.

Ortega et al. (2008) studied the strategies that males of *Artibeus jamaicensis* used to defend their harems to maximize fitness in harem groups. They reported that the harem-holder males performed aggressive to intruding males to protect their female members, but did not perform aggression behavior to subordinate males in the group, because subordinate male appearance can inhibit the intruding males who invaded harem territories.

2.4.7 Mating and courtship

Boonneung (1977) observed mating/courtship behavior in Lyle's flying fox, and revealed that breeding period of the flying foxes were between November and August. The sexual activity mostly occurred in the morning and in the evening. The male bats courted the females by licking at genital area or other part of female body. When the females had positive response for copulation, the males would hold her body by his forearm from backward and mate with females.

Connell et al. (2006) studied mating and courtship behavior in grey-head flying fox, *P. poliocephalus.* They suggested this behavior varied with time of the day and time of the year. Mating and courtship behavior in grey-head flying fox was mostly found in April which was in breeding period (between March and May). Moreover, they found that bats mainly performed this activity in the morning, and then declined continually to the lowest in late afternoon.

Reeder et al. (2006) measured the daily testosterone secretion in Malayan flying foxes (*P. vampyrus*). They revealed that testosterone levels in the flying fox males tended to decrease continuously during the day and the evening. And they also suggested that mating/courtship and aggression activities reached to the highest level in breeding season when testosterone, glucocorticoid and body mass peaked. This can be concluded that these behaviors respond to physiological change.

Melvillea et al. (2012) investigated seasonal changes in male reproductive physiology of *P. alecto* by measure testicular volume, body weight, testosterone secretion and sperm quality. They found that there were seasonal changes in these characteristics. Testicular volume, body weight, testosterone secretion and sperm quality of males *P. alecto* was highest at the beginning of mating season to support the peak mating activity.

Welbergen (2006) suggested that reproductive activity in bats of genus *Pteropus* limited in territories established by dominant males. The territories containing group of females associated with a single male or several males, referred to as “harem’’.

Plowright et al. (2008) described age class of little red flying foxes, *P. scapulatus*, as follow.

(1) 0–1 month; a pup is dependent on its mother, even in foraging flight.

(2) 3 months; the pup is too large to be carried by the mother, but has not yet reached full size

(3) 6 months; the pup is independent, but has not yet reached full size;

(4) Pre-breeding (from 1 to 2 years); bats have a full size, but not sexually mature; in females, nipples are small and surrounded by fur; males have underdeveloped testes regardless of the season.

(5) Mature (from 2 years to at least 16 years old); a full-sized sexually mature animal (potentially breeding); mature males have well developed testes (particularly in the mating season); in females that have bred, nipples are enlarged, irrespective of whether they have lactated recently; also, lactating and post-lactating females have less fur around the nipple.

2.4.8 Maternal care

Like most other mammals, newborn of flying foxes were altricial at birth, helpless condition and require care from parents. In bats, mothers provide protection and rearing their offspring from birth until they were weaned which was about 4 months (Nelson, 1965). During the first 3-4 weeks, offspring need to attach to mother's chest because they could not perch independently. Such a physical contact between mothers and pups provide a relationship, and also maintain body temperature of the pups who have a limited capacity to control body temperature (Kunz and Hood, 2000). However, Mclean and speakman (1997) found that physical touching between mothers and pups of *Plecotus auritus* decreased when the pups increased in age.

Kunz and Hood, (2000) suggested the mothers need to leave their pups alone at roost before flying out at night, because the pups is too large to be carried after the first

3-4 week. When the mothers return from foraging, they can recognize their pups by tactile, acoustic and olfactory senses

Boonneung (1997) investigated the relationship between precipitation and number of juvenile in Lyle's flying foxes. She revealed that Lyle's flying foxes had a highest number of newborns in March and June because this period had food abundant and was enough for rearing their young. The number of newborns became lower during July and October which was heavy rain due to heavy rain might be obstacle for rearing their young.

CHAPTER III

METHODOLOGY

3.1 Study area

The study was conducted at Wat Pho, Amphoe Bang Khla, Chachoengsao Province, Thailand between 2010-2011 (Figure 3-1 and Figure 3-2). It is located at 13° 43' 14.1''N and 101° 12' 9.43''E. The northern part of the study site is adjacent with Bang Pakong River and opposite to the orchard island. The other sides were surrounded by local community. The study area is approximately 0.032 km^2, containing a number of big trees where Lyle's flying foxes roost. This place become to be one of tourist attraction because a large established colony of Lyle's flying foxes, >10 thousands individuals, has been found in this temple (Boongird and Sawai, 2004).

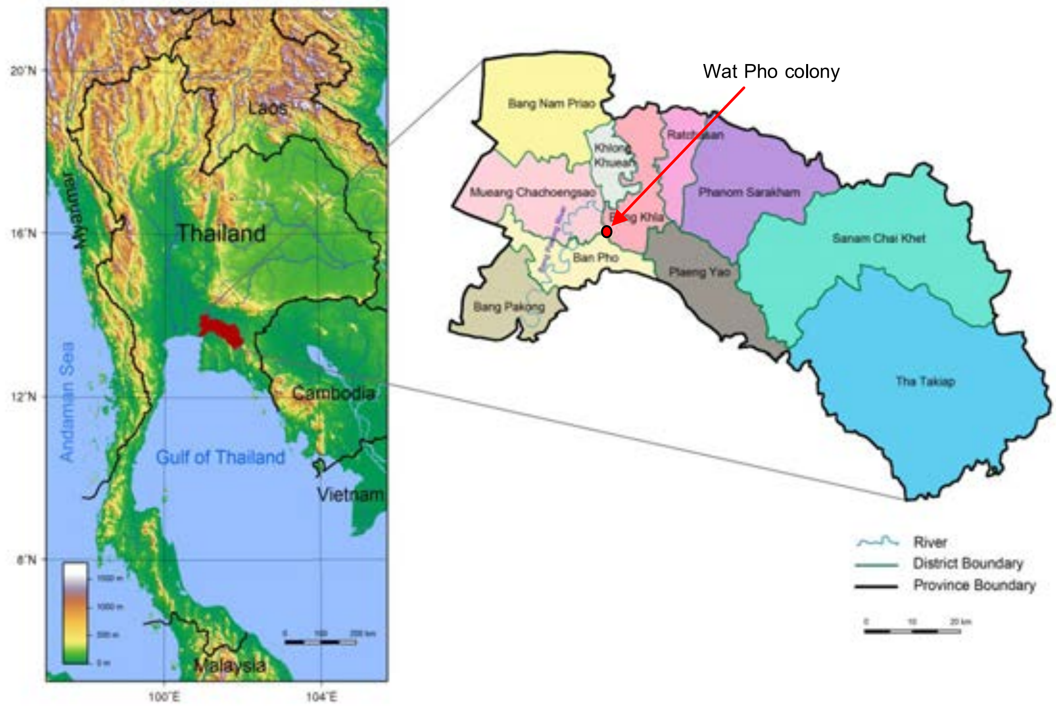

Figure 3-1 Location of Wat Pho Amphoe Bang Khla, Chachoengsao Province (Modified from http://www.toursanook.com/thaiprovinces/chachoengsao.htm)

Figure 3-2 Wat Pho, Amphoe Bang Khla, Chachoengsao Province

3.2 Methods

3.2.1 Preliminary observation

A preliminary survey was carried out to determine the location of bat roost in Wat Pho colony, and the direct count were conducted to determine the proportion between male and female and population size of Lyle's flying fox in the colony.

Data analysis

The population size of Lyle's flying fox were estimated using bounded count method (Choudhary, 1987), as follow.

$$N_0 = 2n_k - n_{k-1}$$

N_0 = Population size

n_k = The first maximum number counted

n_{k-1} = The second maximum number counted

The approximate upper confidence limit N_u is determined as $N_u = n_k + \{(1-\propto)(n_k - n_{k-1})/\propto\}$ where $\propto$ is the significance level (0.05).

3.2.2 Colony-wide emergence study

During the one-year study period (September 2010 to August 2011), monthly observations on colony-wide emergence behavior were carried out for 8 days each. The observations covered full moon and new moon nights of each month. Night shot video-camera was occasionally used to film the main emerging steam and to keep track of number of bats in the steam. Observations were made at dusk. Observer was positioned under the main emergence streams before sunset in order to record the colony-wide emergence timing data of Lyle's flying foxes. The following data were recorded: (a) the onset of the emergence time, (b) emergence time, (c) the end of emergence time, (d) duration of emergence and (e) environmental factors.

According to Welbergen (2008), the onset of the emergence was defined as the moment when ten bats could be seen flying above the colony. The emergence time was defined as the moment when bats could be seen flying out and no longer return to colony. The end of emergence was defined as the first entire minute that no bats could be seen flying above colony. The duration of emergence was defined as the time from the onset of the emergence to the end of emergence.

Environmental factors, i.e. ambient temperature, relative humidity, cloud cover and light intensity were measured in the same area every 30 minutes from 1500 hour until to the end of emergence. The cloud cover was divided into 5 scales as follows:

0 = No clouds, There are no cloud visible.

1 = Clear, clouds are present but cover less than 10 % of the sky.

2 = Isolated clouds, clouds cover between 10 – 25 % of the sky.

3 = Scattered clouds, clouds cover between 25 – 50 % of the sky.

4 = Broken cloud, clouds cover between 50 – 90 % of the sky.

5 = Overcast, cloud cover more than 90% of the sky.

The sunset time and twilight duration at Wat Pho (13° 43' 14.1''N and 101° 12' 9.43''E) were obtained from Thai Astronomical Society. Sunset time refer to the time when the upper edge of the sun's disk is on an ideal horizon. Twilight duration refer to the time between sunset time and the end of astronomical twilight defined as the time when the center of the sun is geometrically 18° below an ideal horizon. Precipitation data at Chachoengsao meteorological station (13° 30' 56.48'' N and 101° 27' 29.8''E) which is located about 20 km from the study site, were obtained from Thai Meteorological Department

Data analysis

Correlation

The Kolmogorov-Smirnov tests were analysed in order to examine whether the data differ from a normal distribution. As the results showed the normal distribution among the data, Pearson correlation and multiple regression were used to evaluate the relationship between the onset of colony-wide emergence time (presented in relative to sunset time) and environmental factors (ambient temperature, relative humidity, cloud cover, light intensity and 24 hrs–precipitation).

Pearson correlation was used to assess the correlation between the colony-wide emergence of Lyle's flying foxes and astronomical data such as the relationship between the onset of colony-wide emergence time and sunset time, and the relationship between duration of colony-wide emergence and twilight duration.

In order to study the effect of lunar phase on colony-wide emergence in Lyle's flying foxes, the onset of colony-wide emergence time and the emergence time between full moon and new moon night (presented in relative to sunset time) were compared by Paired Sample t-test.

All statistical analyses were carried out using SPSS for Window version 17. Significant correlation and significant difference were considered at the probability of $p \leq 0.05$.

3.2.3 Individual emergence study

Individual emergence behavior was investigated for 8 days a month during October 2010 and September 2011. To compare individual emergence times between sex and status, Closed Circuit Television (with Sanyo digital video recorder 2004s) was used to film mixed-sex group containing males, non-lactating-females, lactating females and juveniles for recording to the nearest second of individual emergence time. Filming of focal group started about 1 hour before dusk. During the first 20 minute of filming, the observer classified and recorded sex and age class of mixed-sex group members. Individuals were categorized as juvenile, adult male, adult female (non-lactating female and lactating female). Filming continued until the last member of focal group flew off from its roosting position.

In parallel with Powright et al. (2008) and Welbergen (2006), juveniles of Lyle's flying fox have not yet reached full size , and they were discriminated from adult by their smaller size, their narrower shoulders comparing to their head size, their longer legs comparing to their body length, and their larger eyes relative to the their face. Adult males were distinguished from adult females by the presence of the penis, and lactating females were identified by pup attachment.

Data analysis

In order to study the influence of sex and status on emergence behavior in Lyle's flying foxes, the average emergence time (presented in relative to sunset time) of each status, i.e. juvenile, adult male, non-lactating female and lactating female, were compared using a Kruskal-Wallis test.

All statistical analyses were carried out using SPSS for Window version 17. Significant difference were considered at the probability of $p \leq 0.05$.

3.2.4 Daytime behavior at roost study

Monthly observations on daytime behavior at roosting site were carried out for 4 days each during August 2010 to July 2011. The observation started at 0600 hours and ended at 1800 hours in the roosting area. The observation was conducted monthly at trees containing adults of both sexes. Fifty bats were selected randomly by scanning from one individual to the next every 30 minutes. Behavior, sex and age class of those bats were instantly noted. Environmental factors i.e. ambient temperature, relative humidity and light intensity were concurrently recorded every 30 minutes. The following behaviors of Lyle's flying foxes, as described by Connell et al. (2006) was observed during the daytime.

(a) Sleeping: eyes close and wing wrapped around body

(b) Grooming: licking and scratching body and/or head

(c) Wing spreading: wing wide open, extended on side or in front of body

(d) Movement: climbing along branch or trunk

(e) Wing flapping: fanning body with wing

(f) Aggression: fighting between individuals

(g) Mating and courtship: male attempt to copulate with female

(h) Maternal care: newborn attached/juvenile nursing

Data analysis

The Kolmogorov-Smirnov tests were analysed in order to examine whether the data differ from a normal distribution. As the results indicated that the data were not normally distributed, non-parametric statistics were preformed. The percentages of the number of bats performing each behavioral type were grouped into one-hour blocks in order to determine daytime behavior pattern of Lyle's flying foxes. These percentages were analyzed to determine whether behaviors differ between times of day and time of the year using Kruskal-Wallis test.

In order to examine the sexual differences in activity levels of Lyle's flying foxes, the proportion number of bat performing grooming, wing spreading, movement, aggression and mating/courtship between adult males and females were analyzed using Mann-Whitney U test.

In order to evaluate the effect of seasonal change on daytime behaviors of Lyle's flying foxes, the average percentage of the number of bats performing each behavioral type and average environmental factors (ambient temperature and relative humidity) of each month were analyzed by Spearman correlation.

All statistical analyses were carried out using SPSS for Window version 17. Significant correlation and significant difference were considered at the probability of $p \leq 0.05$.

Figure 3-3 Sleeping: eyes close and wing wrapped around body

Figure 3-4 Grooming: licking and scratching body and/or head

Figure 3-5 Wing spreading: wing wide open, extended on side or in front of body

Figure 3-6 Movement: climbing along branch or trunk

Figure 3-7 Wing flapping: fanning body with wing

Figure 3-8 Aggression: fighting between individuals

Figure 3-9 Mating and courtship: male attempt to copulate with female

Figure 3-10 Maternal care: newborn attached/juvenile nursing

CHAPTER IV
RESULTS

4.1 Preliminary results

From the census of Lyle's flying fox population at Wat Pho, Amphoe Bang Khla, Chachoengsao Province in 2010, it was found that the Wat Pho colony consisted of 9,199 individuals (range between 18,829-7021 individuals) roosting around the colony. The proportion of males and females were on average 48% and 52%, respectively.

4.2 Colony-wide emergence

4.2.1 Emergence behavior

From the observation of emergence behavior throughout the year, it was found that Lyle's flying foxes fly out from their roosting site to forage every day. Shortly after sunset, a few individuals were noticed flying and calling around the colony. After others members in the colony had heard the calling, most of them woke up from sleeping and groomed themselves. The onset of colony-wide emergence defined as ten bats were noticed swarming above the colony began on average at 9.85 ± 0.34 minutes after sunset (range from 2 minutes before sunset until 16 minutes after sunset). Illumination at initial of colony-wide emergence was on average 14.93 ± 0.85 lux (range between 7 - 55 lux). Then, the number of swarming bats continuously increased and reached to critical density, bats flew away from the colony to forage on average 17.78 ± 0.45 minutes (range between 8-27 minutes after sunset) after sunset at light level of 4.99 ± 0.35 lux (range between 3-28 lux).

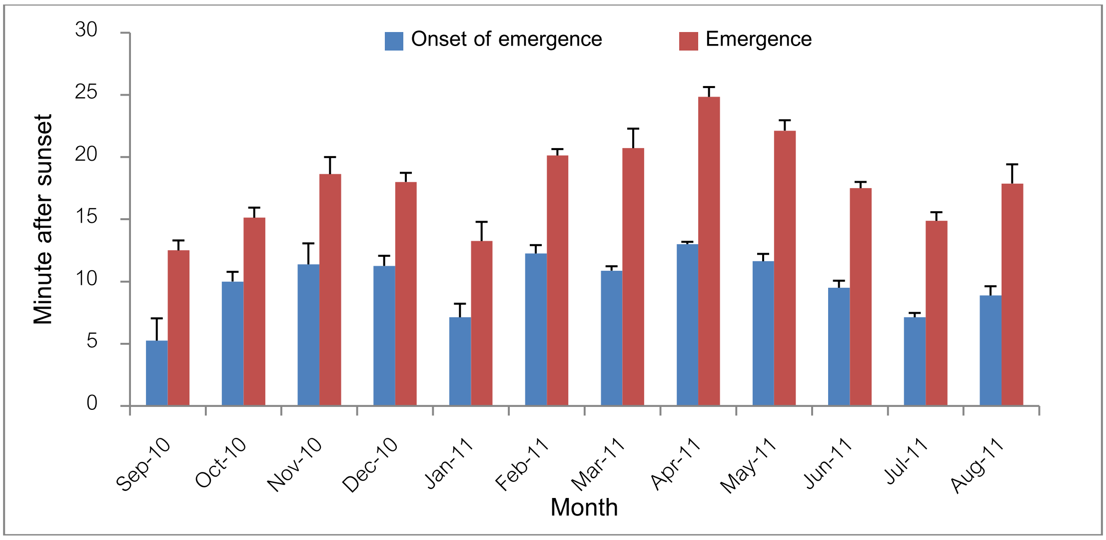

Figure 4-1 The onset of colony-wide emergence and emergence time relative to sunset time between 2010 and 2011

At Wat Pho, Lyle's flying foxes usually emerged in three streams. Two emergence streams directed toward orchards, heading to the north and the west of colony. The other one flew toward the southeast direction. Changes in the proportion of bat in emergence streams were assessed under the two main emergence streams on two evenings in October 2011. The results showed that both streams were similar in out-flight timing of the first bat, emergence pattern and rate of emergence (Figure 4-3 and Figure 4-4).

In this study, however, Lyle's flying foxes performed a different pattern in the emergence behavior between March and April. During these two months, the emergence of the flying foxes did not occur in the stream pattern but proceeded gradually in small groups of individuals. From personal observation, Lyle's flying foxes gave birth and had a number of newborns at this time of the year.

Figure 4-2 Colony-wide emergence stream of Lyle's flying foxes.

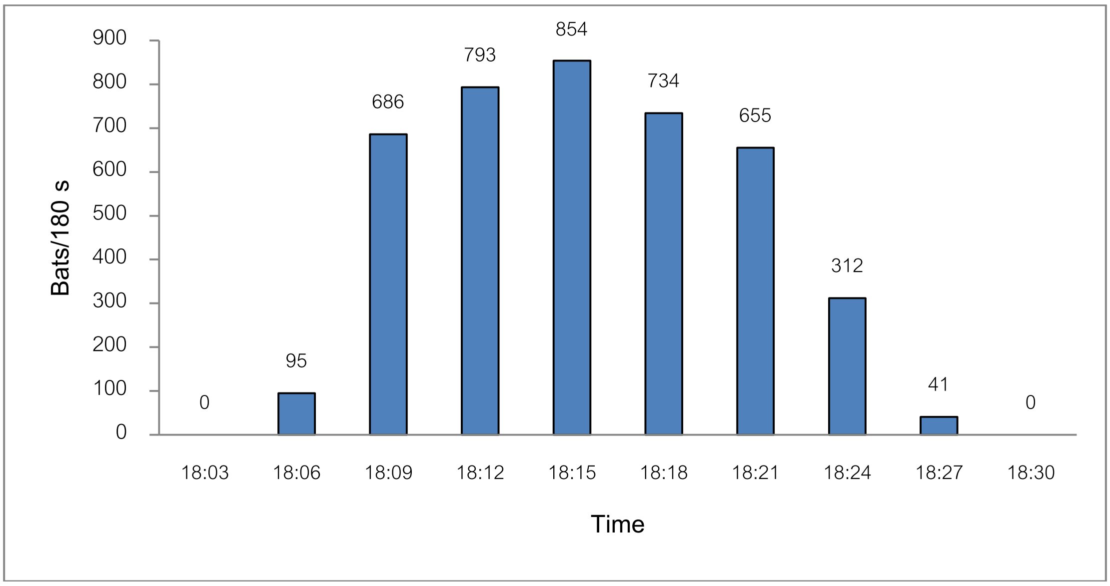

Figure 4-3 Rate of emergence (number of bats/180 s) from the Wat Pho colony on 20 October 2011. Sunset time of this evening was 17:53 pm.

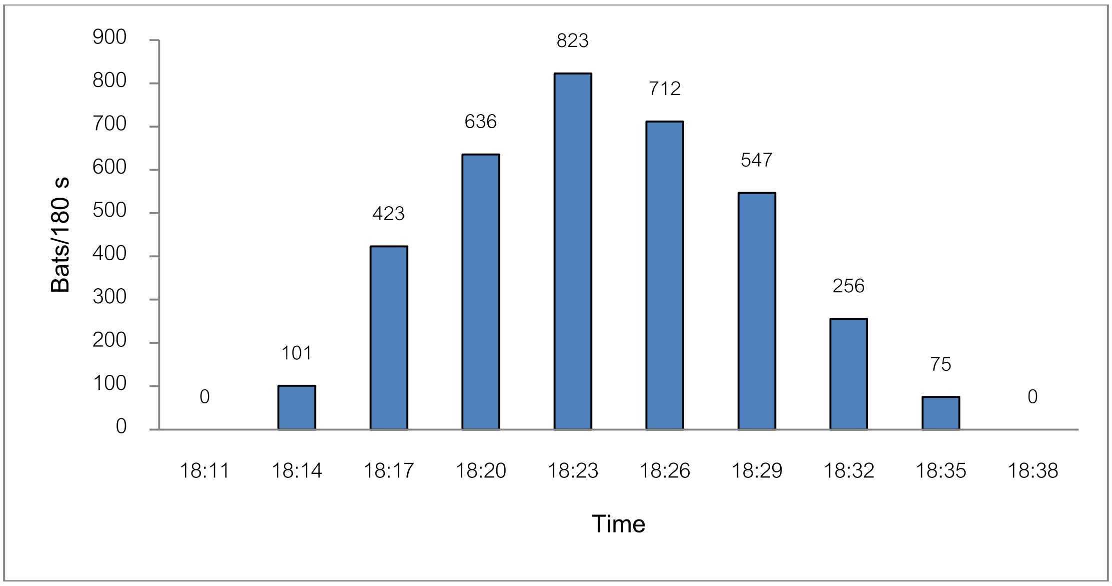

Figure 4-4 Rate of emergence (number of bats/180 s) from the Wat Pho colony on 21 October 2011. Sunset time of this evening was 17:53 pm.

Duration of colony-wide emergence

The above-mentioned that the difference pattern in colony-wide emergence of Lyle's flying foxes were noticed during March and April. Most of them prolonged emergence time by swarming, calling and roosting at tree for several hours after sunset. Due to limitations on observation, the observer was not able to specify the end of emergence time of Lyle's flying foxes. So the accurate data of colony-wide emergence duration were not available in these two months. However, the end of emergence activity could be estimated by listening the background noise created by the flying foxes and observed swarming bats above the colony. Duration of colony-wide emergence between March and April exceeded two hours.

From the emergence behavior observation, it was found that the duration of colony-wide emergence in Lyle's flying foxes varied throughout the year which was highest between March and May (ranged from 52 minutes to over 2 hours), The duration of colony-wide emergence was also high between November and January (45.63±0.98, 42.75±0.72 and 43.00±1.00 minutes ,respectively; Figure 4-5).

From personal observation, Lyle's flying foxes have parturition period in March and April. There were a lot of lactating females with juveniles attached in these two months. Most bats were still roosting on tree for several hours after sunset, and the last groups of emergence tend to be lactating females. However, we noticed that some males and non-lactating females also prolonged their emergence time. Before out-flight activity, some male bats usually climbed along the branch and try to approach in order to copulate with females, while most of lactating females still roosted and looked after their young in the territories.

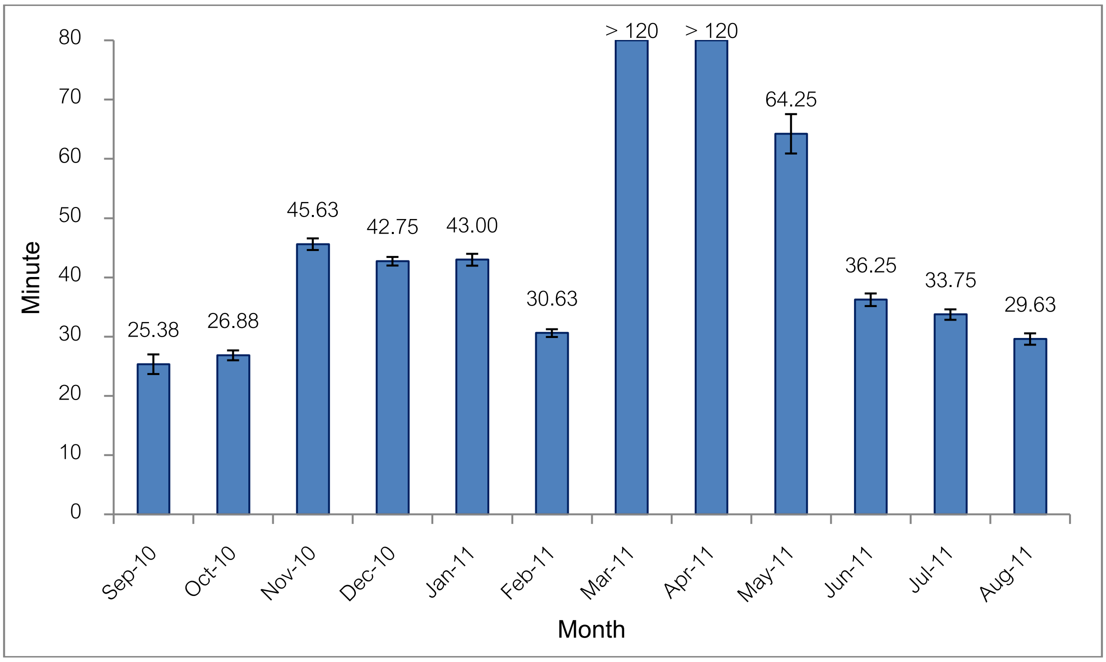

Figure 4-5 Average duration of colony-wide emergence in Lyle's flying foxes in annual observation. During March and April, the duration of colony-wide emergence exceeded 120 minutes.

4.2.2 Relationship between duration of colony-wide emergence and twilight duration

The relationship between the duration of colony-wide emergence and twilight duration was examined to assess the influence of the twilight on the emergence behavior in Lyle's flying foxes. Due to the high variation in emergence duration during March and May, the emergence data in these three months were excluded from the correlation analysis. The results showed that the duration of colony-wide emergence in Lyle's flying foxes was weakly correlated with seasonal changes in twilight duration (Pearson's correlation, $r=0.433$, $p<0.001$; Figure 4-6).

However, the duration of colony-wide emergence in Lyle's flying foxes was strongly correlated with twilight duration (Pearson's correlation, $r=0.846$, $p<0.001$) when the emergence data during lactation period (from March and July) were exclude. Lactating females with juveniles attached were presented during this period.

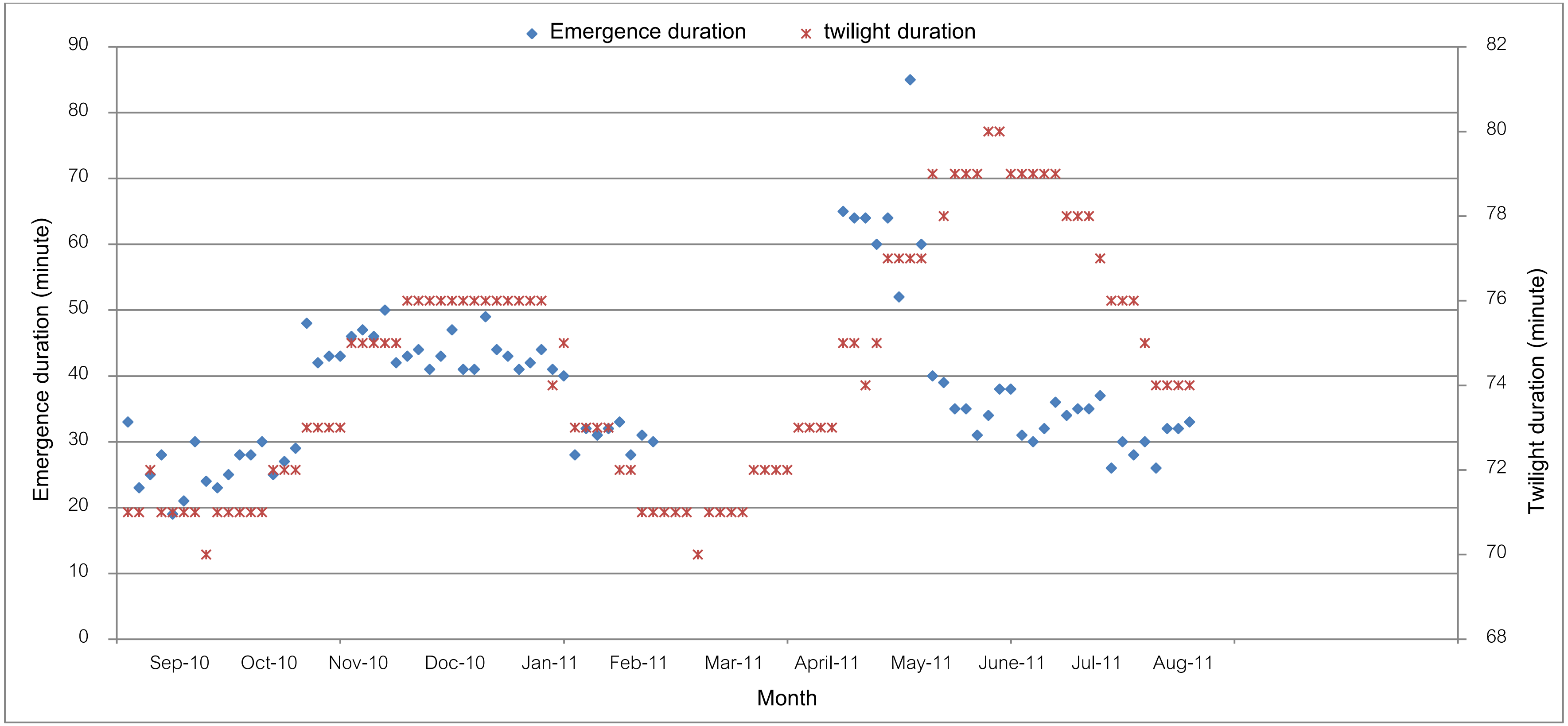

Figure 4-6 Relationship between the duration of colony-wide emergence and twilight duration throughout the year.

4.2.3 Relationship between the onset of colony-wide emergence and environmental factors

From 12 months of observation, it was found that the onset of colony-wide emergence time in Lyle's flying foxes was closely synchronized and positively correlated with seasonal changes in sunset time (Pearson's correlation, $r=0.98$, $p<0.001$; Figure 4-7). Lyle's flying foxes started their emergence behavior progressively in November when the local sunset time was earliest. And their onset of emergence, as well as the sunset time, was latest in July.

The relationships between the onset of colony-wide emergence and environmental factors, i.e. temperature, relative humidity, light intensity, cloud cover and amount of rainfall, were shown in figures 4-8 to 4-12, respectively. Such physical factors fluctuated with seasonal variation. The mean temperature was highest in April, which was the mid hot-dry season, and then decreased to the lowest point in November to January, which was the cold-dry season. The mean light intensity reached the maximum point in April and decreased to the minimum point in October. The mean relative humidity rose up to the maximum point in August and September, which was the rainy season, and then decreased to the minimum point in December. The mean cloud cover was highest in August, and it was lowest in June. The amount of rainfall was highest in September, whereas the minimum amount of rainfall was in November and December.

Table 4-1 shows the relationships between the onset of colony-wide emergence and environmental factors. The results of this study showed that the onset of colony-wide emergence of Lyle's flying foxes was positively correlated with the ambient temperature (Pearson's correlation, $r=0.278$, $p=0.006$; Figure 4-8) and the light intensity (Pearson's correlation, $r=0.202$, $p=0.049$; Figure 4-9), but negatively correlated with the humidity in the air (Pearson's correlation, $r=-0. 513$, $p<0.001$; Figure 4-10).

No correlation between the onset of colony-wide emergence and the cloud cover or the amount of rainfall was detected (Figure 4-11 and Figure 4-12, respectively).

From multiple regression analysis, it was found that the mean ambient-temperature, the mean light intensity, the mean cloud cover and 24 hrs precipitation have no effect on the onset of emergence and emergence time of Lyle's flying foxes (Multiple regression, $p>0.05$). While the mean relative humidity was only one factor which influenced the onset of colony-wide emergence of Lyle's flying foxes (Multiple regression, $r= -0.506$, $p<0.001$; Table 4-2). Hence, relative humidity was main environmental factor that influenced the colony-wide emergence of Lyle's flying foxes.

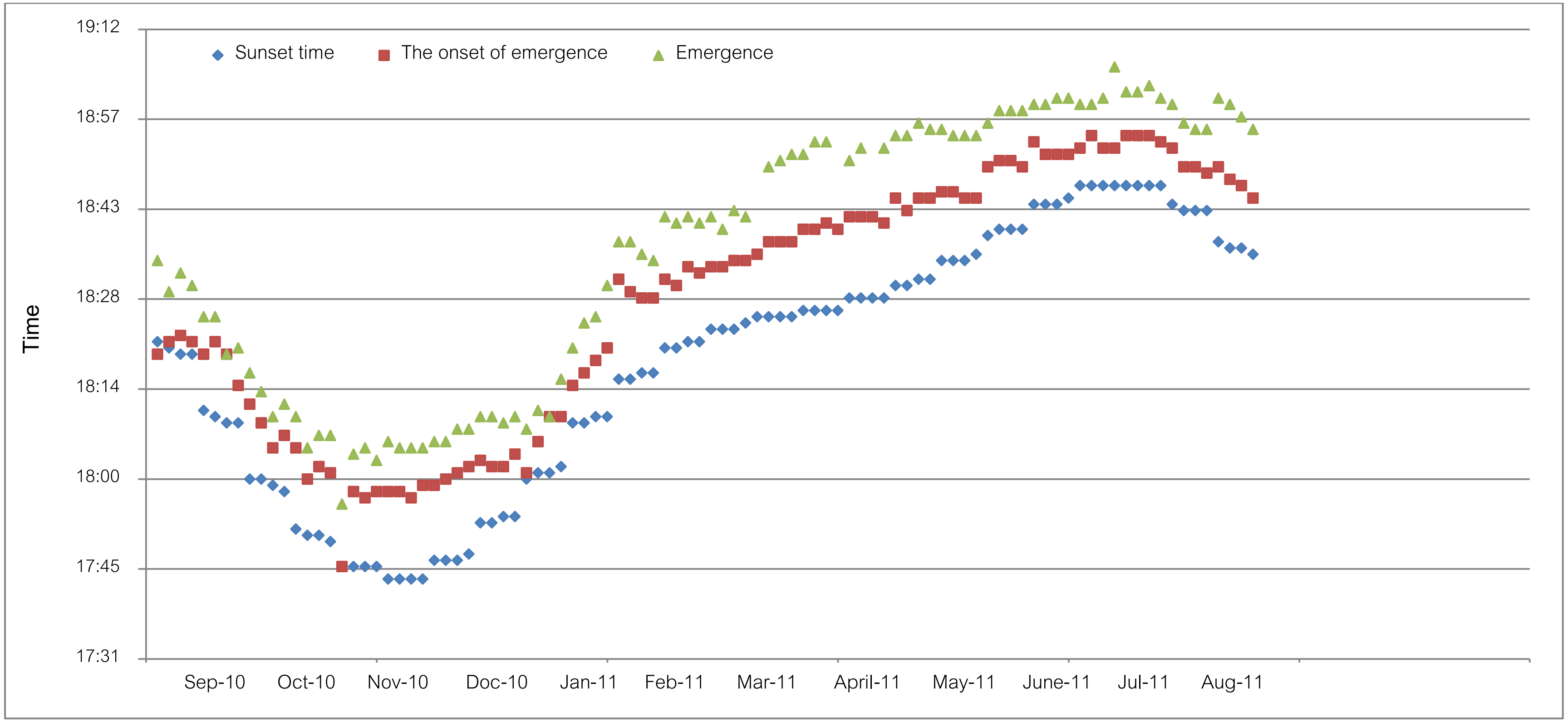

Figure 4-7 Timing of onset of emergence (square symbols) and timing of emergence (triangles) relative to the timing of sunset (diamonds) from the Wat Pho colony during 2010 and 2011. * Emerging data were not available for one day in March and for 2 day in April.

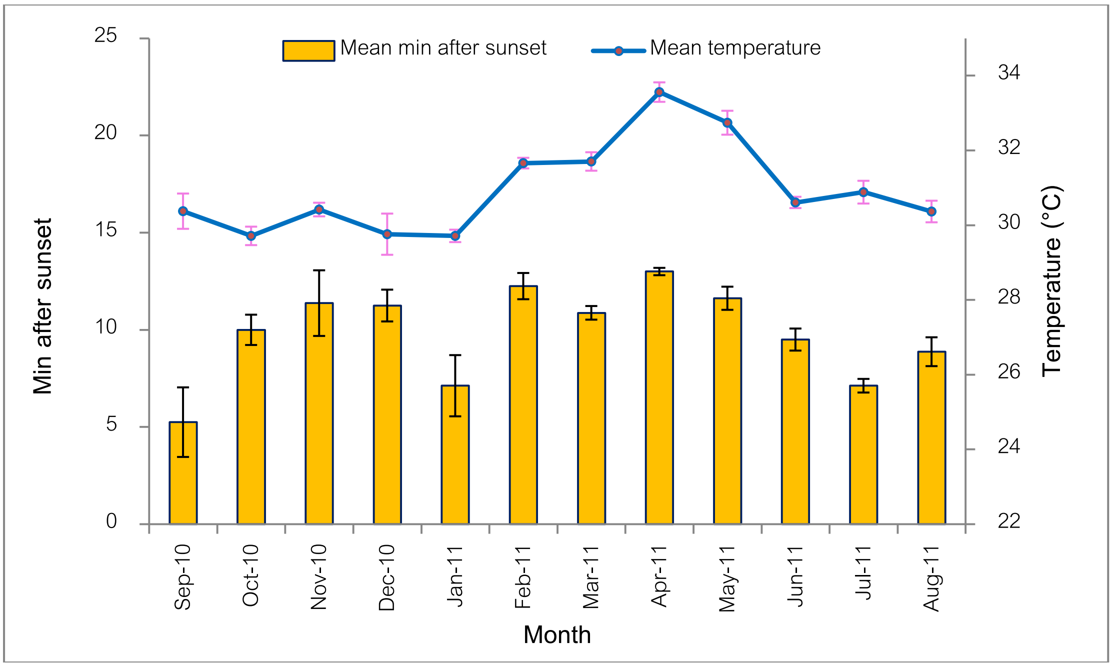

Figure 4-8 Relationship between the onset of emergence in each month and temperature (mean ± SD; r=0.278, p=0.006).

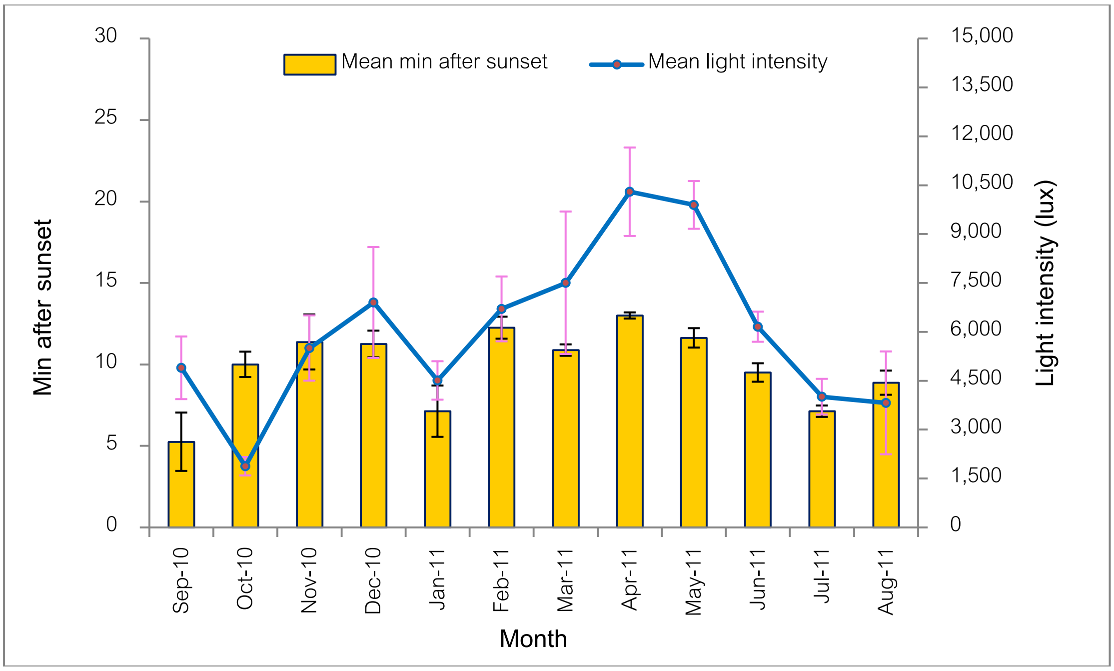

Figure 4-9 Relationship between the onset of emergence in each month and light intensity (mean ± SD; r=0.202, p=0.049).

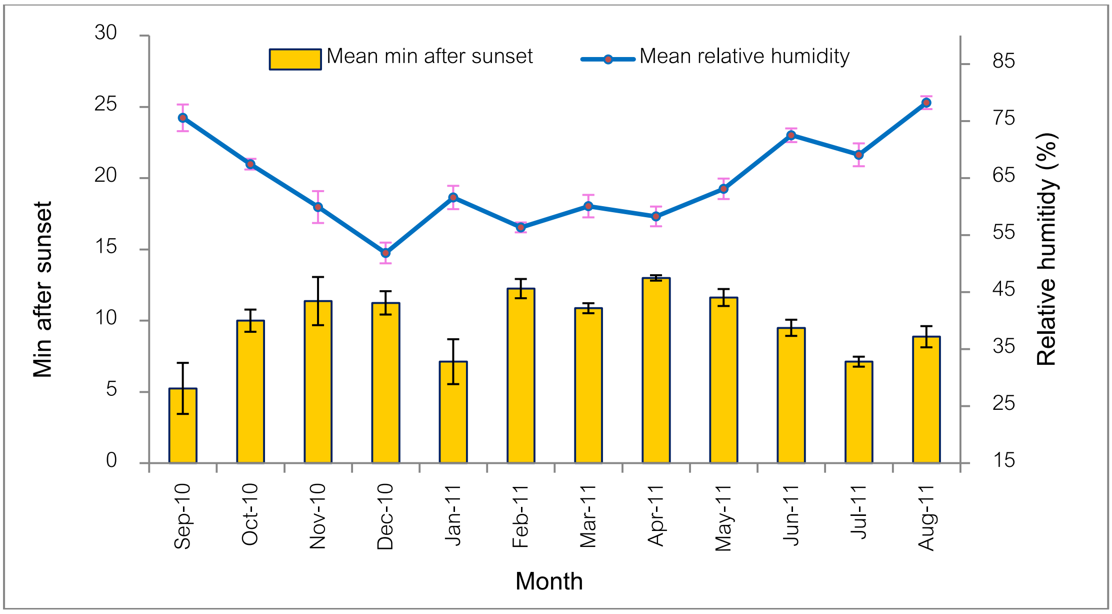

Figure 4-10 Relationship between the onset of emergence in each month and relative humidity (mean ± SD; r=-0. 513, p<0.001).

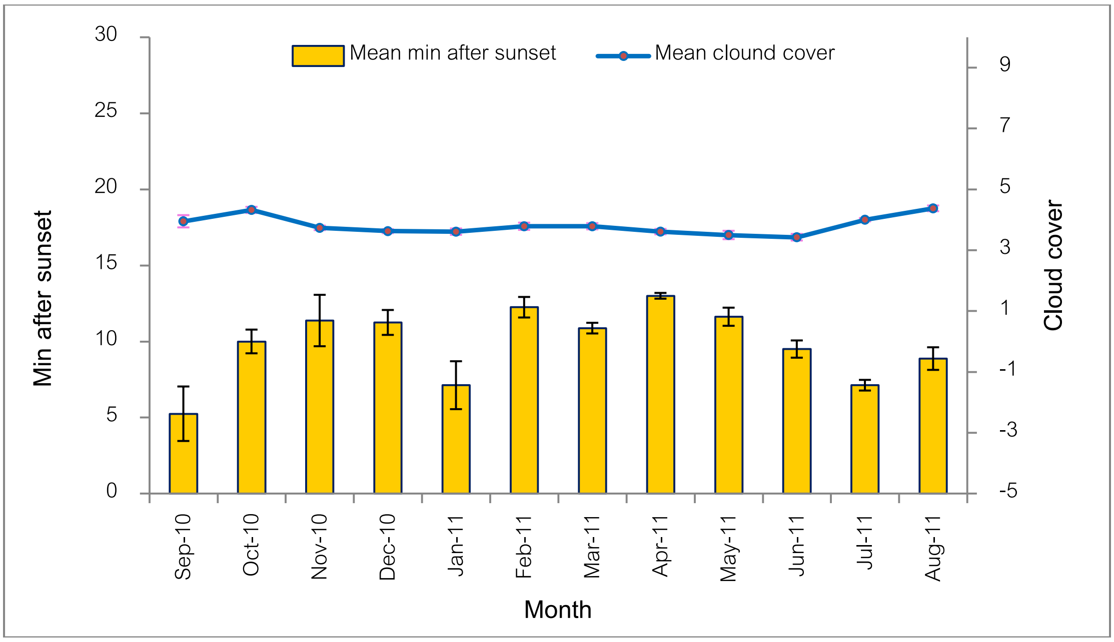

Figure 4-11 Relationship between the onset of emergence in each month and cloud cover (mean ± SD; r=-0.093, p=0.365).

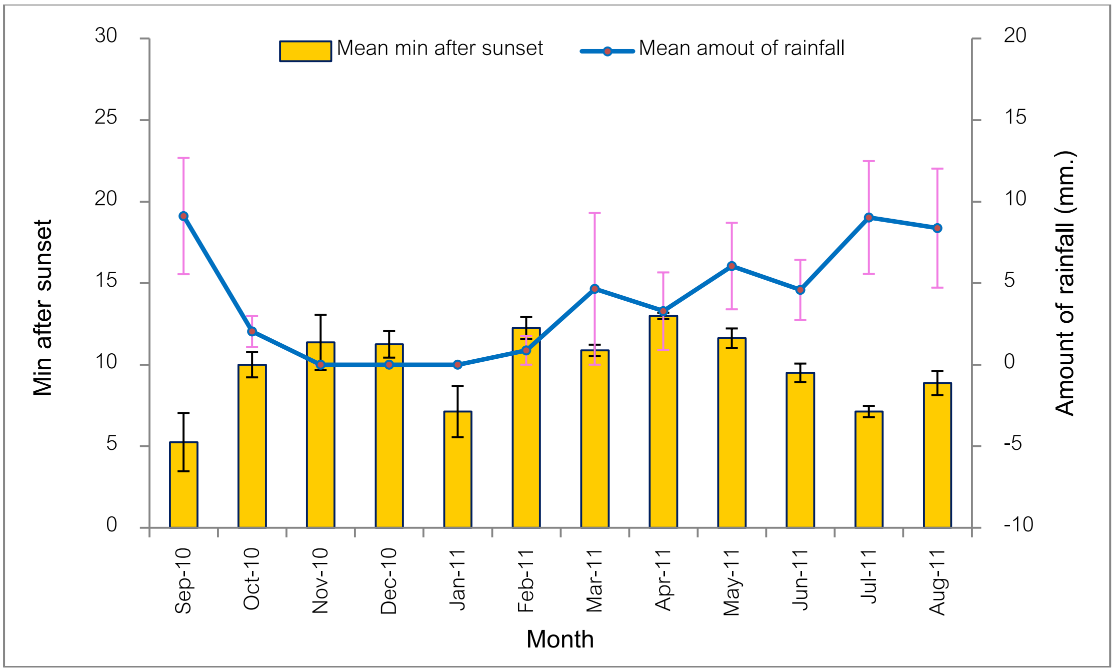

Figure 4-12 Relationship between the onset of emergence in each month and amount of rainfall (mean ± SD; r=-0.181, p=0.078).

Table 4-1 Pearson's coefficient of rank correlation relating the onset of colony-wide emergence and environmental factors, i.e. ambient temperature, relative humidity, light intensity, cloud cover and precipitation.

	The onset of colony-wide emergence	Temperature	Relative humidity	Light intensity	Cloud cover	24 hr Precipitation
The onset of colony-wide emergence	1.000					
Ambient temperature	0.278** (0.006)	1.000				
Relative humidity	-0. 513** (0.000)	-0.235* (0.021)	1.000			
Light intensity	0.202* (0.049)	0.546** (0.000)	0.244* (0.017)	1.000		
Cloud cover	-0.093 (0.365)	-0.255* (0.012)	0.347** (0.001)	-0.346** (0.000)	1.000	
24 hr Precipitation	-0.181 (0.078)	-0.002 (0 .987)	0.396** (0.000)	0.036 (0.728)	0.195 (0.058)	1.000

Remark: number in parentheses represent p-value

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

Table 4-2 Multiple regression between the onset of colony-wide emergence and environmental factors, i.e. ambient temperature, relative humidity, light intensity, cloud cover and precipitation.

Environmental factor	Unstandardized Coefficients		Standardized Coefficients	t	Sig.
	B	Std. Error	Beta		
(Constant)	21.950	2.162		10.151	.000
Relative humidity	-.188	.033	-.506	-5.664	.000*
Ambient temperature	.424	.253	.178	1.675	.097
Cloud cover	1.160	.813	.143	1.427	.157
Light intensity	.000	.000	.030	.270	.788
24 hr Precipitation	-.004	.044	-.009	-.089	.929

Remark: * Correlation is significant at the 0.05 level (2-tailed).

4.2.4 Lunar cycle effect the onset of colony-wide emergence

We investigated the colony-wide emergence time of Lyle's flying foxes on full moon and new moon nights in order to assess the influence of the lunar cycle on the emergence behavior. From the investigation, it was found that there was no significant difference in the onset of colony-wide emergence times between full moon and new moon nights (Paired Sample t-test, t =-1.293, df=11, p=0.223). Bats began their night activity during full moon and new moon nights on average 10.58 ± 0.66 and 8.50 ± 1.70 minutes after sunset, respectively. Furthermore, there was no significant difference in the colony-wide emergence times between full moon and new moon nights (Paired Sample t-test, t =-1.013, df =10, p=0.335). Bats departed from their roost on average 18.36 ±1.10 minutes after sunset around full moon nights and 16.91± 1.67 minutes after sunset around new moon nights.

4.3 Individual emergence

During the observation period, males, females and juveniles were noticed throughout the year. Lactating females with juvenile attached were found between March and July. From video recording and scanning observation, it was found that a number of newborns were observed only between March and April, indicating parturition period during that time of the year.

Owing to technical problem in video-recording, individual emergence data between March and April 2011 were not available, and data between March and April 2012 were collected and used instead.

From video recording data, the emergence time relative to sunset time in males, females, lactating females and juveniles tended to increase between January to April. Thereafter, the emergence time of those declined gradually from May to September. Comparing between males, females and juveniles, differences in emergence time of each sex and status were found only in three months, between February and April (Kruskal-Wallis tests, $p<0.05$, Figure 4-13).

In February, juveniles emerged earlier than adult males and non-lactating females (Kruskal-Wallis test, $H=7.5$, $df=2$, $p=0.023$). While, there were no significant difference in emergence times between adult males and non-lactating females in this month (Mann-Whitney U test, $Z=-0.57$, $p=0.56$). The average emergence time of adult males, adult females and juveniles were 58.21 ± 2.36, 57.92 ± 2.19 and 49.69 ± 0.92 minutes after sunset, respectively.

During March and April, lactating females flew out from roosting branch later than adult males, non-lactating females and juveniles (Kruskal-Wallis test, $H=10.9$, $df=3$, $p=0.012$). Difference in emergence time between adult males, non-lactating females and juvenile were not found in these two months (Kruskal-Wallis test, H=5.8, df=2, p=0.53). In March, the average emergence time of lactating females, adult males, non-lactating females and juveniles were 184.25±17.60, 109.00±10.10, 112.94±22.75 and 92.33±35.54 minutes after sunset, respectively. In April, the average emergence time of lactating females, adult males, non-lactating females and juveniles were 87.09±7.42, 63.77±9.49, 52.34±5.19 and 41.25±1.25 minutes after sunset, respectively.

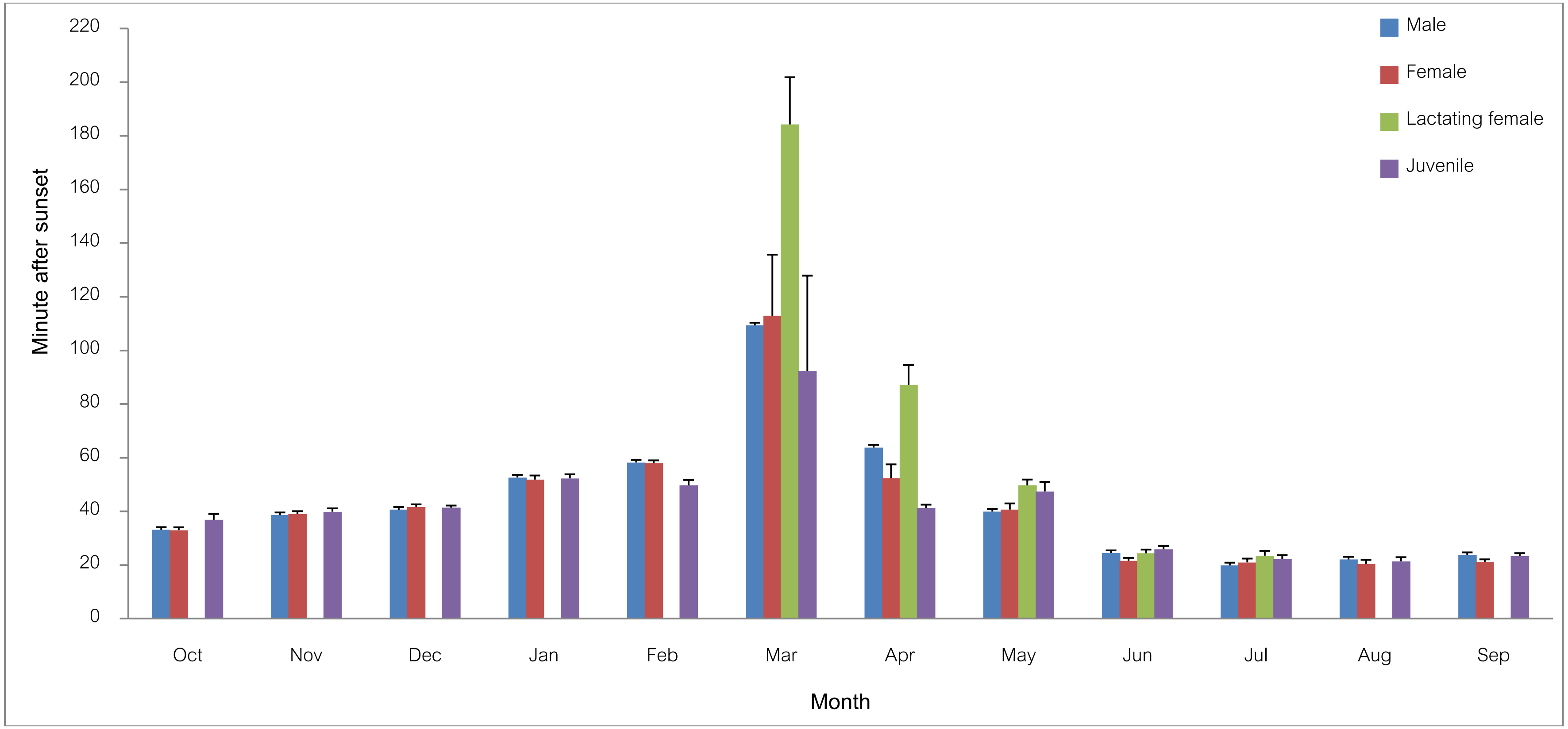

Figure 4-13 Emergence times relative to sunset time (mean and SD) of Lyle's flying foxes relation to sex, age and reproductive status. Data were collected between October 2010 and September 2011 except for March and April when data between March and April 2012 were used instead.

4.4 Daytime Behavior

Sleeping, grooming, wing spreading, movement, wing flapping, aggression, mating and courtship and maternal care were activities observed in Lyle' flying foxes. Most activities occurred everyday during the observations. However, sleeping, grooming and wing flapping were the most common behaviors which were performed by the bats during the day. Furthermore, there were monthly and daily variation in the percentages of bat performing these behaviors as follows.

4.4.1 Sleeping

Sleeping patterns in Lyle's flying foxes varied significantly throughout the day (Kruskal-Wallis test, $H=220.3$, $df=11$, $p<0.001$; Figure 4-14). In general, sleeping occurred mostly in the morning (0700 to 1100 hours) and the evening (1600 to 1800 hours).

Sleeping patterns in Lyle's flying foxes varied significantly throughout the year (Kruskal-Wallis test, $H=42.8$, $df=11$, $p<0.001$). The lowest percentage of sleeping bats was recorded in April, while the highest percentage was recorded between January and February, and between June and July (Figure 4-15).

Sleeping activity was negatively correlated with ambient temperature (Spearman correlation, $r=-0.565$, $p<0.001$; Figure 4-16) and relative humidity (Spearman correlation, $r=-0.309$, $p=0.034$; Figure 4-17).

Sexual differences in sleeping activity could not be examined because it was very difficult to identify the sex of sleeping bats.

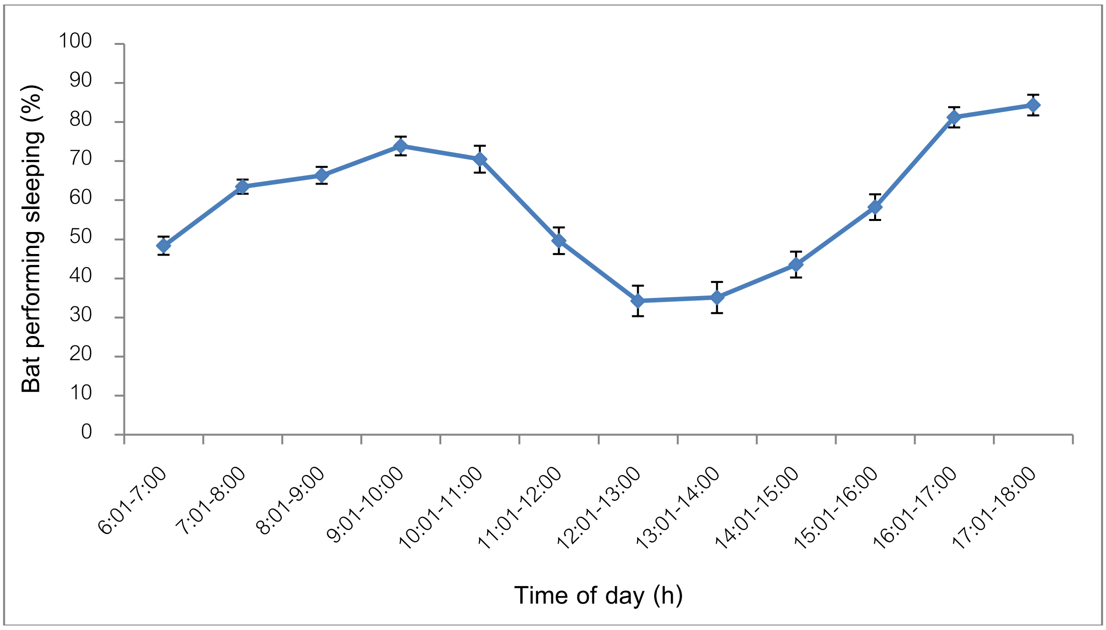

Figure 4-14 The percentage of bats performing sleeping behavior between 0600 and 1800. Data are shown in the mean ± standard errors.

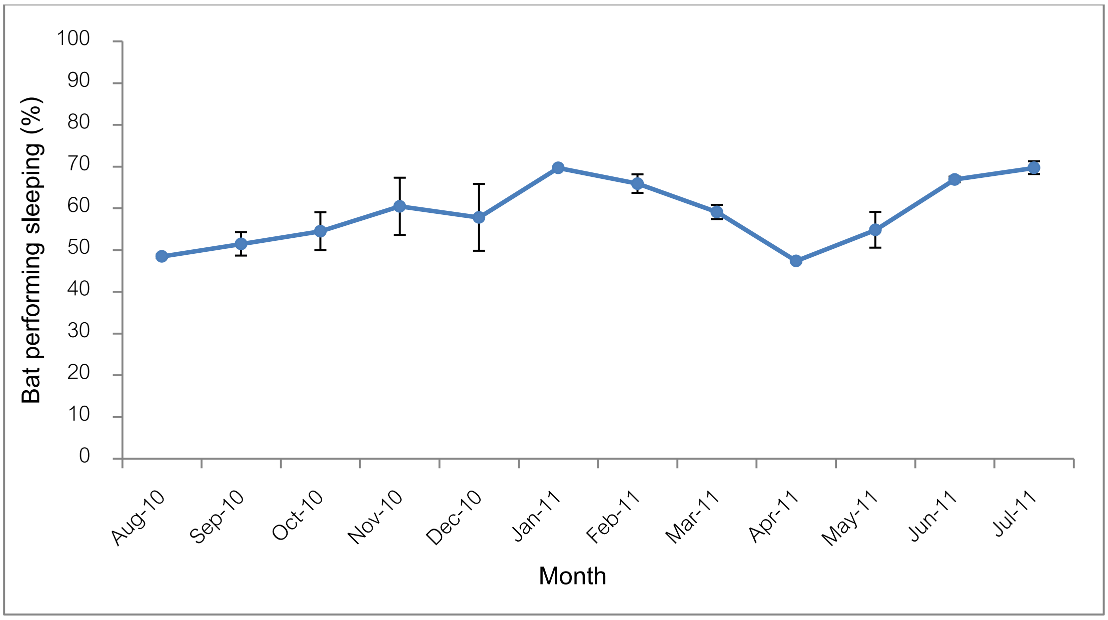

Figure 4-15 The percentage of bats performing sleeping behavior between August 2010 and July 2011. Data are shown in the mean ± standard errors.

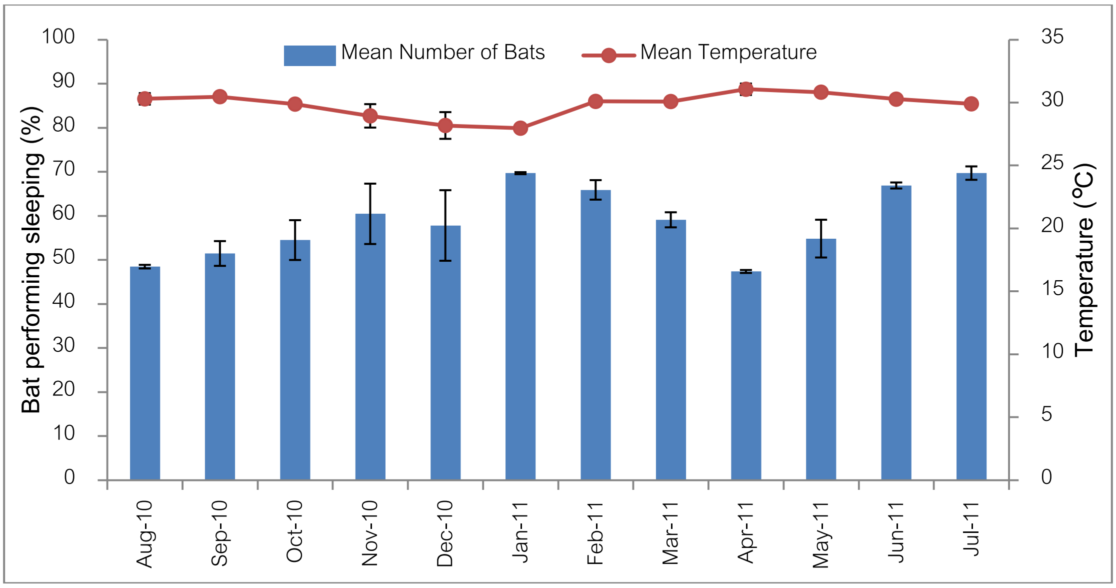

Figure 4-16 Relationship between the percentage of bats performing sleeping behavior in each month and ambient temperature (mean ± SD; r=-0.565, p<0.001).

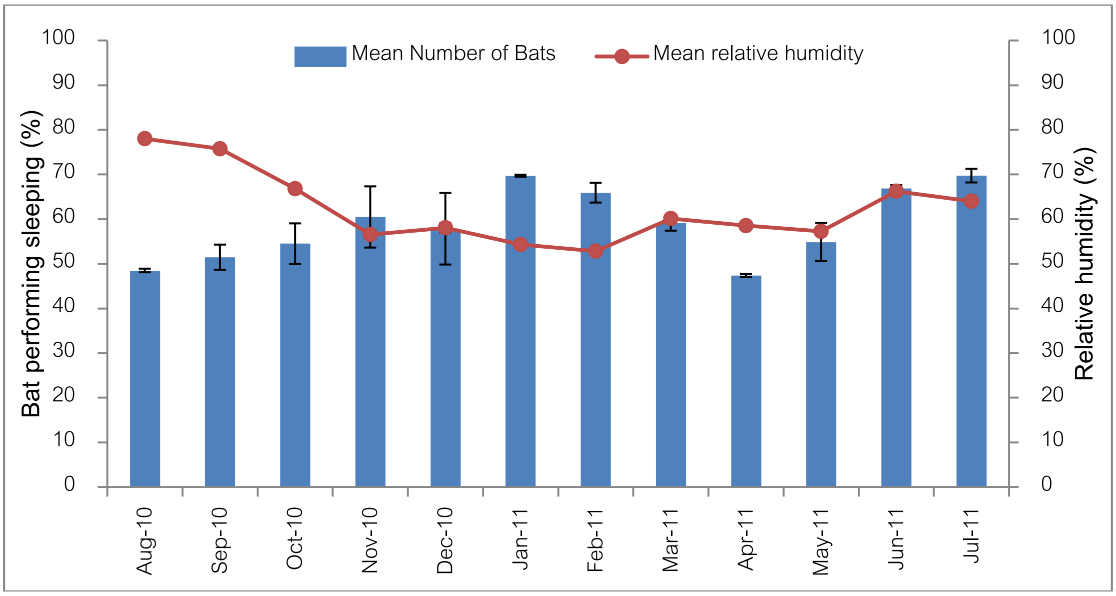

Figure 4-17 Relationship between the percentage of bats performing sleeping behavior in each month and relative humidity (mean ± SD; r=-0.309, p=0.034).

4.4.2 Grooming

From comparisons of grooming activity level between daytime, it was found that grooming in Lyle's flying foxes varied significantly throughout the day (Kruskal-Wallis test, H=177.4, df=11, p<0.001). In general, grooming activity occurred mostly in early morning (0600 to 0700 hours), and this behavior steadily decreased to the lowest in the afternoon (1200 to 1700 hours). Concordant with the emergence observations, grooming behavior of flying foxes increased before their nightly emergence (Figure 4-18).

Grooming activity in Lyle's flying foxes varied significantly throughout the year (Kruskal-Wallis test, H=124.7, df=11, p<0.001). The highest percentage of grooming bats was recorded during August and October, and the lowest percentage was observed between March and April (Figure 4-19).

Grooming activity was not correlated with ambient temperature (Spearman correlation, r=-0.082, p=0.585; Figure 4-20), but was positively correlated with relative humidity (Spearman correlation, r=0.585, p<0.001; Figure 4-21)

Proportion of grooming bats was significantly different between sexes. Adult females performed grooming behavior higher than adult males (Mann-Whitney U test, Z=-4.2, p<0.001).

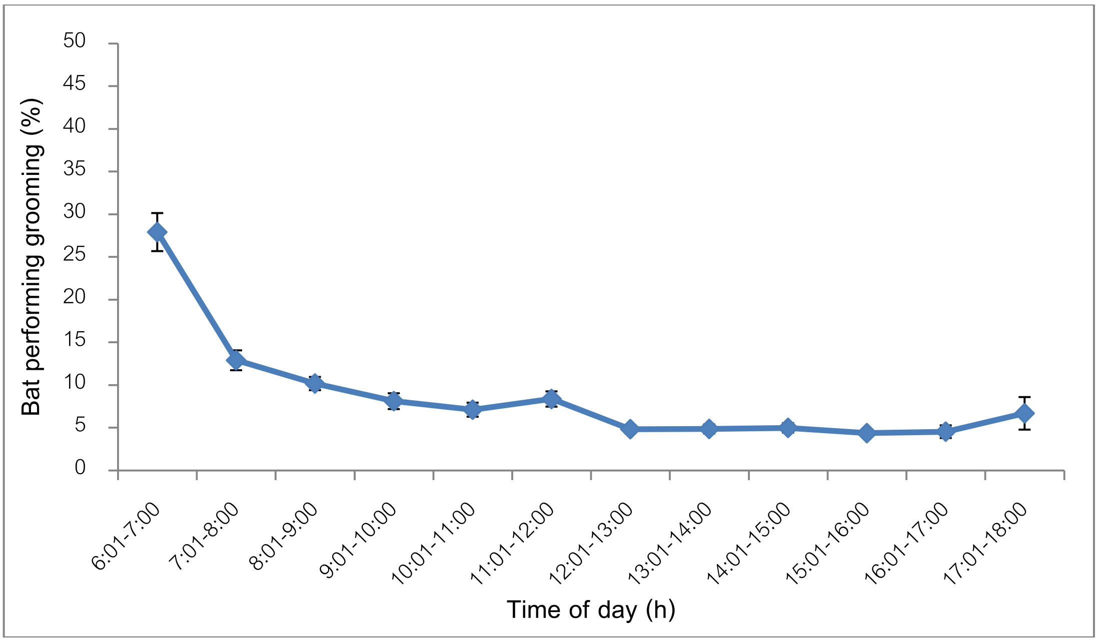

Figure 4-18 The percentage of bats performing grooming behavior between 0600 and 1800. Data are shown in the mean ± standard errors.

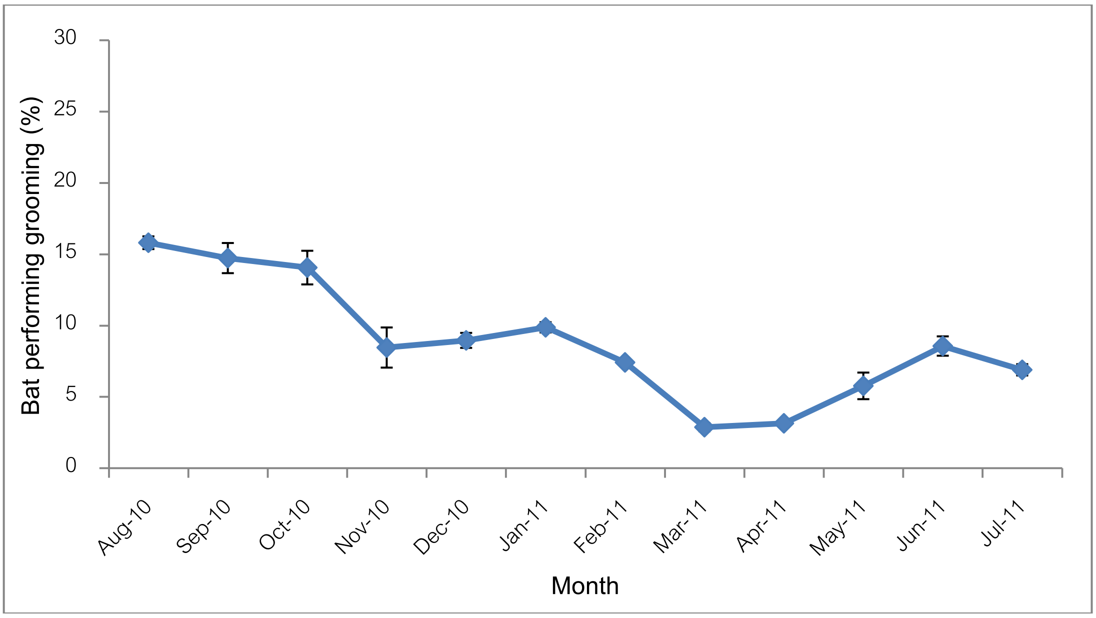

Figure 4-19 The percentage of bats performing grooming behavior between August 2010 and July 2011. Data are shown in the mean ± standard errors.

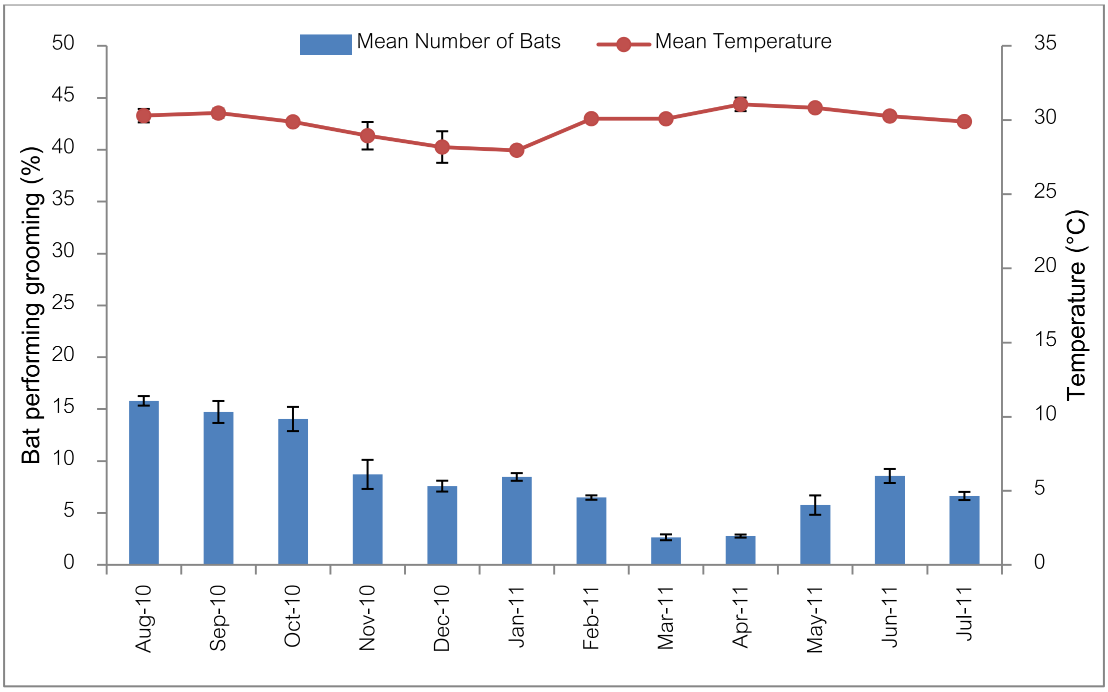

Figure 4-20 Relationship between the percentage of bats performing grooming behavior in each month and ambient temperature (mean ± SD; r=-0.082, p=0.585).

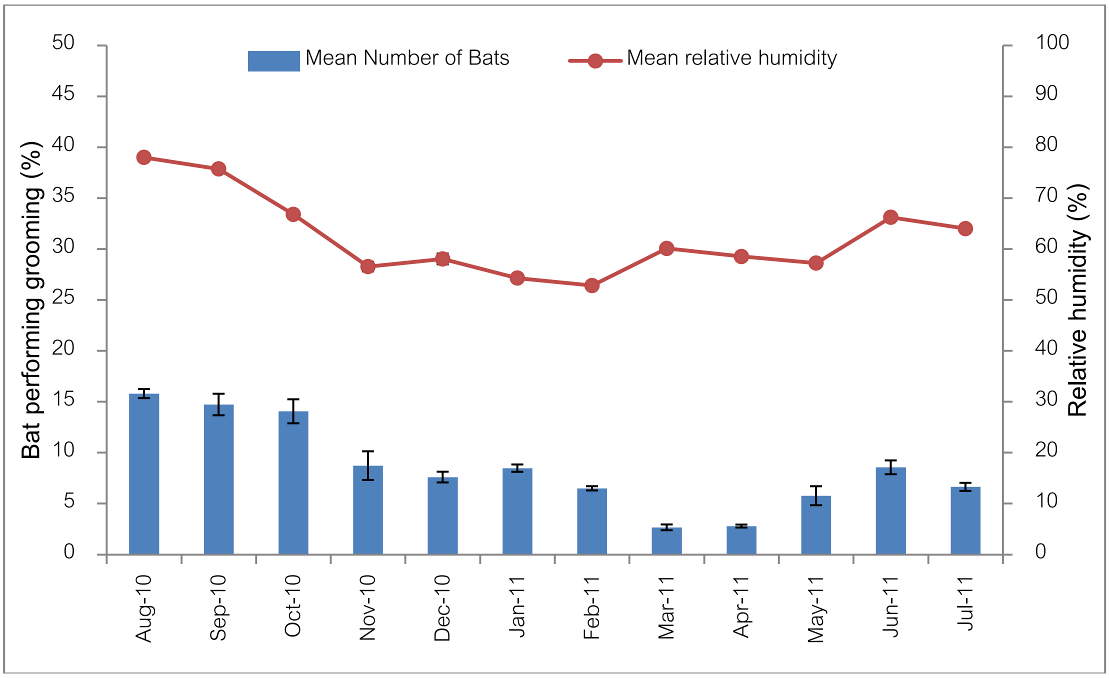

Figure 4-21 Relationship between the percentage of bats performing grooming behavior in each month and relative humidity (mean ± SD; r=0.585, p<0.001).

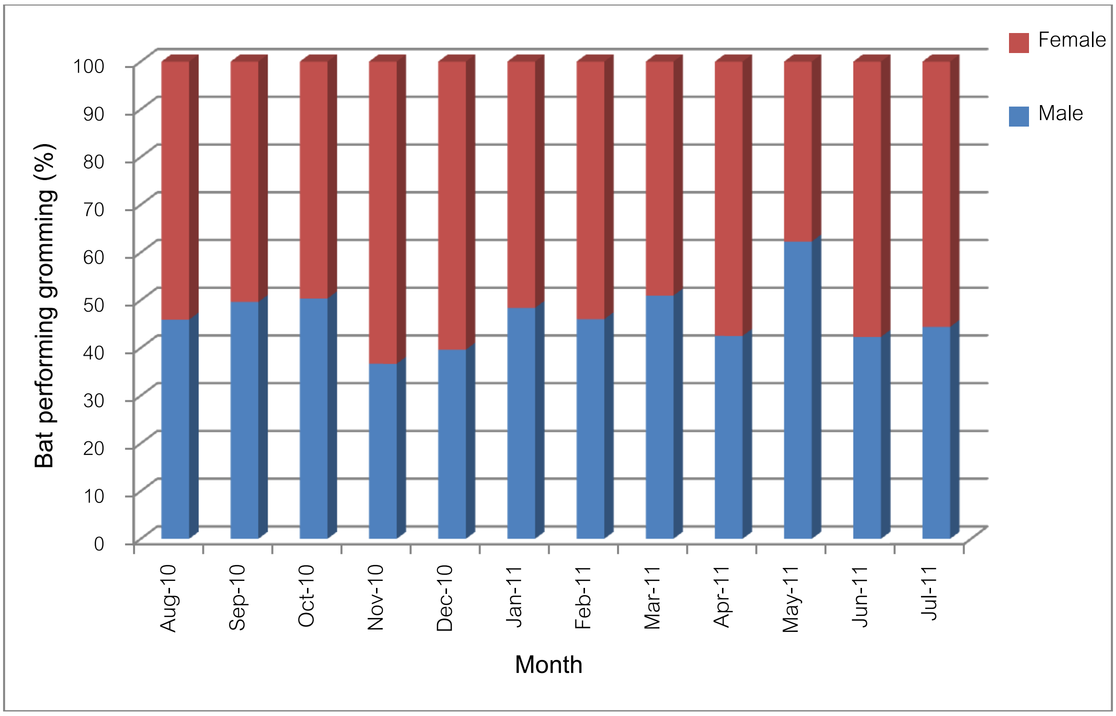

Figure 4-22 The percentage of males and females exhibited grooming behavior between August 2010 and July 2011.

4.4.3 Wing spreading

The wing spreading activity of Lyle's flying foxes significantly varied during the day (Kruskal-Wallis test, H=94.4, df=11, p<0.001; Figure 4-23). The highest percentage of wing spreading bats mostly occurred in the morning (0800 to 0900 hours), then this behavior steadily decreased to the lowest in the evening (1700 to 1800 hours).

Wing spreading pattern in Lyle's flying foxes differed significantly between times of the year (Kruskal-Wallis test, H=163.5, df=11, p<0.001). The highest percentage of wing spreading bats was recorded during August and October, and the lowest percentage occurred in March and April (Figure 4-24).

The wing spreading activity was not correlated with ambient temperature (Spearman correlation, r=-0.113, p=0.448; Figure 4-25), but weakly correlated with relative humidity (Spearman correlation, r=0.417, p=0.004; Figure 4-26).

There were significant differences in number of bats performing wing spreading behavior between sexes. This behavior usually displayed by adult males (Mann-Whitney U test, Z=-21.6, p<0.001; Figure 4-27).

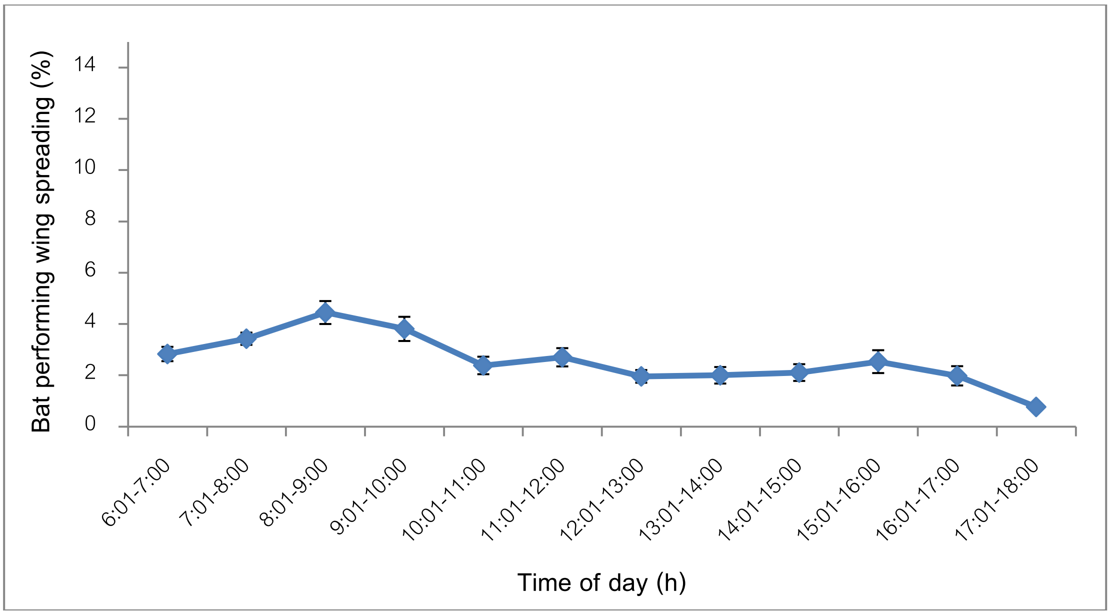

Figure 4-23 The percentage of bats performing wing spreading behavior between 0600 and 1800. Data are shown in the mean ± standard errors.

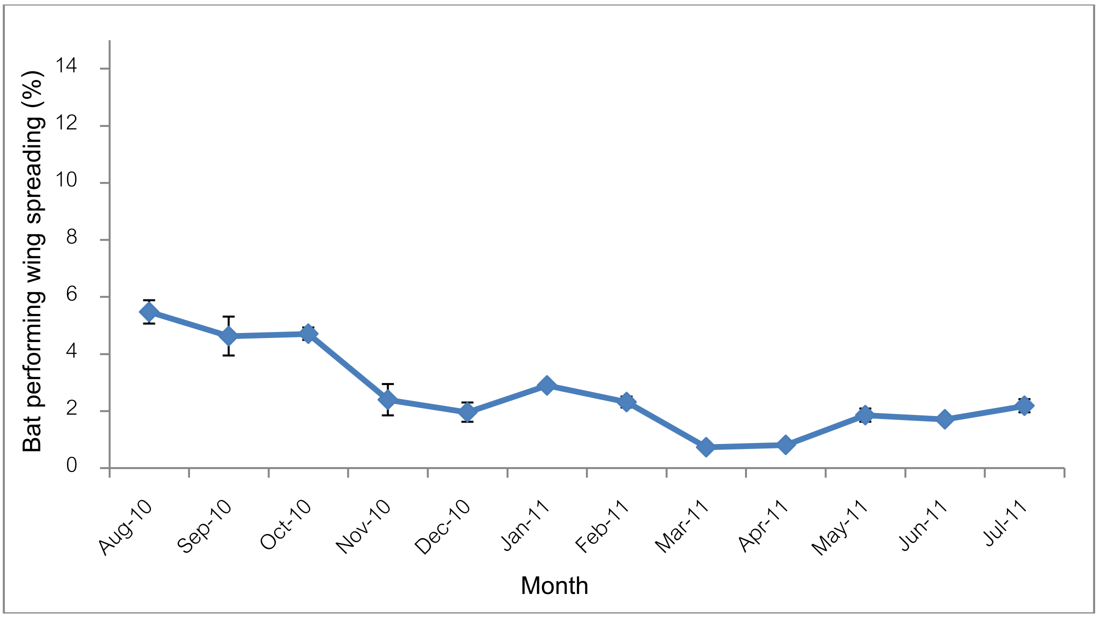

Figure 4-24 The percentage of bats performing wing spreading behavior between August 2010 and July 2011. Data are shown in the mean ± standard errors.

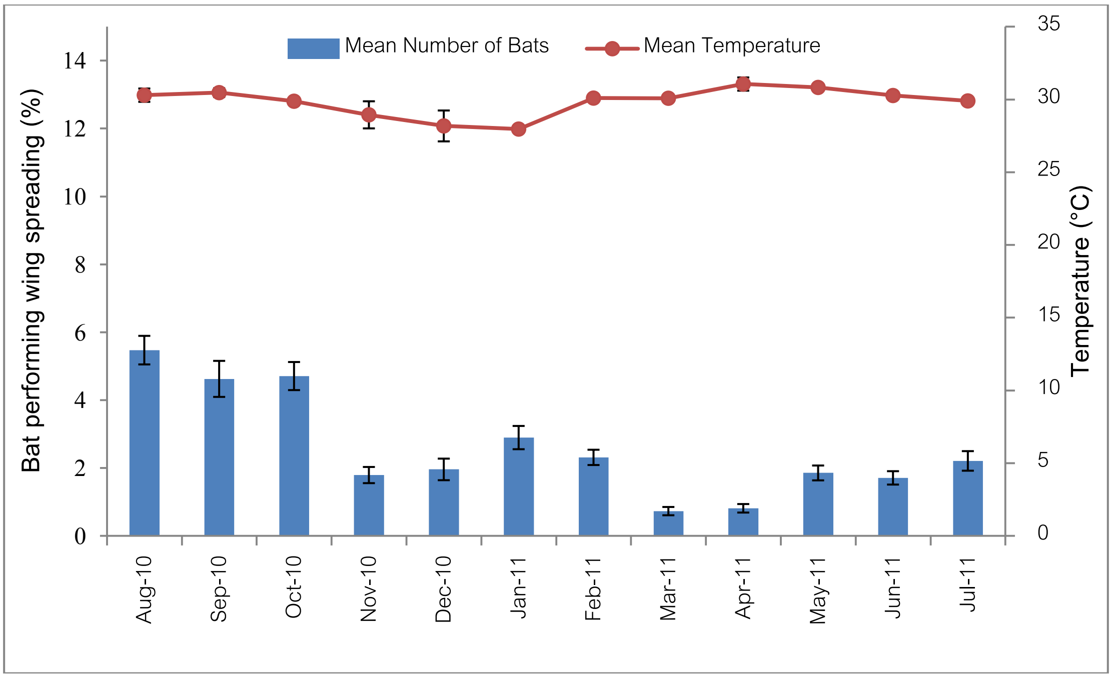

Figure 4-25 Relationship between the percentage of bats performing wing spreading behavior in each month and ambient temperature (mean ± SD; r=-0.113, p=0.448).

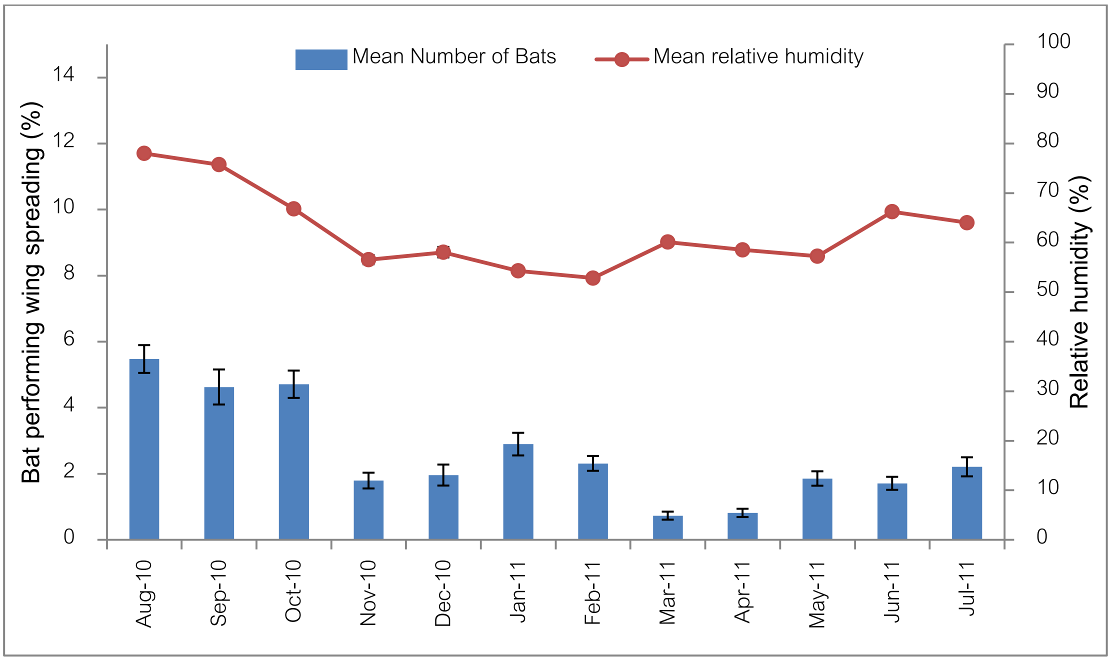

Figure 4-26 Relationship between the percentage of bats performing wing spreading behavior in each month and relative humidity (mean ± SD; r=0.417, p=0.004).

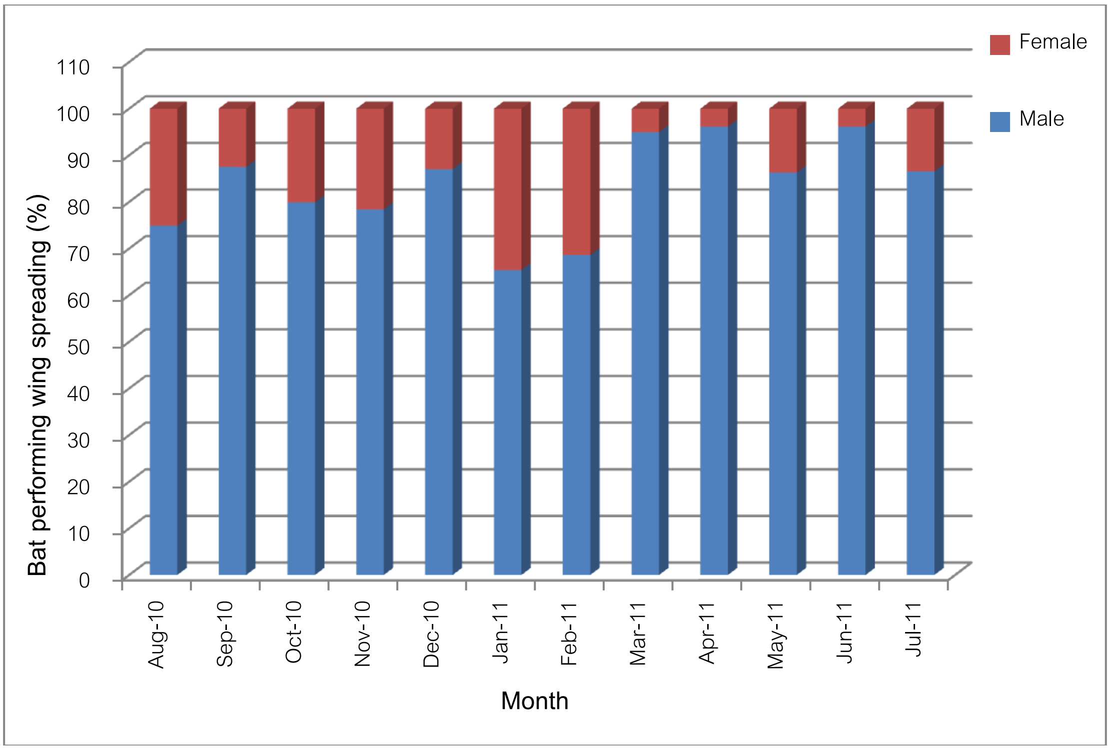

Figure 4-27 The percentage of males and females exhibited wing spreading behavior between August 2010 and July 2011.

4.4.4 Movement

There was slightly but significant difference in the percentages of bats performing movement during the day (Kruskal-Wallis, test, H=95.1, df=11, p<0.001; Figure 4-28). The highest percentages of movement activity occurred in early morning (0600 to 0700 hours) and at noon (1200 to 1300 hours), while the lowest occurred in late afternoon (1600 to 1700 hours).

There was little significant difference in the percentages of bats performing movement at various times of the year (Kruskal-Wallis test, H=81.8, df=11, p<0.001). The highest percentage of movement activity was observed in August and October, whereas the lowest percentage was presented in March and April (Figure 4-29).

The movement activity was not correlated with ambient temperature (Spearman correlation, r=0.099, p=0.509; Figure 4-30, but strongly correlated with relative humidity (Spearman correlation, r=0.664, p<0.001; Figure 4-31).

The proportion of bat performing movement activity significantly differed between sexes. The movement activity was found in adult males more frequently than in adult females (Mann-Whitney U test, Z=-13.3, p<0.001; Figure 4-32).

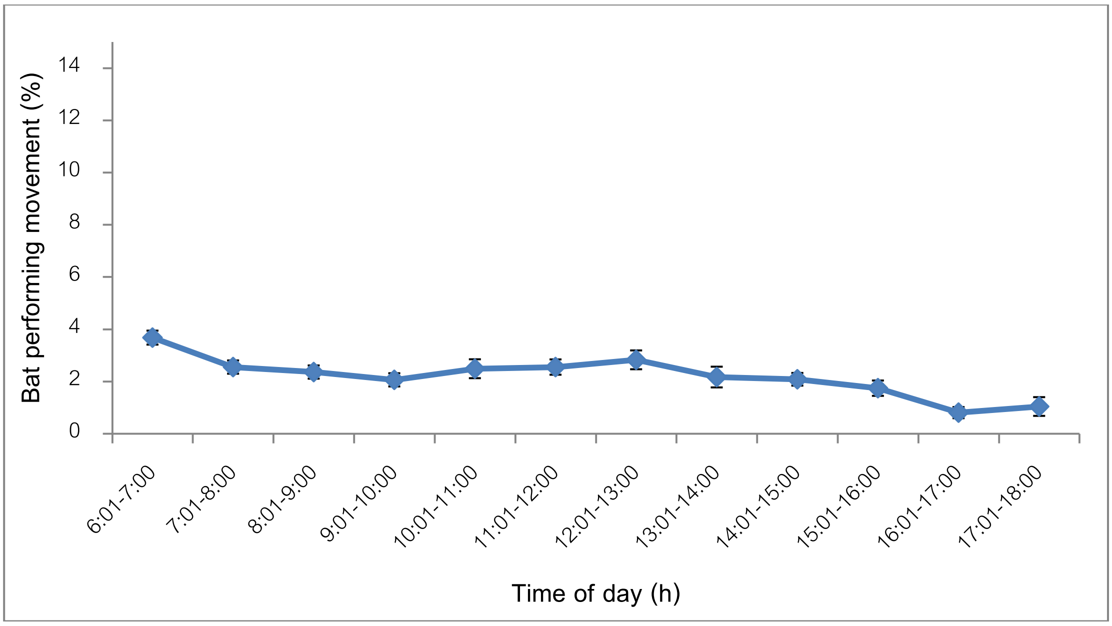

Figure 4-28 The percentage of bats performing movement behavior between 0600 and 1800. Data are shown in the mean ± standard errors.

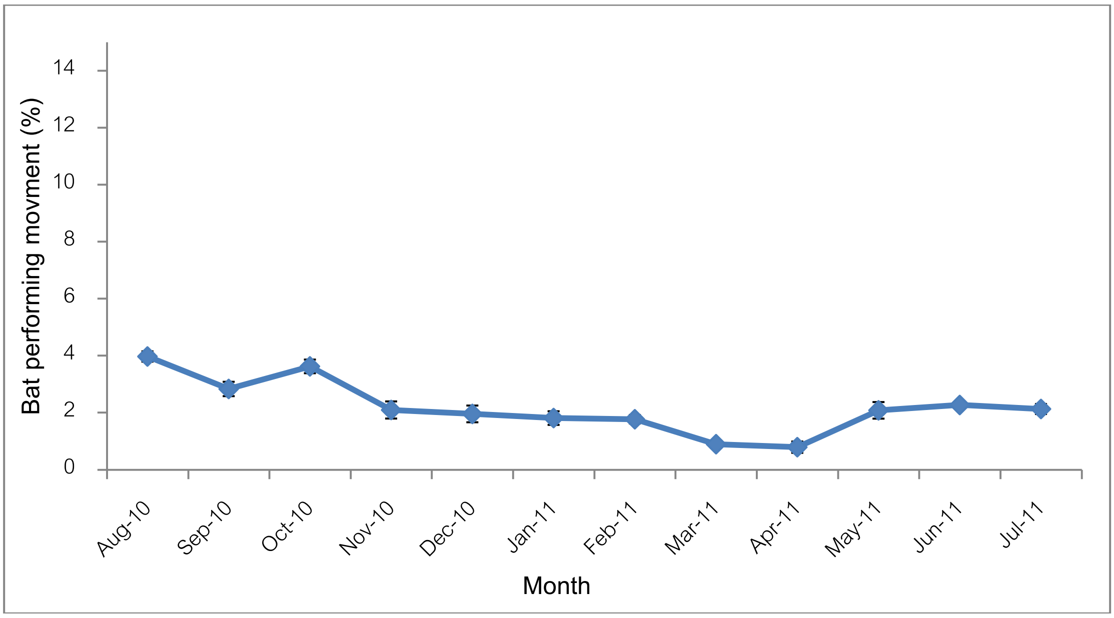

Figure 4-29 The percentage of bats performing movement behavior between August 2010 and July 2011. Data are shown in the mean ± standard errors.

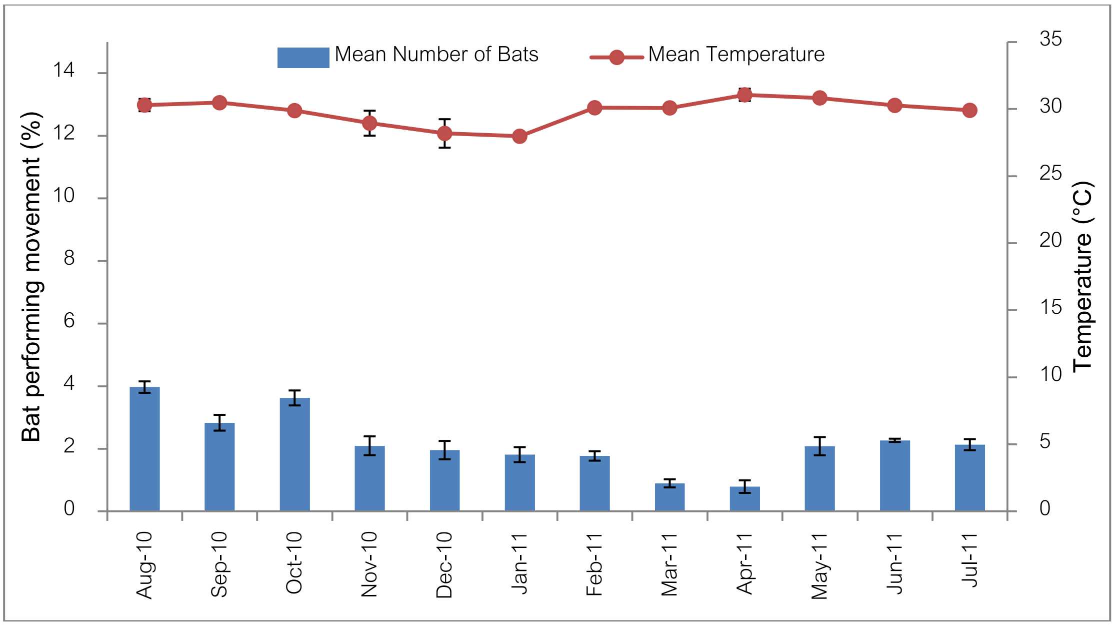

Figure 4-30 Relationship between the percentage of bats performing movement behavior in each month and ambient temperature (mean ± SD; r=0.099, p=0.509).

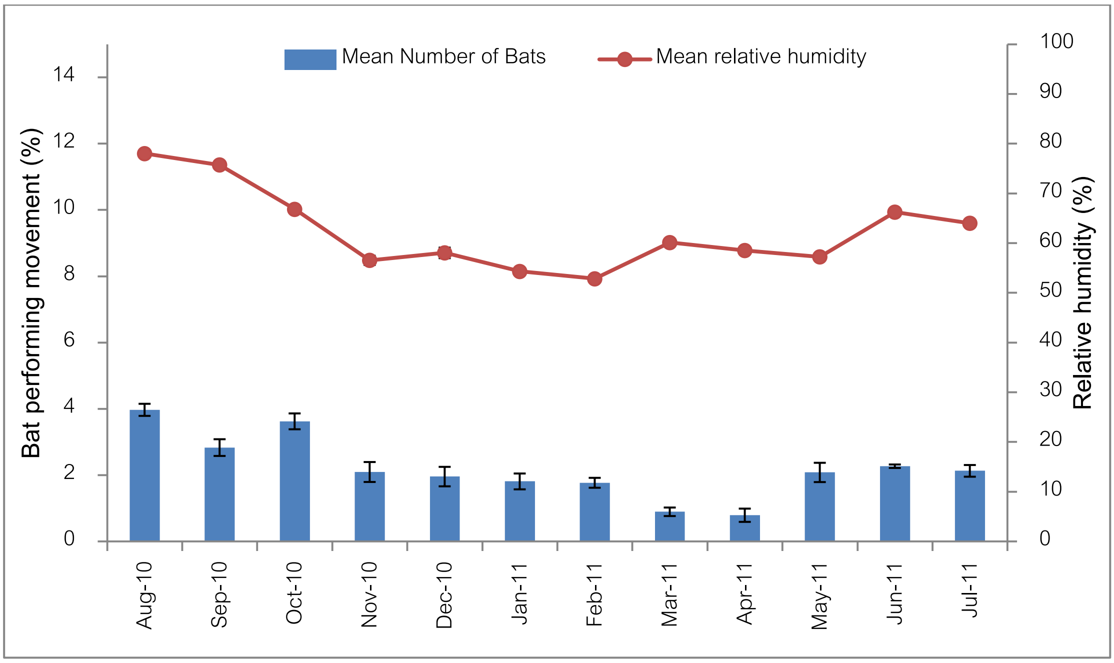

Figure 4-31 Relationship between the percentage of bats performing movement behavior in each month and relative humidity (mean ± SD; r=0.664, p<0.001).

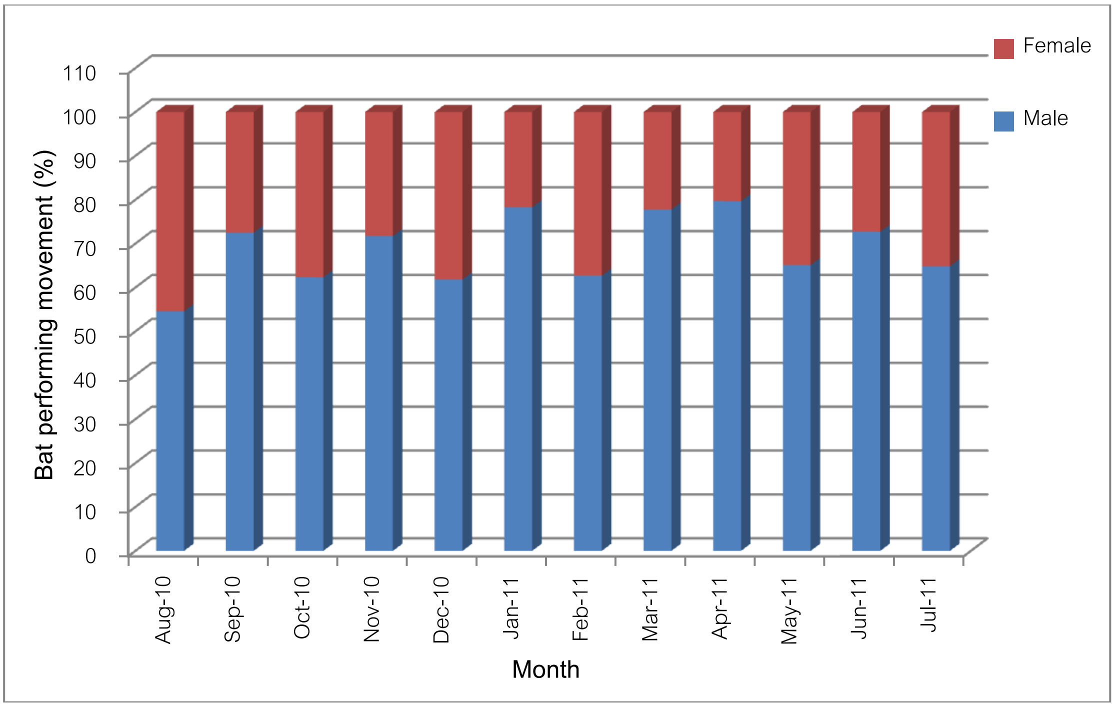

Figure 4-32 The percentage of males and females exhibited movement behavior between August 2010 and July 2011.

4.4.5 Wing flapping

There were significant differences in the percentage of bats performing wing flapping during the day (Kruskal-Wallis test, $H=415.8$, $df=11$, $p<0.001$; Figure 4-33). Wing flapping was observed from late morning until late afternoon (1000 to 1700 hour). This activity increased rapidly in late morning and reached to the highest at noon, then this behavior gradually decreased to the lowest in late afternoon.

Wing flapping activity of Lyle's flying foxes varied significantly throughout the years (Kruskal-Wallis test, $H=27.4$, $df=11$, $p<0.05$; Figure 4-34). The lowest percentage of wing flapping activity was found during January and February, while the highest percentage was observed in April.

This activity was positively correlated with ambient temperature (Spearman correlation, $r=0.611$, $p<0.001$; Figure 4-35), but not correlated with relative humidity (Spearman correlation, $r=0.198$, $p=0.182$; Figure 4-36).

Sexual differences in wing flapping activity cloud not be examined due to the difficultly in sex identification when bats performed wing flapping.

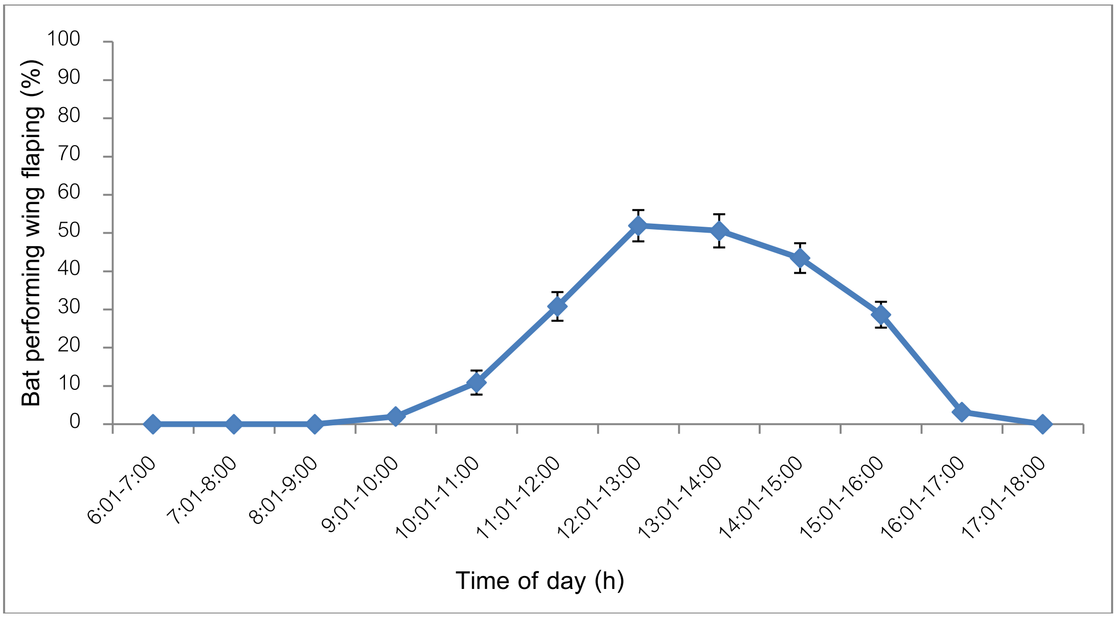

Figure 4-33 The percentage of bats performing wing flapping behavior between 0600 and 1800. Data are shown in the mean ± standard errors.

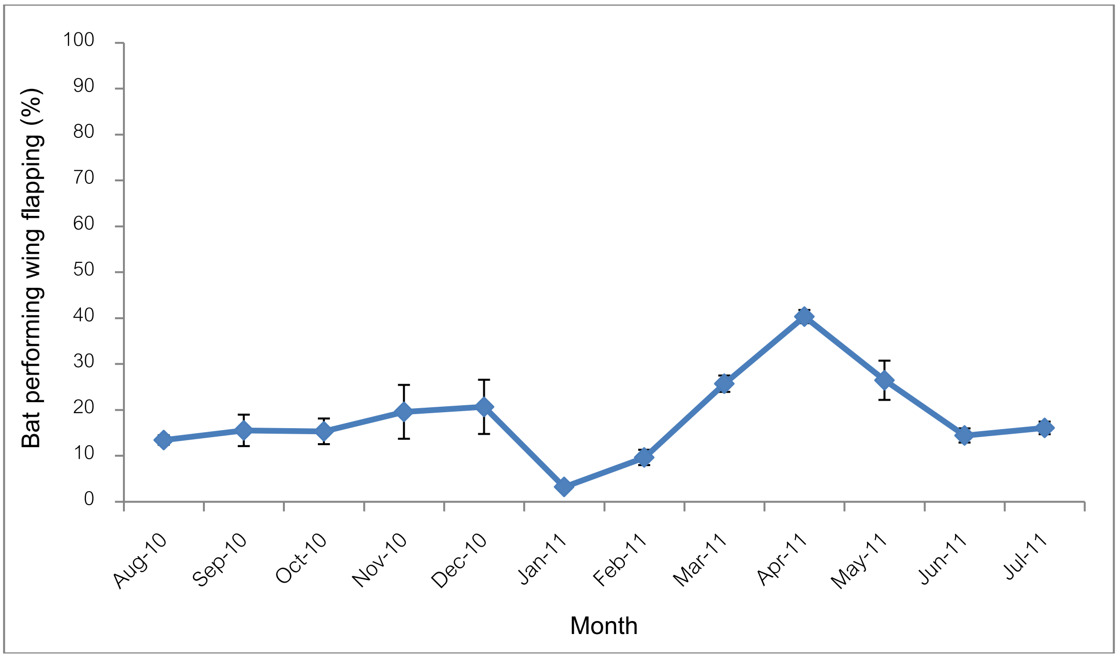

Figure 4-34 The percentage of bats performing wing flapping behavior between August 2010 and July 2011. Data are shown in the mean ± standard errors.

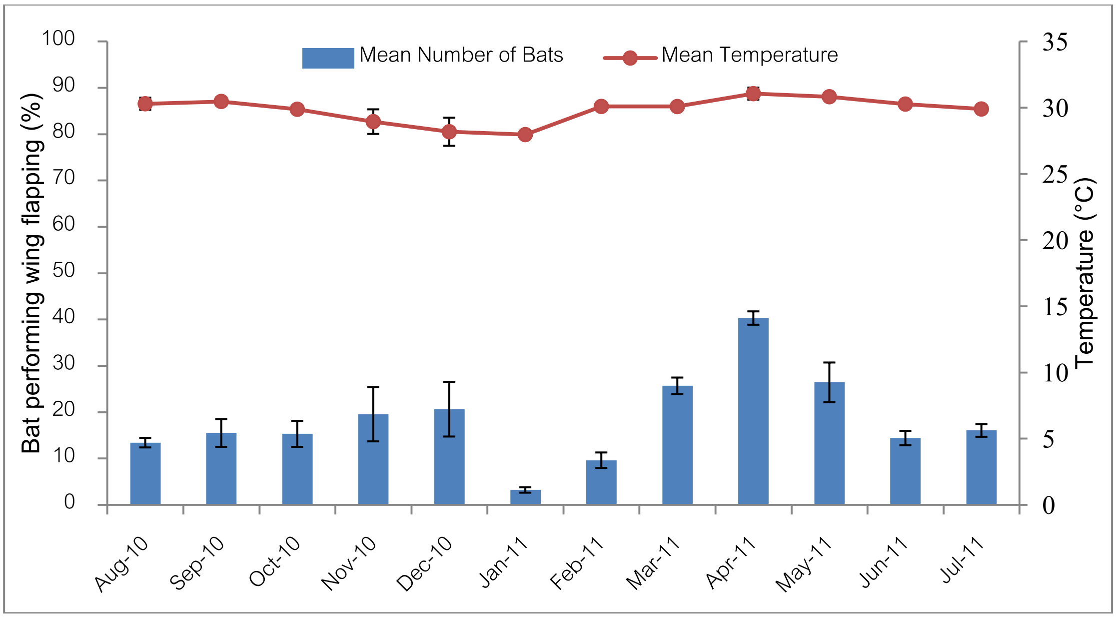

Figure 4-35 Relationship between the percentage of bats performing wing flapping behavior in each month and ambient temperature (mean ± SE; r=0.611, p<0.001).

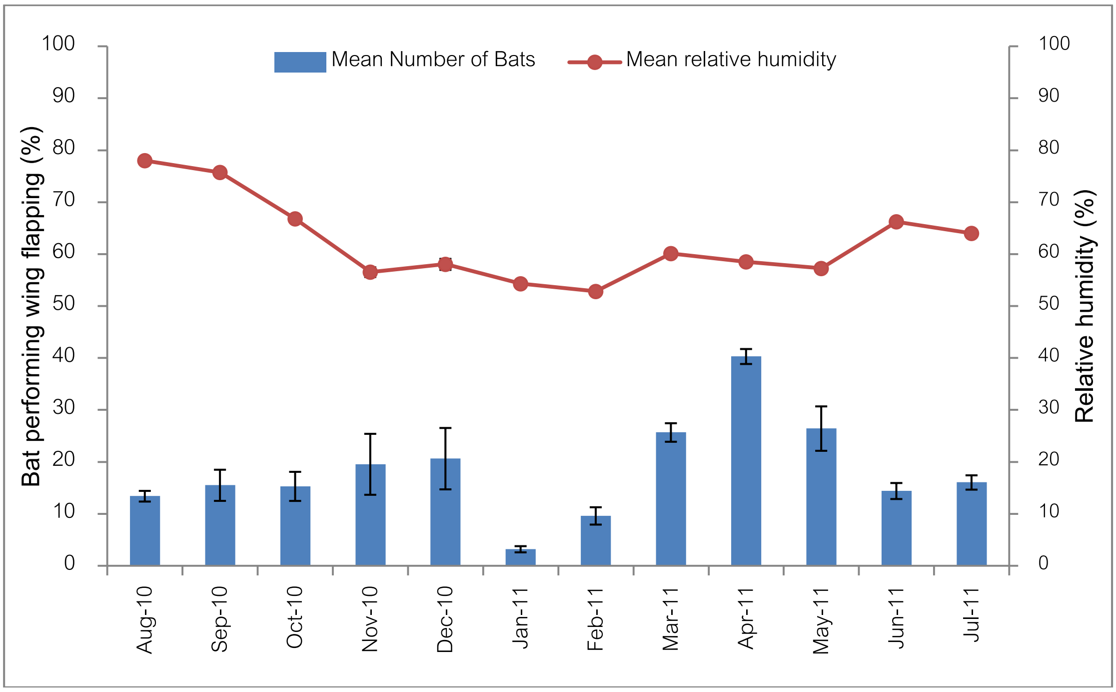

Figure 4-36 Relationship between the percentage of bats performing wing flapping behavior in each month and relative humidity (mean ± SE; r=0.198, p=0.182).

4.4.6 Aggression

Lyle's flying fox performed aggression differently at times of day. (Kruskal-Wallis test, H=102.6, df=11, p<0.001; Figure 4-37). Aggressive behavior mostly occurred in the morning (0700 to 0900 hours), and decreased to the lowest in the evening (1700 to 1800 hours).

There was slightly but significant difference in aggression activity throughout the entire observation period (Kruskal-Wallis test, H=47.1, df=11, p<0.001; Figure 4-38). The highest percentage of bat performing aggression was found in January and February.

The aggression in Lyle's flying foxes was not correlated with ambient temperature (Spearman correlation, r=-0.015, p=0.922; Figure 4-39), but was weakly correlated with relative humidity (Spearman correlation, r=-0.381, p=0.008; Figure 4-40).

There were significant differences in number of bats performing aggression behavior between sexes. Adult females performed aggressive behavior more frequently than adult male (Mann-Whitney U test, Z=-3.1, p=0.002; Figure 4-41).

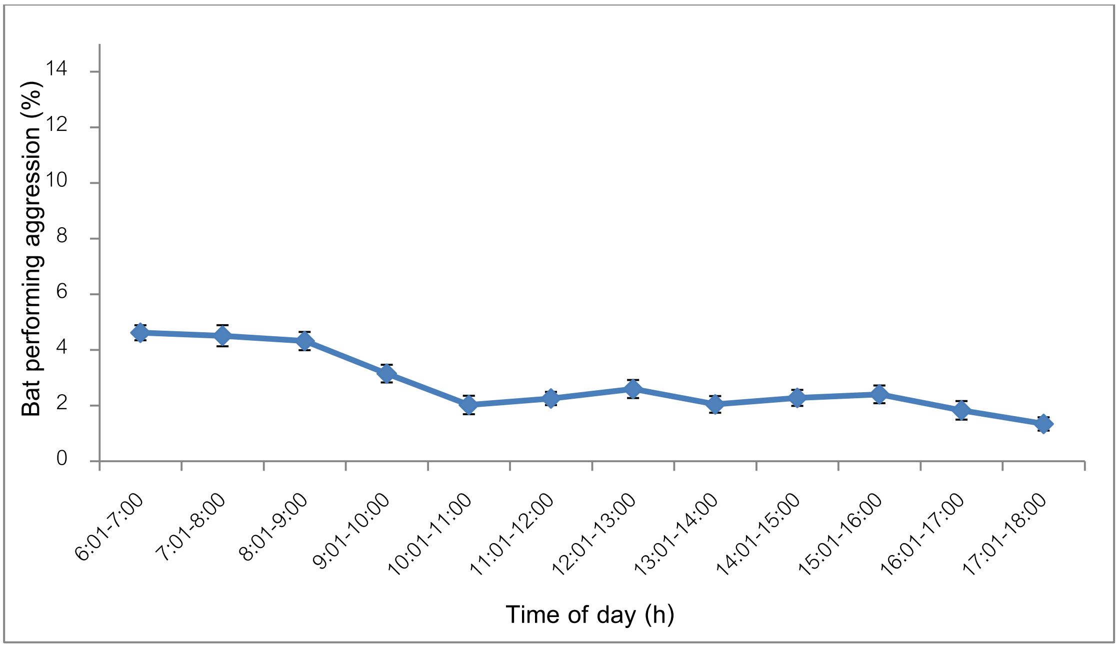

Figure 4-37 The percentage of bats performing aggressive behavior between 0600 and 1800. Data are shown in the mean ± standard errors.

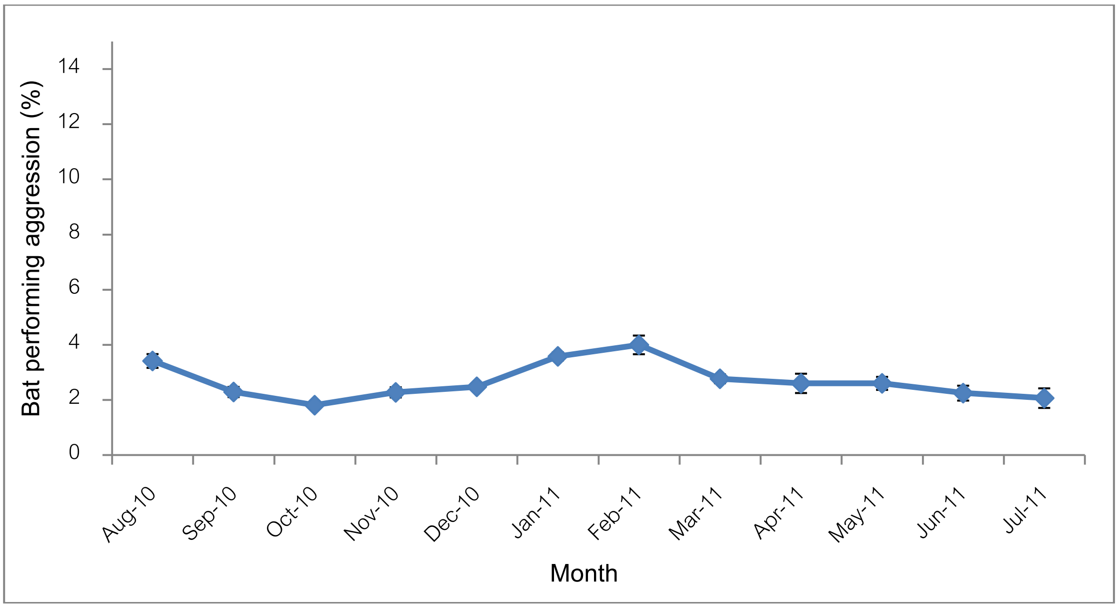

Figure 4-38 The percentage of bats performing aggressive behavior between August 2010 and July 2011. Data are shown in the mean ± standard errors.

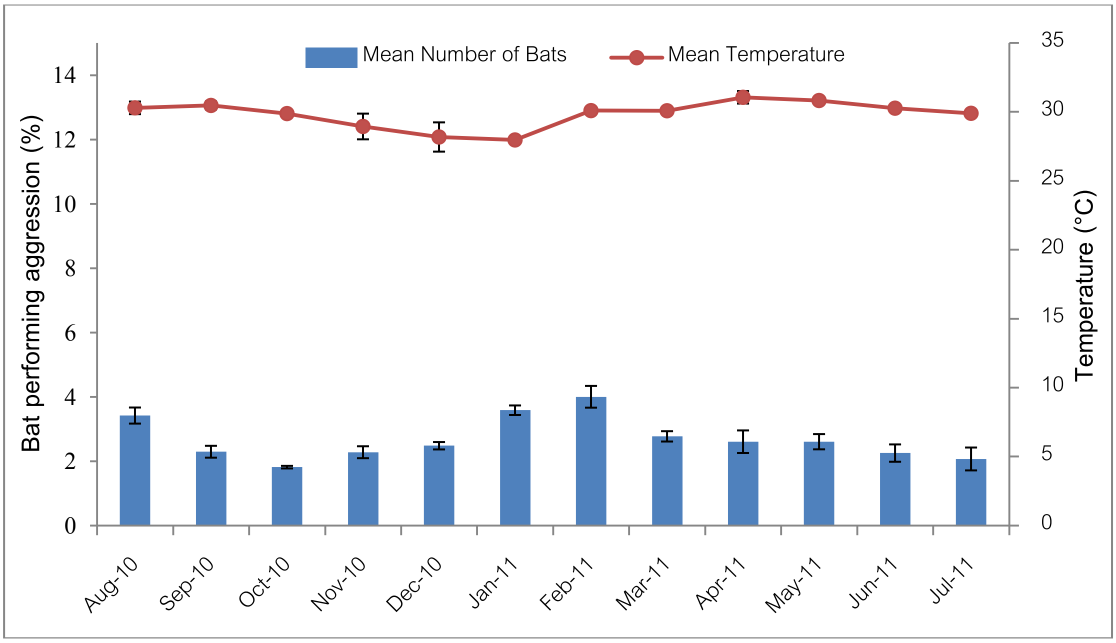

Figure 4-39 Relationship between the percentage of bats performing aggressive behavior in each month and ambient temperature (mean ± SE; r=-0.015, p=0.922).

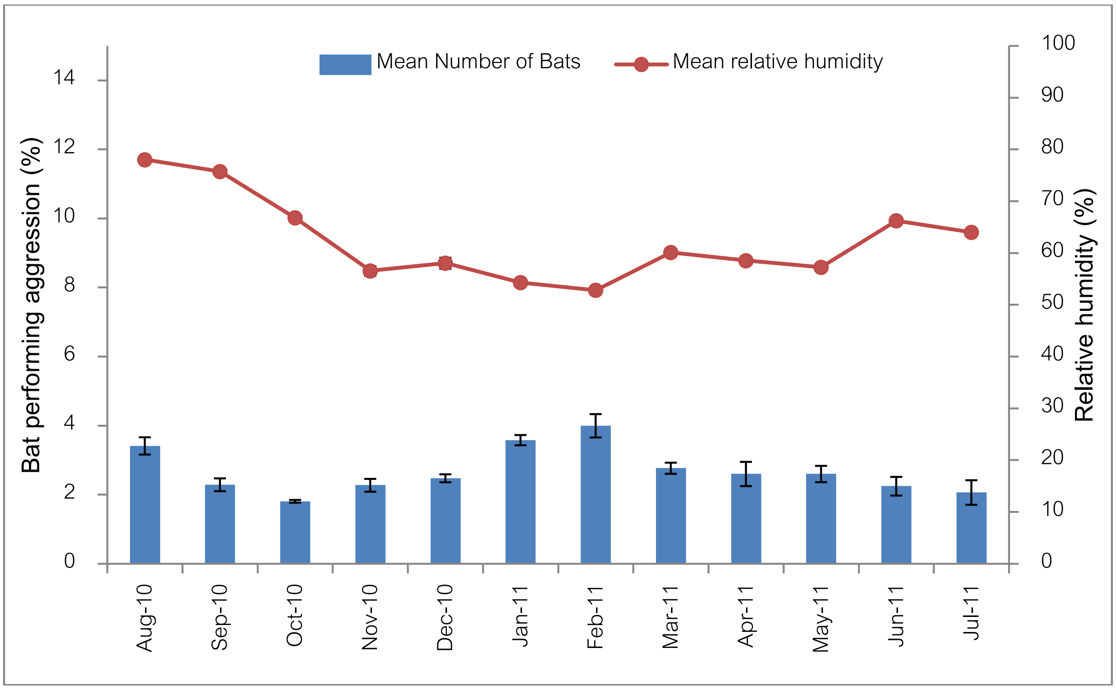

Figure 4-40 Relationship between the percentage of bats performing aggressive behavior in each month and relative humidity (mean ± SE; r=-0.381, p=0.008).

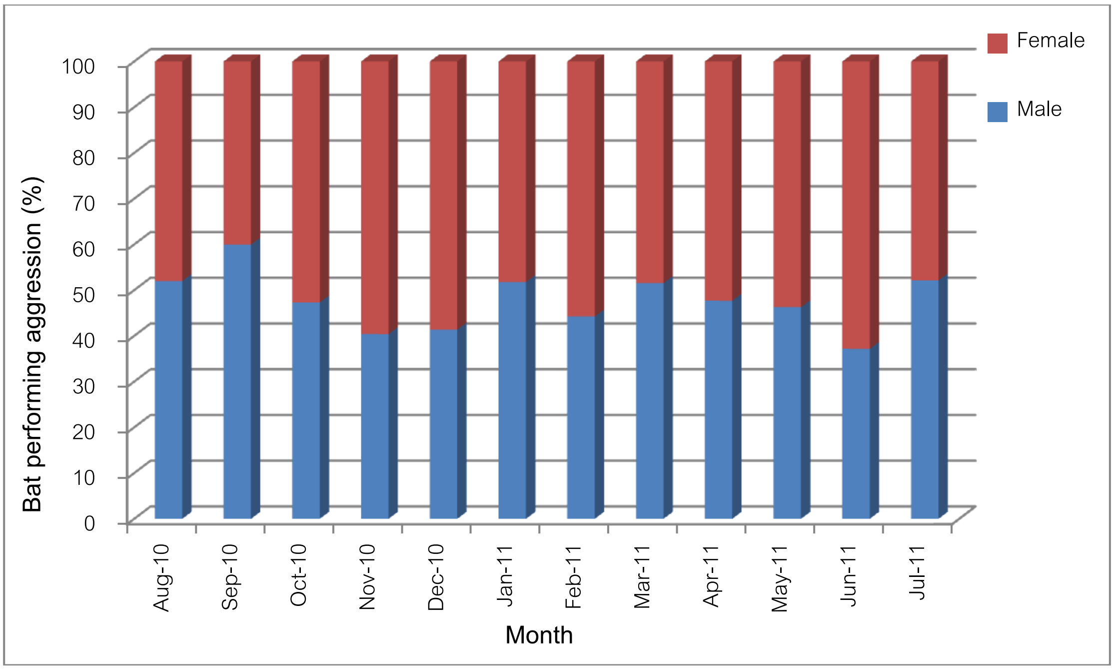

Figure 4-41 The percentage of males and females displayed aggressive behavior between August 2010 and July 2011.

4.4.7 Mating and courtship

There were significant differences in the percentages of bats performing mating and courtship behavior throughout the day (Kruskal-Wallis test, H=233.1, df=11, p<0.001; Figure 4-42). This behavior mostly occurred in the morning (0700 to 0900 hours), and decreased to the lowest in the afternoon (1200 to 1500 hours). Then, this activity rose up again in the evening (1600 to1800 hours).

Mating and courtship activity were observed and significantly varied throughout the year (Kruskal-Wallis test, H=78.7, df=11, p<0.001; Figure 4-43). The percentage of bats performing mating and courtship behavior peaked in August, January and February, while the percentage reached the lowest in June and July.

This behavior was not correlated with ambient temperature (Spearman correlation, r=-0.074, p=0.620; Figure 4-44) and relative humidity (Spearman correlation r=0.066, p=0.660; Figure 4-45).

However, there were significant differences in number of bats performing mating and courtship between sexes. Adult males performed mating and courtship behavior more frequently than females (Mann-Whitney U test, Z=-16.7, p<0.001; Figure 4-46).

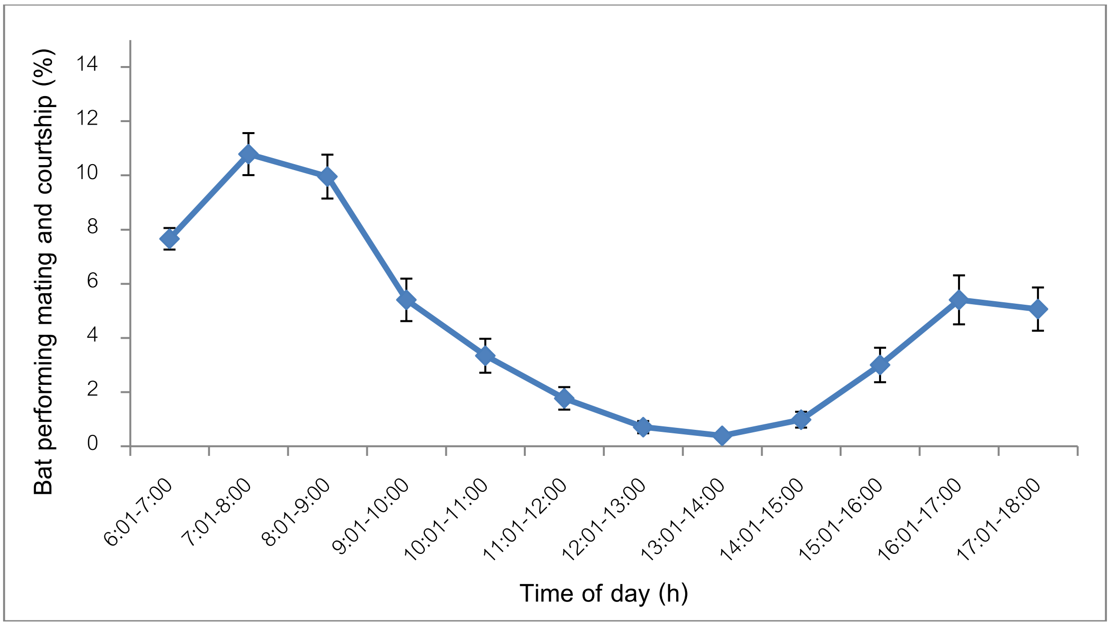

Figure 4-42 The percentage of bats performing mating and courtship behavior between 0600 and 1800. Data are shown in the mean ± standard errors.

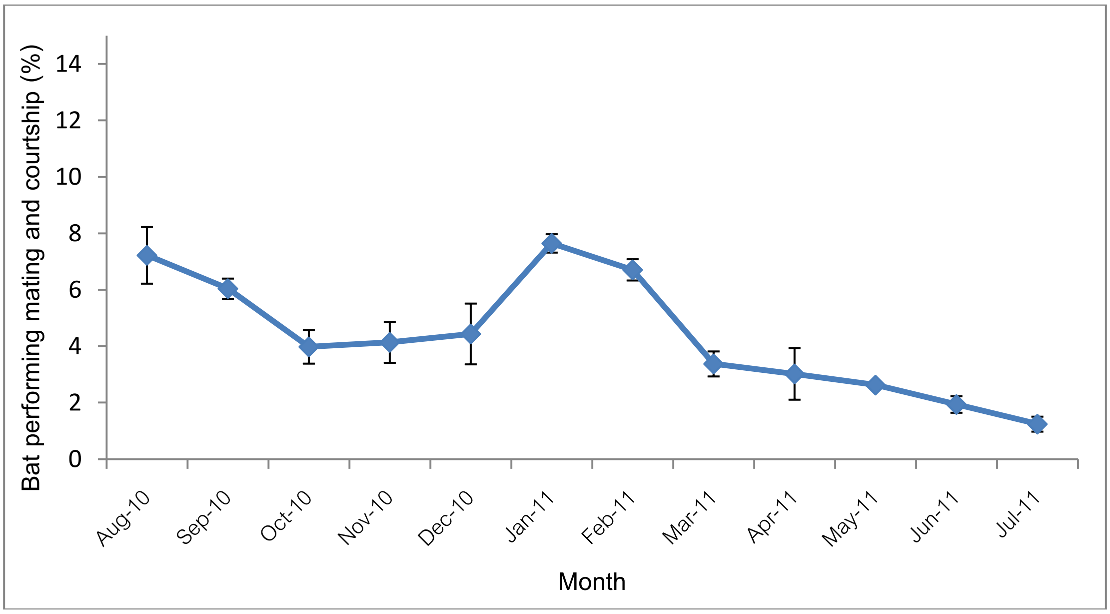

Figure 4-43 The percentage of bats performing mating and courtship behavior between August 2010 and July 2011. Data are shown in the mean ± standard errors.

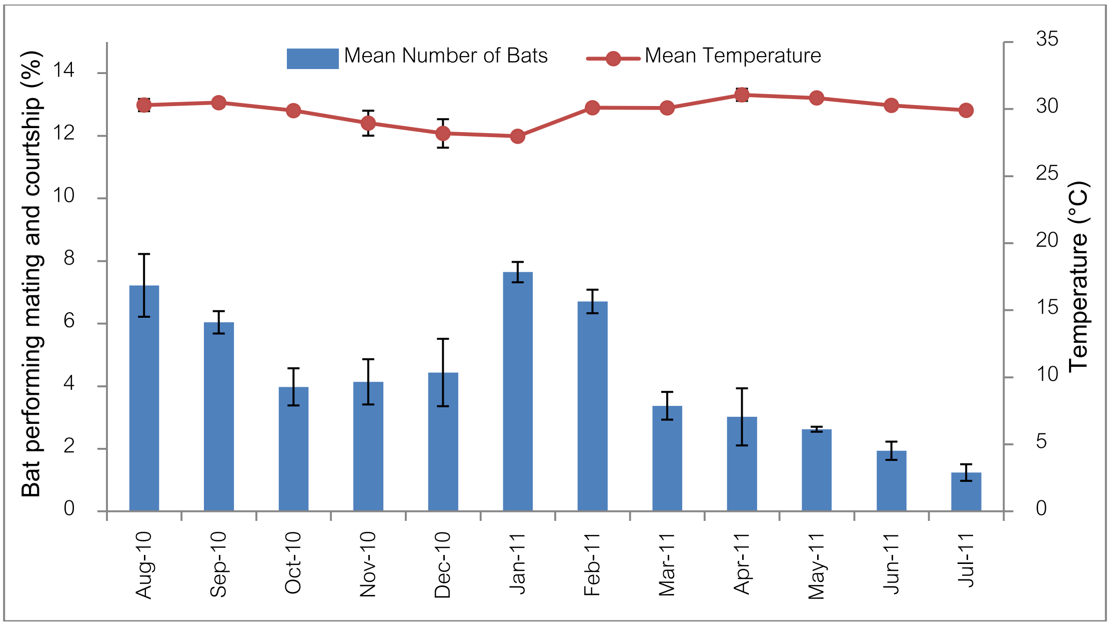

Figure 4-44 Relationship between the percentage of bats performing mating and courtship behavior in each month and ambient temperature (mean ± SE; r=-0.074, p=0.620).

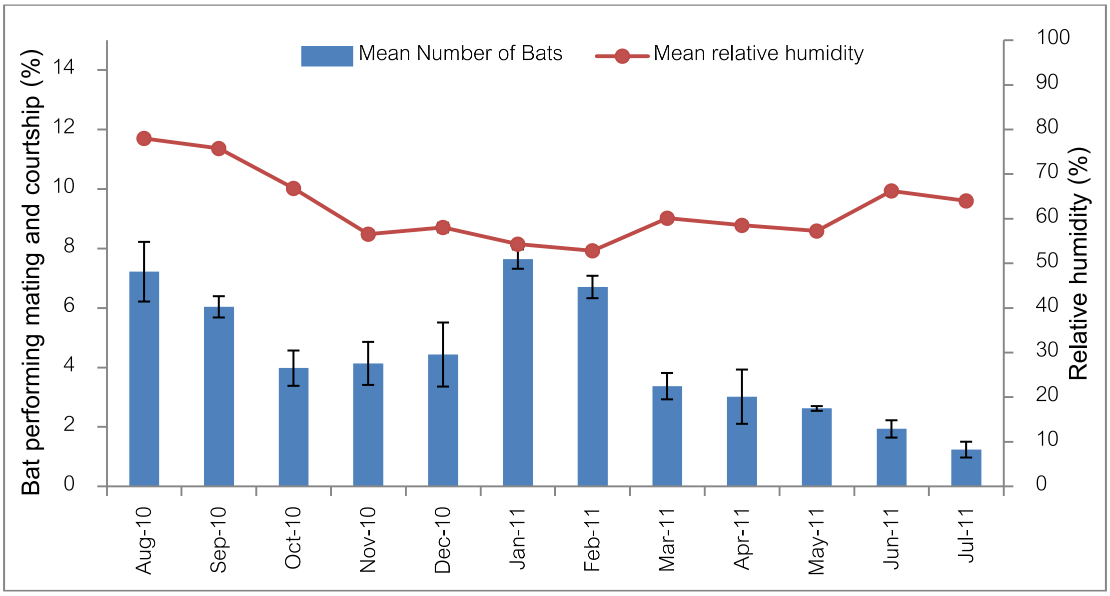

Figure 4-45 Relationship between the percentage of bats performing mating and courtship behavior in each month and relative humidity (mean ± SE; r=0.066, p=0.660).

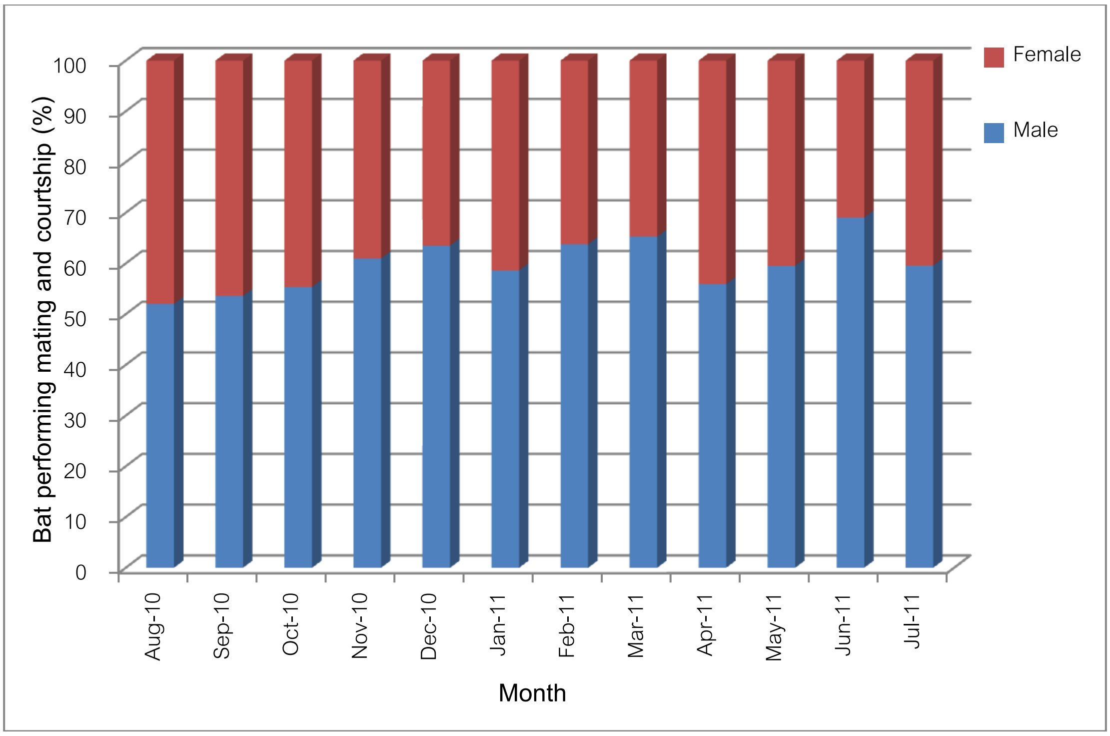

Figure 4-46 The percentage of males and females performed mating and courtship behavior between August 2010 and July 2011.

4.4.8 Maternal care

Maternal care was not statistically analyzed because it is difficult to observe lactating female with newborn attached when they were sleeping during early lactation period (March and April). Therefore, the present study provided the description of mother and young behaviors.

From field observation, a number of newborns in Lyle's flying fox occurred between March and April, and the lactating females with juveniles attached were observed between March and July. The newborns were altricial at birth. During the first lactation months (March and April), the newborns could not perch independently, they need to attach to mother's chest for all time, so lactating females must carry their offspring all time even in foraging flight. Maternal grooming such as licking was usually found throughout the day during this period.

Between May and July, I was found that lactating females leave their young at roosting site before emergence because the juvenile was too large to be carried while foraging. However, lactating females always came back to visit their young at the roosting site and flew out again to forage during the night. Nevertheless, the frequency of roost visit was currently unknown. When lactating females came back at dawn, they located their young and finally holded them by wing membranes. Maternal grooming was found throughout the day, but this behavior was frequently observed before and after foraging flight.

Form video recording study, it was found that juveniles of Lyle's flying fox began their flight developing skill by flapping their wing membranes when they were leave at roost during the night in May. During this period, the temporality of independently perching beside mother was observed in juveniles, and these occurred more frequently as they grew up. However, mothers always pulled their offspring for grooming and embrace.

During field observations, the caregiving behavior of Lyle's flying fox was only exhibited by females. However, adult males defended females and pups within their territories from other males.

CHAPTER V
DISSCUSSION

5.1 Colony-wide emergence

5.1.1 Emergence behavior

Although Lyle's flying fox is a large frugivorous bat, it is still considered to be a small mammal. It has a high metabolic rate and low body reserve because they feed on diet which is high in carbohydrate but low in lipids, which constitute fat storage (McNab, 1976). So they must consume sufficient food to fuel up their energetic demands by foraging every night. As expected, Lyle's flying foxes emerged to forage everyday. Shortly after sunset, a few individuals were noticed flying and calling above the colony. Boonneung (1977) believed that these behaviors are signal of nightly emergence used for calling to awake other members from sleeping. After acoustic stimulation, other members in the colony woke up and prepared their night departure by grooming themselves to clean their wing membranes and fur, as suggested by Burnett and August (1981). When, the number of bats flying around the colony increased and reached the critical number, the leader of them will decide to leave the roosting site at particular light intensity with respect to predation risk, and others will follow resulting in the emergence streams heading towards the direction of food resources. The similar patterns have been found in the emergence study of *P. alecto* and *P. poliocephalus* by Welbergen (2008). The mixed-species colony contained up to 26,000 individuals of *P. alecto* and *P. poliocephalus,* and their emergence consisted of six snakelike streams. Due to the smaller population size, the emergence of Lyle's flying fox at Wat Pho colony only consisted of three sinuous streams. Circling and wheeling above the colony before emergence of flying fox may be related to information transfer, or just warming up to travel for long distances (Hall and Richards, 2000). Tuttle (1994) mentioned that *Tadarida brasiliensis* swirl higher and higher to gain some altitude in the sky, before forming a stream and flying off to forage.

Furthermore, Glover and Altringham (2008) mentioned that flying in and around caves was a swarming behavior among species of Microchiroptera. The functions of this swarming in temperate bats were supposed to serve the purposes of hibernation site assessment as well as information transfer between adults and juveniles about the site of hibernation or mating strategy because the swarming site facilitated gene flow between populations (Fenton, 1969; Furmankiewicz and Altringham, 2007).

Duration of colony-wide emergence

Furthermore, this study found crucial evidence that Lyle's flying foxes had changed emergence behavior by extending emergence time in parturition and early lactation period, usually in during March and April, as suggested by Boonneung (1977). During these two months, Lyle's flying foxes gradually emerged later for several hours after sunset, resulting in the longest duration of colony-wide emergence between March and April. From personal observation and video recording, most bats prolonged emergence time were lactating females. During their first month, newborns are dependent on their mothers and need to be carried by their mothers even during foraging flight (Plowright et al., 2008). So the maternal care including juvenile attachment might affect flight performance and delay the emergence of lactating females, which prolonged the duration of colony-wide emergence in Lyle's flying foxes between these times of the years.

In May, the age of pups was about two months, and they were too large to be carried by their mothers while foraging (Tidemann, 1987). Lactating females need to separate themselves from their young temporarily and leave them in the roosting site. That process might take a long time and hence prolong the duration of colony-wide emergence in Lyle's flying foxes. From personal observation, infant mortality was probably highest during this period when the young were left at the roosting site before they cloud fly. Infant mortality occurs when they fall from their perch and are unable to climb back up the tree (Nelson, 1965).

The high duration of colony-wide emergence was also found between November and January. Sexual behavior such as mating and courtship display should occur mostly around this time of the year. Because Lyle's flying foxes have four to five months gestation period, before giving birth in March and April (Boonneung,1977). Such sexual behavior might delay the emergence time of Lyle's flying foxes.

5.1.2 Relationship between duration of colony-wide emergence and twilight duration

For year-round observation, the present study showed the seasonal changes in twilight duration had a little positive relationship on the duration of colony-wide emergence in Lyle's flying fox. However the strong positive impact was found in the study by Welbergen (2006). He demonstrated that the duration of colony-wide emergence in *P. poliocephalus* and *P. alecto* was strongly correlated with seasonal variation in twilight duration.

This can be explained by the difference of twilight duration between equator and higher latitude. The length of twilight defined as the time interval between the sunset and the end of astronomical twilight, not only depend on the time of year, but it also depend on the latitude. Twilight duration is shorter at the equator than at higher latitudes. Because sun's path toward the horizon is more nearly vertical at equator than at higher latitudes (Ahrens et al., 2012). Therefore, bats living at higher latitude such as *P. poliocephalus* and *P. alecto* are encountered with longer length of twilight which covered the whole duration of colony-wide emergence. That might result in the strong positive relationship between the duration of colony-wide emergence and twilight duration in Australia. Lyle's flying fox living at equator encountered with shorter length of twilight which did not cover the whole duration of colony-wide emergence throughout the year. That might result in the weakly positive relationship between the duration of colony-wide emergence and twilight duration in Thailand.

However, the strongly positive relationship between the duration of colony-wide emergence in Lyle’s flying fox and twilight duration was found outside lactation period. This suggests that not only geographical variation in twilight duration but reproductive state and paternal care also play a crucial role in the colony-wide emergence of Lyle’s flying fox. Further detailed study in the duration of colony-wide emergence in Lyle’s flying fox should be taken into account.

5.1.3 Relationship between the colony-wide emergence time and environmental factors

The result supported previous research on many bat species including insectivorous and frugivorous bats (Kunz and Anthony, 1996; Welbergen, 2006; Reichard et al., 2009) in that the onset of colony-wide emergence of Lyle's flying foxes was highly correlated with seasonal changes in sunset time. Moreover, Erkert (1978) suggested that the end of flight acitivity in tropical bats is also closely related to times of sunrise. For all mammals, sunset and sunrise play an important role as timing cues for daily or circadian rhythms. The rhythms are endogenously generated which is roughly 24 hour cycle in physiology processes of life beings such as sleeping, waking up and eating. In bats, they sleep as usual during daytime and endeavor to fly out for foraging at night. Neuweiler (2000) suggested that bat colonies used sunset as external cues to time their emergence. Particular illuminances during dusk twilight normally trigger the beginning of emergence activity in bats (Isaac and Marimuthu, 1993). So the time of bats emergence in the evening sustains a constant time correlation with the time of sunset throughout the year. In addition, a delicately balanced combination of sunlight, high pressure and dry air, air-borne dust particles and cloud cover can produce a prolonged sunset. This can delay bat emergence (Fure, 2006).

This study found that the onset of colony-wide emergence in Lyle's flying foxes was significantly correlated with ambient temperature, relative humidity, and light intensity, but insignificantly correlated with cloud cover and amount of rainfall. However, the results from multiple regression analysis indicated that relative humidity was main meteorological variable that influenced on the onset of colony-wide emergence of Lyle's flying foxes.

This can be explained by physical factors association. When ambient temperature was low, relative humidity was high resulting in increased cloud cover and reduced light intensity from the sun. Corresponding to the suggestion by Welbergan (2006), the meteorological variables that significantly affected the onset of emergence in *P. poliocephalus* were cloud cover and relative humidity. Cloud cover is correlated with increased humidity and reduced light available from the sun. Light intensity has an influence on bat emergence time serving as a time giver to synchronize circadian rhythm (Erkert, 1982). Furthermore, reduction in light intensity probably triggered the emergence activity in advance because several species of bats used particular light levels as a cue for when to fly out, with respect to predation risk from diurnal aerial predators whose visualization declines with falling light intensity (Reymond, 1985). For cave dwelling bats, some of those bats will venture in between the cave entrance to sample the light intensity outside. When the light level reached a threshold level, all of the bats left the cave to forage. Yapa et al. (2005) suggested that the onset and the end of flight activity in three bat species were closely related with the light intensity prevailed at the cave entrances. Even though they are sympatric living in the same roost, the different species of bats have different threshold levels for light intensity. For example, *Rhinolophus rouxii* has a tolerance for higher light intensity than *Hipposideros lankadiva* and *R. leschenaultia*, so it can emerge earlier than *H. lankadiva* and *R. leschenaultia*.

However, several factors are referred to have influences on bat emergence only in some regions. Subbaraj and Chandrashekaran (1977) suggested that ambient temperature may directly influence the emergence behavior in temperate bats but not in tropical bats. For heterothermic bat species in temperate regions, ambient temperature plays a crucial role as a factor controlling seasonal timing and course of hibernation (Erkert, 1982). Laufens (1973) reported the earlier emergence of heterothermic bats in the day with high ambient temperature. In addition, Shirley et al. (2001) revealed that ambient temperature on previous day is crucial in determining the number of *Myotis. daubentonii* emergence, and suggested that the bats used ambient temperature as a cue of prey abundance.

In the present study, precipitation has no influence on the onset of emergence in Lyle's flying foxes. This agrees with many studies on frugivorous bats. Welbergen (2006) found that precipitation did not impact the onset of colony-wide emergence in *P. poliocephalus.* Thies et al. (2006) mentioned that light or moderate rain did not interrupt flight activity in *C. castanea*, a small fruit-eating bat. However, several studies mentioned about the influence of rain on emergence time of insectivorous bats. Entwistle et al. (1996) found that heavy rain delayed emergence time in *P. auritus.* In 1996, Kunz and Anthony reported that heavy precipitation delayed the onset of emergence, and prolonged the duration of emergence in *M. lucifugas*. While light rain appeared to have little effect on the onset of emergence in the bat species. From personal observation, Lyle's flying foxes usually cover their body and head by wing membrane during a medium or heavy rain in daytime.

The above-mentioned is about the influence of environment factors on emergence time in bats. However, there is also the study that mentioned the effect of social interaction on bat emergence behavior. Marimuthu et al. (1981) reported that social cues such as noise of the wingbeats of the first bats to leave the cave, active vocal signaling and specific pheromones released when they prepare to leave for foraging can serve as crucial cues to out-flight time in cave-dwelling bat, *H. speoris.*

5.1.4 Lunar cycle effect the onset of colony-wide emergence

Similar to other studies on fruit-eating bats, the results from the present study revealed that lunar phase has no influence on the onset of emergence in Lyle's flying foxes. However, this contrasts sharply with many studies on insectivorous bats emergence. Lang et al. (2006) reported that *L. silvicolum* emerged from their roost earlier around full moon than new moon night. They suggested that lunar phase has indirect effect on insectivorous bat emergence because insect activity level is depended on moon light. In new moon night, insects were active throughout the night, whereas the peaks of insect activity occur only at the beginning and the end of night around full moon. Hence, insectivorous bats need to emerge early in full moon rather than new moon night in order to be in foraging areas at the period of highest insect activity. Jones and Rydell (1994) suggested that insectivorous species usually begin their emergence before sunset, thus maximizing predation risk from aerial predators, in order to take advantage of the peaks in insect activity at dusk. That is likely to be a trade-off between resource availability and predation risk.

Contrast to insectivorous bats, frugivorous bats feed on fruit which has no influence from light emitted by the moon, so they can emerge later in order to minimize the risk of predation at dusk. Thies et al. (2006) revealed that the emergence time and the time spent in flight of *C. castanea* have not been affected by moonlight. However, some fruit-eating bats minimize predation risk in the bright night during full moon as shown by Elangovan and Marimuthu (2001). They found that the flight activity during foraging of *C. sphinx* was higher during the phase of new moon compared to the phase of full moon night. The restriction of flight activity during the bright nights is normally interpreted as an adaptation to keep away from nocturnal predators.

5.2 Individual emergence

Parturition period of Lyle’s flying fox during March and April, suggests that their pregnancy period occurs between November and February because flying foxes have four gestation months. And they have lactation period during March and July because juvenile bats are independent and wean at about four months from birth.

This study revealed that Lyle's flying foxes experience larger change in emergence time during reproductive period. In pregnancy period, the female bats emerged later as gestation progressed. The similar emergence patterns have been observed by Duverge et al. (2000). They reported that females of greater horseshoe bats, *Rhinolophus ferrumequinum* and lesser horseshore bats, *R. hipposideros* emerged gradually later as gestation proceeded. The late evening emergence of pregnancy can be explained by the enlargement of wing loading, which might effects flight performance and increased risk of aerial predator (Hughes and Rayner, 1993).

It was surprising that not only female of Lyle's flying foxes prolonged their emergence time during reproductive period, but other members within group including adult males, non-lactating females and juveniles also extended their emergence time. Some male bats that remained at roosting site attempted to approach and mate with females when possible (personal observation). Males possibly delayed their emergence to increase their opportunity for mating with females. Welbergen (2006) suggested that the harem-holding males adjusted their emergence time to the time when their last female member had left from the roost in order to reduce mating opportunities and cuckoldry by other males. While the female bats adjusted thier emergence time related to their body condition. This supports the hypothesis that, male and female have the differences in factors that restrict their reproductive success (Trivers, 1972). Under this hypothesis, male reproductive success is limited by ability to attract or arouse females, while female reproductive success does not appear to be restricted by ability to attract males, but it appears to be primary limited by resource available

Due to less developed flight skill and mother's milk supporting in energetic demands, juvenile bats would be expected to emerge later than adults. This hypothesis was supported by many studies in *P. poliocephalus* (Welbergen, 2006), in *E. nilssonii* (Duverge, et al., 2000) and in *M. lucifucus* (Kunz and Anthony, 1966). Furthermore, an advantage of later emergence not only reduce the risk of predation but also minimize acoustic clutter from adults that interrupt the development of flight and echolocation skills of juveniles in insect-eating bats (Kunz and Anthony, 1966). Unexpectedly, the present study found that there was no obvious difference in emergence times between juveniles and adults of Lyle's fling foxes. The earlier emergence of young after the early stage of volancy development were observed in *Tadarida brasiliensis mexicana* (Lee and McCracken, 2001) and in *Desmodus rotundus* (Wilkinson, 1985). It is possible that the flight performance increased rapidly with age, and the young bats may adjust their emergence to follow their mother when foraging. Because information exchange about feeding area mostly occur between mothers and their offspring. Nelson (1965) mentioned that bats of genus *Pteropodidea* adjust their emergence time to that of the other members within the group. The roost group members may emerge and forage together within the same feeding site.

Interestingly, this study found the difference pattern of emergence time in lactating female which never been reported in previous study. During the first two months of lactation period, lactating females of Lyle's flying foxes emerged so later than adult males, non-lactating females and juveniles that contrast with many studies on individual emergence. For example, Welbergen (2006) studied the individual emergence time of grey-head flying fox, *P. poliocephalus,* and found the earlier emergence of lactating females. The similar pattern has been observed by Duverge et al. (2000), which the emergence time of lactating females become earlier in greater horseshoe bats, *R. ferrumequinum*, and lesser horseshore bats, *R. hipposideros*, as lactation proceeded. During lactation, metabolizable energy intake (MEI) of lactating females in fruit-eating bat, *Rousettus aegyptiacus* increased by 80 %, compared to that of nonreproductive females, resulting in higher energetic demands, and consequently, higher food consumption (Korine et al., 2004). Early emergence of lactating females in many bat species will benefit to the food availability, but maximize the predation risk at dusk. However, this kind of trade-off adaptation has not yet been observed in Lyle's flying foxes, and further investigation should be emphasized during lactation period.

5.3 Daytime behavior

It is well-known that flying foxes are active at night for foraging as nocturnal species, but daytime is also surprisingly busy for these animals. During the day, Lyle's flying foxes always performed many activities such as sleeping, grooming, wing spreading, movement, wing flapping, aggression, mating/courtship and nursing/maternal behavior. However, the data from this study revealed that these activities were affected by time of day and by time of year, as follows.

5.3.1 Sleeping

Sleeping is the most common behavior in Lyle's flying foxes. The percentage of sleeping behavior in bat varied significantly during the day and throughout the year. In common, sleeping occurred mostly in late morning and late afternoon to the evening. This pattern is consistent with the study by Connell et al. (2006). They showed that sleeping in *P. poliocephalus* was most common in middle of the day and late afternoon. The highest percentage of sleeping activity during that time may indicate that the flying foxes are sleeping in order to preserve their energy before nightly emergence. In addition, Funakoshi et al. (1991) suggested that the major period of sleeping in *P. dasymallus* occurred in the first half of the day. The sleeping activity in the first half of the day may indicate that bats are resting after their foraging at night.

For monthly variation, the highest percentage of sleeping in Lyle's flying foxes occurred in January and July, while the lowest percentage of this behavior occurred in April. From the analysis of relationship between sleeping activity and weather variables analysis, sleeping activity was negatively correlated with ambient temperature. The activity tends to be reduced during both hot seasons, and it tends to increase during cold season. The results agreed with the study by Funakoshi et al. (1991) who studied on seasonal change in activity of *P. dasymallus*. They suggested that the time spent for sleeping activity in *P. dasymallus* was closely correlated with ambient temperature. Flying foxes spent most of their time sleeping during the months when ambient temperatures were low. During adverse environmental condition or food shortage, bats usually enter a torpor state by reducing their activity level, body temperature and metabolic rate in order to conserve fat storage for future energy deficiency (Zubaid et al., 2006). This can explain why bats often spend more time sleeping in the cold months (Ambient temperature ranged from 21-32°C) rather than in hot months. (Ambient temperature ranged from 24-36 °C).

5.3.2 Grooming

Grooming behavior is a common behavior in Lyle's flying foxes which can be seen throughout the day, but this behavior changed significantly during the observation period. During daytime, grooming activity in Lyle's flying foxes usually occurred in early morning. The similar patterns have been observed in other bat species including both frugivorous bats and insectivorous bats. Grooming activity in fruit-eating bat, *P. poliocephalus* occurred more frequently in the morning (Connell et al., 2006). Burnett and August (1981) found that insect-eating bat, *M. lucifugus* often groomed themselves in the morning when they return from foraging in order to clean their wing membranes. And they groomed again before nightly emergence, corresponding with our study on emergence behavior in Lyle's flying foxes, we noticed that Lyle's flying foxes usually groomed themselves before emergence. This may indicate that bat grooming in the evening is to prepare their night departure.

During the year of study, the highest percentage of grooming in Lyle's flying foxes occurred in August and October which was in rainy period, while the lowest percentage of this behavior occurred in March and April which was in hot-dry period. This corresponded with the relationship between grooming activity and weather variables, as the grooming activity was positively correlated with relative humidity.

Hence, the grooming activity in Lyle's flying foxes tends to increase in rainy season rather than in dry season. This can be explained by ectoparasite density difference between wet and dry seasons. Bat ectoparasites density is higher in wet season more than in dry season (Linhares and Komeno, 2000). Ter Hofstede and Fenton (2005) suggested that grooming is a behavioral strategy which bats use to reduce the ectoparasite density. So, bats with high ectoparasite densities need to scratch more than those with low ectoparasite densities. These results indicate that grooming behavior is affected by season.

The present data revealed that self-grooming in Lyle's flying foxes was different among sexes. Adult females had more frequency in self-grooming during the day than those in adult males. This can be explained by the behavioral adaptation difference between males and females. Czenze and Broders (2011) suggested that the prevalence and density of ectoparasite was affected by roost group size of bats. Male bats roosting solitary tended to have ectoparasite density less than the males roosting with a large number of females. This may be behavioral adaptation to reduce the ectoparasite prevalence in male bats.

In addition, Pearce and O’Shea (2007) reported the significant differences between adult and juvenile *of E. fuscus* in prevalence and intensity of ectoparasites. Ectoparasites were normally more prevalent and had higher intensities on adult bats rather than juvenile bats. As juveniles are sparsely furred, this may allow parasite removal by grooming to be more effective. Because of relatively larger skin surface area of adult bats, they may allow more ectoparasite species and ectoparasite density. Presley and Willig (2008) reported that greater host body size may reduce interspecific and intraspecific competition of ectoparasites. Furthermore, Rudnick (1960) suggested that adult bats have experienced longer lifes than juvenile bats, which caused adults to be more exposed to infestations rather than juveniles. So, adult bats with high ectoparasite density need to groom themselves more frequently than juveniles with low ectoparasite density.

In contrast to self-grooming, social grooming was found to serve a significant function rather than cleaning and parasite control in species with complex social behavior such as bats. Nelson (1965) suggested that social grooming in genus *Pteropus* can establish social bonds, especially between mother – offspring pairs or between group members. Wilkinson (1985) studied the grooming behavior in the common vampire bat, *Desmodus rotundus,* and found that there is positive relationship between social grooming and food sharing in vampire bats. Food sharing by regurgitation usually occurred after the donor was groomed by its partner.

5.3.3 Wing spreading

Wing-spreading is a common behavior in Lyle's flying foxes which can be seen throughout the day. However, this behavior changed significantly during the observation period. During daytime, wing spreading was frequency obseved in morning and but not in evening. That pattern was similar with the aggressive pattern in Lyle's flying foxes. This may indicated that wing spreading may be related with aggressive behavior. Connell et al. (2006) suggest that wing spreading was related with aggression behavior in *P. poliocephalus.* Since these behaviors occurred more frequently when the bats were performing peak in mating and courtship behavior.

For year-round activity, wing spreading patterns in Lyle's flying foxes differed significantly between times of the year which was highest in August and October (rainy season), and was lowest in March and April (hot-dry season). This results agreed with the analysis of relationship between wing spreading activity and weather variables, the wing spreading activity was weakly positively correlated with relative humidity. Hence, this activity tends to increase during rainy season rather than in hot-dry season. Sellers (1995) suggested that wing spreading is one of the most characteristic features of the behavioral repertoire in avian species which were used for wing-drying when their plumages were wet. This function might be used in bats also, especially in wet condition.

According to the present data, this behavior was mostly observed in males rather than females of Lyle's flying foxes as suggested by Connell et al. (2006). They observed that wing spreading was often used by male bats when they wanted to protect their territories which were mostly established in the breeding period. From personal observation, Lyle's flying foxes always performed wing spreading and wing shaking when they wanted to discourage other bats from landing in their territories. In addition, Markus (2002) reported that the function of wing spreading in *P. alecto* is to serve as a threat display.

5.3.4 Movement

Movement in tree and climbing along branch were behaviors which occurred less frequently in Lyle's flying foxes, corresponding with the study in *P. poliocephalus.* Connell et al. (2006) also suggested that movement in tree was rare occurrence behavior in *P. poliocephalus.* However, this behavior changed significantly during the observation period. During the day, movement in tree or climbing along branch occurred mostly in early morning and noon, but less frequently in late afternoon. The least movement activity in late afternoon corresponded to the peak in sleeping at this time of day. In early morning, Lyle's flying foxes located their territories or appropriate perches for resting after their foraging (personal observation), and hence resulted in the high movement activity. Boonneung (1977) reported that Lyle's flying foxes usually climbed along branch to escape the sun light during noon, suggesting that movement activity may be affected by ambient temperature.

However, from the present study, movement activity in Lyle's flying foxes was not associated with ambient temperature, but it was related with relative humidity. Neuweiler

(2000) suggested that flying foxes of the genus *Pteropus* spent daytime roosting on the tree, which exposed to sunlight, did not move to another place when ambient temperature begins to rise in the middle of the day because they have potential strategies to control their body temperature efficiently. While microchiroptera bats roosting on tree have clever ways to avoid the sunlight in middle of the day by crawling into lower branch to avoid overheating.

Movement activity in Lyle's flying foxes was exhibited by both sexes, but this activity has been exclusively found in males rather than in females. According to the observations, males of Lyle's flying foxes often moved to approach the female, or moved to search for receptive females which were ready to breed, as suggested by Boonneung (1977). In addition, Nelson (1965) revealed that flying foxes usually moved when they were disturbed.

5.3.5 Wing flapping

Wing flapping is common behavior in Lyle's flying foxes which varied significantly during the day. Wing flapping mostly occurred in noon and afternoon, while this activity had not been found in early morning or in evening. The highest percentage of wing flapping in Lyle's flying foxes occurred in April, when ambient temperature was high, while the lowest percentage of this behavior occurred in January and February when ambient temperatures were lower. The results indicated that the relationship between wing flapping behavior and ambient temperature as wing flapping tended to increase during hot periods.

In tropical zone, flying foxes roosting on the tree might be exposed to sunlight or high ambient temperature in the middle of the day, and they also lack sweat glands to balance their body temperature and ambient temperature by evaporation (Robinson and Morrison, 1957). Hence, they need to have behavioral strategies in order not to overheat. Ochoa-Acun and Kunz (1999) demonstrated that wing flapping behavior is an important role of thermoregulation in *P. hypomelanus* as this species tended to increase the frequency of wing-fanning behavior when ambient temperature reached a maximum at about 36 °C. The range of the thermoneutral zone in large flying foxes lies between 24 °C - 35 °C (Neuweiler, 2000). In addition, salivation and body licking appeared to be the last effective way in respond to overheating (Ochoa-Acun and Kunz, 1999).

Unlike flying fox in genus *Pteropus,* microchiroptera avoid intense heat through day roost selection. They roost in cave or cracks in rocks which provide an ideal environment, stable temperature in the thermoneutral zone (Neuweiler, 2000). Leitner and Nelson (1967) reported that wing flapping behavior has not been found in *Rousettus aegyptiacus* and *Macroderma gigas,* both cave-dwelling bats. In temperate zone, wing flapping rarely occurs in *P. poliochephalus* due to moderate temperature (Connell et al., 2006).

5.3.6 Aggression

Aggression is common behavior in Lyle's flying foxes which varied significantly during the observation period. Peak in aggression activity had been obviously seen in the morning, corresponding with the peak in mating/courtship behaviors. For monthly variation, the maximum percentage of aggression in Lyle's flying foxes occurred in January and February, corresponding with the peak in mating/courtship behaviors. The minimum percentage of this behavior occurred between September and November and between June and July which corresponded to the reduction in mating/courtship behaviors. The results demonstrated the relationship between aggression and mating/courtship behaviors.

Reeder et al. (2005) suggested that animal behavior involves several factors, including the hormone regulation and the environment. In term of hormonal regulation, the sustained elevations of glucocorticoid in *P. vampyrus and*

P. pumilus were considered a mark of the stress response, and were most pronounced in the breeding males who attempted to compete or fight for mating access during breeding season. Furthermore, Nelson (1965) revealed that males of flying foxes became more aggressive as they began to establish their territories, and was less intense when the territories were learned. Ortega et al. (2008) reported that dominant males of *Artibeu jamaicensis* displayed defensive behavior by wing flicking, engagement in short chases, and attempting to bite satellite males to protect their harem, but did not perform aggressive displays to subordinate males in the group. The presence of subordinate males reduced the number of satellite males which invaded the roosting site.

For weather influences, this study found that aggression activity was weakly correlated with relative humidity. However, we are unable to interpret such a relationship because there are no other investigations to confirm or contradict this result.

The present study suggested that the sexes have influence on aggressive behavior in Lyle's flying foxes as female bats performed higher than male bats in aggression. This results contradict with the study by Nelson (1965). He suggested that male of flying foxes is more aggressive than females, especially in breeding season. From personal observation, adult of both sexes were more aggressive than juveniles, which can be explained by hierarchical status. Flying foxes varied in hierarchical status according to their sizes (Ortega et al., 2008). So aggression behavior was less in juveniles, who had not reached the full body size, and tended to avoid fighting with adults.

5.3.7 Mating and courtship

During the observation period, males of Lyle's flying foxes attempted to copulate with females by mutual grooming or by licking the genital area of females. However, the frequency mating/courtship activity seems to vary between time of the day, which was highest in the morning and in the evening, as suggested by Boonneung (1977). Nevertheless, these contradicted with the study by Connell et al. (2006). They suggested that the highest percentages of mating/courtship activity in *P. poliochephalus* have been found in the morning, and then declined continually to the lowest in late afternoon. This can be explained by the variation in testosterone secretion during the day. It is well-known that testosterone, working to increase sexual desire has a circadian rhythm which varies between times of day (Mazur and Booth, 1998). Reeder et al. (2006) studied the testosterone secretion in Malayan flying foxes (*P. vampyrus*), and revealed that testosterone levels in males tended to reduce steadily during the day to the evening. However, there was no information available on testosterone secretion in Lyle's flying foxes which would be a crucial evidence for interpreting the result from present study.

Males of Lyle's flying foxes attempted to copulate with females throughout the year, but the peak in mating/courtship activity occurred in August, January and February. Breeding season of Lyle's flying foxes are ranging between November and August (Boonneung, 1977). The mating effort of males in non-breeding season may facilitate harem maintenance. Melvillea et al. (2012) demonstrated that testicular volume, body weight, testosterone secretion and sperm quality of males *P. alecto* was highest at the beginning of mating season in order to support the peak mating activity, suggesting that sexual behavior involves the regulation of hormonal system.

Reproductive activity in bats of genus *Pteropus* restricted to mating territories, which was established by dominant male before breeding season (Welbergen, 2006; Nelson, 1965). The territories containing a group of females associated with a single male, referred as “harem’’ (Neuweiler, 2000). During mating season, dominant males became more aggressive by wing flicks, and attempted to bite another male who invaded their territories that cause more energy expenditure (Ortega et al., 2008). However, the group organization in bat species obviously provided reproductive success to the dominant male because all of the newborn in the group inherited the genes of the dominant male (Neuweiler, 2000).

From personal observation, mating/courtship activity was rarely observed in juvenile of Lyle's flying foxes. Since juveniles or immature bats have not yet reached full size or sexual maturity, having underdeveloped sexual organs, until they are two years old (Plowright et al. 2008).

5.3.8 Maternal care

The neonates of Lyle’s flying foxes were altricial, requiring feed or nurse from mothers. Hence, mothers need to protect and rear their offsprings from birth until they were weaned to facilitate rapid development of young. During the first month, the youngs could not perch independantly and need to attach to mother’s chest which facilitated a stable body temperature (Nelson, 1965). Mothers always groomed their offspring to clean the fur and wing membranes of their young. In addition, maternal grooming helped to establish social bonds between mothers and their young (Kunz and Hood, 2000).

When the age of youngs were about three to four weeks, lactating females of Lyle’s flying foxes leave their young at roosting site before emergence because the youngs were too large to be carried while foraging. However, lactating females always visited to the roost during night. Mclean and Speakman (1997) observed the highest number of nightly returns to the roost made by lactating females of *P. auritus* in early lactation, and the number of those declined as lactation proceeded. This indicated that the maternal care declined as the young grew. After return to colony, mothers were able to recognize their offspring by tactile, acoustic and olfactory senses (Kunz and Hood, 2000).

Bat of genus *Pteropus* were considered to be polygynous species, one male mates with more than one female (Nelson, 1965). So the paternal care was provided by females only. Nevertheless, the males of some bat species defend their territories or harem, especially in the period which pregnant females and young are present, and the effort of males could be included as paternal care (Kunz and Hood, 2000).

In addition, Boonneung (1997) suggested that Lyle's flying foxes usually gave birth and had a number of newborns during March and June which was in hot season and early rainy season because such a period had abundant food available for feeding their young. Low number of newborns was observed during July to October, and heavy rain in that period was considered to be an obstacle for nursing youngs. From her study, none of newborn was found from late October until February which was in cold-dry season possibly because of food shortage which was not enough to support energetic demands of lactating females and their young.

CHAPTER VI
CONCLUSIONS AND RECOMMENDATIONS

6.1 Conclusions

6.1.1 Colony-wide emergence

Lyle's flying foxes are nocturnal feeder. They began their emergences by swarming and calling above the colony on average ten minutes after sunset at light level of 15 lux. Then they emerge to forage on average 18 minutes after sunset at light level of 5 lux. The emergence after sunset could be reflected from the trade-off between predation risks and foraging needs.

The duration of colony-wide emergence in Lyle's flying foxes varied significantly throughout the year which was longest in parturition and early lactation period. During these periods, the flying foxes changed their emergence pattern by prolonged emergence time and proceeded emergence gradually with the small group of individuals. Most bats prolonged emergence time were lactating females with newborn attracted. Later emergence may be resulted from reduction in flight performance of lactating-females with juveniles attached. So the maternal care might affect flight performance and delay night departure of lactating females, which prolonged the duration of colony-wide emergence between these times of the year.

The environmental factors that explained a significant variation in the onset of the colony-wide emergence time were sunset time and relative humidity. The emergence activity in bats may accompany with illumination during sunset. The relative humidity also associated with other physical factors that cause reduction of light penatrating from the sun. In general, nocturnal species reduce predation risk by foraging at low light intensity when visualization of diurnal predator decline.

Contrast to insectivorous bats, difference in the onset of colony-wide emergence time as well as the colony-wide emergence time between full moon and new moon nights was not found in Lyle's flying fox which is frugivorous bat.

6.1.2 Individual emergence

The effect of reproductive state on emergence time of Lyle's flying fox was found in this study. Reproductive females prolonged their emergence times during late pregnancy and lactation periods. The later emergence during pregnancy and lactation can be reflected from the enlargement of wing loading, which has been effect a flight performance and increase risk of predation in reproductive female. However, not only reproductive females prolonged their night departure, but adult males, non-reproductive females and juveniles also prolonged their out-flight also. Different sexes and status of bats may have different reasons to emerge later during that times. Males possibly delayed their emergence to increase reproductive success. Non-reproductive and young bats may adjust their emergence to that of the other members within the group because information exchange about feeding site mostly occur between roost-group members, and it is possible that they forage together within the same feeding areas.

6.1.3 Daytime behavior

Lyle's flying fox performed all of daytime behaviors differently between times of day and times of the year. However, there were only four behaviors: sleeping, grooming, wing flapping, mating/courtship, which had obvious different pattern of occurrence at various times. Sleeping, grooming and mating/courtship behaviors mostly occur in morning, late afternoon and evening, while wing flapping usually occurred in noon and early afternoon. The bats spend most of daytime to sleep during cold months, and they mostly groomed themselves during rainy months. The peak of bat with wing flapping was found in summer, whereas the highest levels of mating/courtship occurred in cold months. So, the present study can conclude that times of day and seasons are crucial factors that influence on daytime behaviors of Lyle's flying foxes because living on trees provide them experience the weather fluctuation during the day and seasons.

In addition, sex has influenced on daytime behavior of Lyle’s flying foxes, especially in wing spreading, movement, mating/courtship and maternal care behaviors. Wing spreading, movement along branch and mating/courtship has been exclusively found in males rather than females, while maternal care was exhibited by female only. This can be explained by hypothesis that male and female have the difference in goal of reproductive success. The goal of reproductive success in male is to pass thier genes onto the next generation by mating with several females. Wing spreading, movement and courtship displays might be strategy that the male used for female attraction. The goal reproductive success in female is to increase offspring survival. Maternal care may have evolved as a strategy to maximize offspring survival.

6.2 Recommendations

6.2.1 For further understanding about the emergence behavior of Lyle’s flying fox, more detailed study in emergence and foraging behavior at individual level should be conducted using satellite telemetry, especially in reproductive period.

6.2.2 The hormonal variation between times of day and time of the year should be investigated because some behaviors may respond to the change in physiological factors.

6.2.3 Parental care in Lyle’s flying foxes should be observed for further understanding.

6.2.4 In many areas of Thailand, Lyle’s flying fox is vulnerable species due to hunting by local people, and roosting sites are declining due to habitat change by humans. Hence, habitat management should be considered in advance to satisfy conservation.

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APPENDICES

APPENDIX A

Daytime behavior

Percentage of bats performing in each behavior type during the day in August 2010 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Aggression	Mating/Court ship	Maternal care
6:01-7:00	26.00±4.000	59.33±5.696	3.00±1.000	6.67±.667	.00±.000	2.67±.333	1.67±.882	.67±.333
7:01-8:00	51.67±4.096	24.33±2.333	4.00±1.528	5.00±1.000	.00±.000	3.67±2.028	10.00±1.155	1.33±.882
8:01-9:00	40.33±4.256	18.33±4.256	8.67±4.256	3.33±4.256	.00±4.256	6.33±4.256	18.67±4.256	4.33±4.256
9:01-10:00	47.33±4.333	18.00±1.000	7.00±.577	3.67±.333	6.33±1.667	4.33±.333	9.33±1.764	4.00±.577
10:01-11:00	53.00±4.000	18.00±2.887	4.00±1.528	3.67±1.764	3.33±1.333	4.00±2.000	12.00±1.528	2.00±.577
11:01-12:00	33.00±2.646	6.67±2.186	5.00±1.528	5.33±.333	38.67±6.960	3.00±.577	6.00±1.155	2.33±.667
12:01-13:00	12.67±1.333	4.67±1.202	5.00±.000	5.67±1.202	67.67±1.202	3.33±1.453	.67±.667	.33±.333
13:01-14:00	45.33±2.333	8.67±2.603	5.33±.882	2.33±.667	32.67±3.930	1.67±.882	1.33±1.333	2.67±1.453
14:01-15:00	54.00±1.732	12.00±2.082	6.67±.333	4.67±.667	8.00±2.082	4.33±.882	6.00±3.055	4.33±1.856
15:01-16:00	57.67±3.383	8.67±.333	8.67±1.764	4.67±.882	3.67±1.856	4.00±.577	11.00±3.786	1.67±.882
16:01-17:00	67.00±7.937	9.33±2.028	5.67±1.333	2.67±1.764	.67±.667	3.67±1.856	8.67±4.667	2.33±.333
17:01-18:00	93.67±1.667	1.67±.882	2.67±.333	.00±.000	.00±.000	.00±.000	1.33±1.333	.67±.667

Percentage of bats performing in each behavior type during the day in September 2010 (Mean±SE)

(data obtained from four observation days)

Time of day	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Agression	Mating/Courtship	Maternal care
6:01-7:00	49.25±3.728	35.25±4.270	1.75±.854	2.75±.629	.00±.000	2.25±.750	4.75±1.601	4.00±1.581
7:01-8:00	59.50±9.023	19.25±3.591	4.50±.866	2.00±.577	.00±.000	3.25±1.887	10.00±3.240	1.50±.645
8:01-9:00	44.00±2.708	15.25±1.493	8.25±1.436	5.00±.707	.00±.000	5.75±.854	16.25±1.750	5.50±.645
9:01-10:00	48.25±1.250	20.25±1.250	11.00±1.414	3.50±1.323	1.50±1.500	2.00±1.155	10.25±.250	3.25±.250
10:01-11:00	60.00±1.871	13.25±.750	3.75±1.031	4.50±1.190	9.50±2.901	2.00±.000	5.00±3.000	2.00±.408
11:01-12:00	41.75±6.129	16.25±1.750	4.25±.479	2.75±1.181	31.50±4.518	2.25±.250	.00±.000	1.25±.750
12:01-13:00	15.75±.854	7.25±1.109	3.50±.289	4.00±.408	63.50±1.323	5.00±1.633	.00±.000	1.00±.408
13:01-14:00	33.25±10.250	6.75±1.652	3.00±1.780	1.75±.629	52.50±14.379	1.00±.577	.00±.000	1.75±.750
14:01-15:00	52.00±6.721	10.75±.629	5.25±1.750	4.25±.250	24.00±10.255	1.00±.577	.50±.500	2.25±1.315
15:01-16:00	66.50±2.958	7.50±.866	5.25±3.198	1.25±.946	3.75±2.250	2.00±.816	11.50±1.708	2.25±.479
16:01-17:00	70.50±7.533	9.25±3.521	3.75±1.601	.75±.250	.00±.000	1.00±.707	10.25±3.224	4.50±.645
17:01-18:00	76.75±11.600	15.75±8.538	1.25±.629	1.50±.866	.00±.000	.00±.000	4.00±3.082	.75±.750

Percentage of bats performing in each behavior type during the day in October 2010 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Agression	Mating/Court ship	Maternal care
6:01-7:00	48.50±2.327	32.50±4.291	4.25±1.031	5.00±.408	.00±.000	1.75±1.031	4.25±.750	3.75±.946
7:01-8:00	54.75±7.273	13.0±3.488	4.50±.289	3.00±1.472	.00±.000	5.75±1.315	17.75±2.394	1.25±.479
8:01-9:00	64.25±3.198	7.25±1.315	7.50±1.756	2.75±1.031	.00±.000	5.00±.577	11.00±3.000	2.25±.250
9:01-10:00	70.50±7.599	11.75±3.119	7.00±.707	3.75±.854	.00±.000	2.50±.957	2.75±2.136	1.75±.479
10:01-11:00	59.50±8.846	10.50±3.500	6.75±.629	6.75±1.315	13.75±5.452	1.00±.577	.00±.000	1.75±.854
11:01-12:00	40.50±6.131	17.50±1.443	7.751.031±	4.00±1.155	27.75±7.064	1.00±.577	.00±.000	1.50±.645
12:01-13:00	23.75±5.105	8.00±1.291	4.75±.250	6.00±.707	54.5±06.564	1.00±.408	.00±.000	2.00±.816
13:01-14:00	32.00±3.240	11.00±1.472	6.25±.854	1.25±.250	47.00±4.416	1.00±.577	.00±.000	1.50±.645
14:01-15:00	47.75±11.807	5.75±1.652	3.50±1.652	2.75±1.031	37.75±9.169	.25±.250	.50±.500	1.75±.629
15:01-16:00	85.75±6.303	3.50±1.500	2.00±.816	.25±.250	3.00±1.915	.50±.500	2.50±2.500	2.50±1.190
16:01-17:00	90.75±3.497	4.00±1.472	2.25±.854	.00±.000	.00±.000	.00±.000	2.50±1.500	.50±.289
17:01-18:00	36.00±2.345	44.00±1.915	.00±.000	8.00±1.683	.00±.000	2.00±1.155	6.50±1.258	3.5±0.500

Percentage of bats performing in each behavior type during the day in November 2010 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Agression	Mating/Courtship	Maternal care
6:01-7:00	34.00±4.223	38.55±3.750	2.00±.000	4.00±.707	.00±.000	6.00±.707	13.5±1.109	2.00±.408
7:01-8:00	64.25±6.210	15.50±3.797	3.25±.479	2.75±.479	.00±.000	4.00±.913	9.25±1.181	1.00±.707
8:01-9:00	71.50±6.837	12.00±2.273	2.50±.957	2.50±.500	.00±.000	2.25±.629	8.50±3.379	.75±.750
9:01-10:00	80.00±4.637	5.75±1.974	2.50±.957	3.00±1.080	.00±.000	3.00±.707	5.50±2.327	.25±.250
10:01-11:00	90.00±5.370	3.75±1.797	1.25±.946	1.25±.946	.00±.000	.50±.289	2.50±1.190	.75±.750
11:01-12:00	69.75±1.109	8.75±3.614	1.75±.750	2.00±.707	14.50±3.500	1.75±.250	1.50±.866	.00±.000
12:01-13:00	41.00±17.944	1.00±.408	1.25±.750	1.75±.629	54.50±17.628	.50±.500	.00±.000	.00±.000
13:01-14:00	40.50±18.209	2.50±.289	.75±.250	1.00±.707	54.50±19.081	.75±.479	.00±.000	.00±.000
14:01-15:00	36.00±15.530	1.00±.707	.75±.479	2.00±.707	56.00±17.753	2.75±1.377	1.50±.957	.00±.000
15:01-16:00	39.25±9.801	4.00±1.225	1.75±.854	2.25±.854	46.50±12.926	2.75±1.601	3.00±.577	.50±.289
16:01-17:00	65.50±6.357	7.25±1.315	4.00±1.080	1.00±.577	8.75±4.308	5.00±.577	8.25±.577	.25±.250
17:01-18:00	93.75±1.493	3.50±.866	.75±.479	.50±.500	.00±.000	.00±.000	1.50±.957	.00±.000

Percentage of bats performing in each behavior type during the day in December 2010 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Agression	Mating/Courtship	Maternal care
6:01-7:00	37±5.393	32.5±3.092	2±0.408	4.5±0.629	.00±.000	7.0±1.19	16.50±2.25	0.50±0.25
7:01-8:00	63.75±9.34	18±6.988	2.25±0.479	3±0	.00±.000	3.75±1.25	8.75±2.287	0.5±0.289
8:01-9:00	71.25±8.138	10.75±2.689	4.25±1.436	3.25±1.315	.00±.000	3.25±1.25	6.75±1.887	0.5±0.5
9:01-10:00	74.5±4.628	9.75±0.479	3.75±0.75	2±0.913	.00±.000	3.5±0.5	5.75±2.81	0.75±0.75
10:01-11:00	85±1	4.75±0.479	1.75±0.25	2±0.408	.00±.000	2.5±0.645	4±1.291	0±0
11:01-12:00	73.5±6.551	8.25±2.25	2.25±0.946	2.5±1.19	11±6.285	1.75±0.854	0.75±0.479	.00±.000
12:01-13:00	40.75±20.357	1.25±0.629	0.75±0.25	0.25±0.25	56.25±20.381	0.75±0.75	.00±.000	.00±.000
13:01-14:00	31.5±14.292	2±0.707	0.5±0.289	0.25±0.25	65±15.519	0.5±0.5	0.25±0.25	.00±.000
14:01-15:00	37.75±16.418	1.5±0.957	0.25±0.25	1±0.707	58.75±17.269	0.5±0.5	0.25±0.25	.00±.000
15:01-16:00	37.5±7.9	4.25±1.181	1.5±0.866	3.75±2.462	46±10.173	4±2.16	2.75±0.946	0.25±0.25
16:01-17:00	52.25±14.902	11.5±5.008	4.5±2.398	3±1.472	10.75±5.764	4.25±2.016	12.75±7.087	1±0.707
17:01-18:00	91.5±1.323	3±1.354	0.75±1.354	0.25±0.25	.00±.000	1.5±0.5	3±1.915	.00±.000

Percentage of bats performing in each behavior type during the day in January 2011 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Agression	Mating/Courtship	Maternal care
6:01-7:00	42.00±2.345	33.5±2.562	4.50±.750	4.50±.479	.00±.000	2.5±.479	12.00±.408	1.00±.500
7:01-8:00	48.50±2.255	17.25±1.601	5.25±.854	4.25±1.315	.00±.000	6.25±1.652	17.50±1.190	1.00±.408
8:01-9:00	52.00±1.080	15.25±.854	6.75±1.109	4.25±.250	.00±.000	6.00±1.291	15.00±1.080	.75±1.080
9:01-10:00	67.50±.957	7.25±.629	4.75±.854	2.25±.479	.00±.000	6.50±.500	11.25±.750	.50±.289
10:01-11:00	62.75±1.797	12.75±1.652	4.00±.707	1.75±.854	2.00±2.000	6.75±.854	10.00±.577	.00±.000
11:01-12:00	62.50±2.217	15.25±1.797	4.50±.645	1.25±.479	3.25±1.109	4.50±.500	8.75±.500	.00±.000
12:01-13:00	70.00±2.345	7.00±2.345	3.00±.408	2.25±1.031	9.00±1.915	4.00±.707	4.75±1.315	.00±.000
13:01-14:00	86.25±2.175	2.50±.289	1.75±.479	1.50±.645	5.25±1.931	1.50±.866	1.25±.866	.00±.000
14:01-15:00	80.00±6.557	3.25±1.109	1.00±.408	1.50±.645	10.25±3.473	2.25±.854	1.50±.645	.25±.250
15:01-16:00	85.00±5.612	2.00±1.080	1.00±.577	.50±.500	8.00±4.637	1.50±.866	2.00±1.683	.00±.000
16:01-17:00	94.25±2.016	1.00±.707	.00±.000	.00±.000	.75±.750	.25±.250	3.75±1.931	.00±.000
17:01-18:00	85.50±2.754	1.50±.645	.50±.289	.00±.000	.00±.000	2.25±.629	10.00±2.582	.00±.000

Percentage of bats performing in each behavior type during the day in February 2011 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Agression	Mating/Courtship	Maternal care
6:01-7:00	49.00±1.190	22.00±.816	4.00±.408	4.00±.408	.00±.000	7.00±1.041	11.0±.500	3.0±.645
7:01-8:00	58.25±2.323	13.00±1.780	3.75±.750	3.50±.500	.00±.000	4.75±1.109	13.25±1.887	3.50±.500
8:01-9:00	58.00±2.415	14.00±1.472	5.25±.854	1.50±.645	.00±.000	4.75±.750	13.75±1.109	2.75±.479
9:01-10:00	64.75±2.016	7.00±1.581	3.00±.408	2.00±.408	.00±.000	5.75±.629	15.00±1.780	2.50±.645
10:01-11:00	73.25±3.065	6.00±2.041	2.75±1.109	2.00±.913	6.25±3.750	3.50±.957	6.25±	.00±.000
11:01-12:00	81.00±3.342	3.75±.750	1.50±.289	1.25±.629	8.00±3.391	2.50±3.391	2.00±3.391	.00±.000
12:01-13:00	67.75±.854	4.75±.854	1.75±.250	2.00±.408	17.75±2.097	5.25±.479	.75±.250	.00±.000
13:01-14:00	62.00±3.719	4.00±.577	2.50±.500	2.25±.250	22.25±2.955	5.75±1.109	1.25±.479	.00±.000
14:01-15:00	56.00±7.927	4.50±.866	1.75±.250	1.50±.500	32.00±7.394	3.50±.957	.75±.479	.00±.000
15:01-16:00	59.25±6.562	3.00±.408	1.50±.289	1.25±.289	29.25±5.483	3.50±.500	2.25±.854	.00±.000
16:01-17:00	84.75±3.521	4.50±1.323	1.50±.500	.75±.479	.00±.000	2.00±.816	6.50±2.062	.00±.000
17:01-18:00	79.25±2.562	2.50±.645	.50±.289	1.25±.750	.00±.000	3.25±.479	13.25±1.493	.00±.000

Percentage of bats performing in each behavior type during the day in March 2011 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Aggression	Mating/Courtship	Maternal care
6:01-7:00	67.5±.854	6.5±.479	.00±.000	1.5±.479	.00±.000	10.00±1.472	9.5±1.601	5.0±.500
7:01-8:00	67.25±2.496	3.00±.408	1.75±.629	2.00±.707	.00±.000	7.50±.866	14.00±1.871	4.50±.500
8:01-9:00	75.50±2.062	2.75±.479	1.75±.250	1.25±.479	.00±.000	6.25±1.031	10.00±.913	2.50±.500
9:01-10:00	93.50±2.398	1.50±.645	1.00±.408	.50±.289	.00±.000	2.50±1.041	.5±.289	.50±.289
10:01-11:00	96.50±.957	2.00±.408	.75±.250	.75±.479	.00±.000	.00±.000	.00±.000	.00±.000
11:01-12:00	50.25±6.005	3.25±1.109.	1.25±.250	2.25±.854	40.25±4.715	1.50±.866	.25±.250	1.00±1.000
12:01-13:00	26.75±8.673	2.00±.408	.00±.000	1.50±.500	65.75±7.761	2.50±1.190	.00±.000	1.50±.866
13:01-14:00	7.00±4.601	1.75±.629	.25±.250	.75±.479	73.50±12.142	2.00±.816	.00±.000	2.25±1.031
14:01-15:00	10.50±4.113	4.00±1.958	.50±.289	.25±.250	82.75±7.016	.75±.479	.00±.000	1.25±.479
15:01-16:00	42.75±9.595	5.75±.250	.50±.289	.75±.250	44.25±9.936	2.50±.500	1.00±.577	2.50±.289
16:01-17:00	94.00±2.041	1.25±.629	.00±.000	.00±.000	1.75±.000	.75±479	1.25±.750	1.00±.577
17:01-18:00	85.75±6.223	1.50±.645	1.00±.577	.00±.000	.00±.000	2.00±1.225	8.75±3.544	1.00±.707

Percentage of bats performing in each behavior type during the day in April 2011 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Aggression	Mating/Courtship	Maternal care
6:01-7:00	71.00±.500	8.5±.629	1.5±.479	1.5±.479	.00±.000	6.5±.250	8.5±.250	2.5±.250
7:01-8:00	78.25±4.110	7.75±.479	1.75±.250	.50±.289	.00±.000	10.25±.629	3.75±2.926	1.75±.479
8:01-9:00	79.75±2.898	4.50±.866	1.75±.479	1.00±.408	.00±.000	4.75±.750	6.50±2.255	1.75±.629
9:01-10:00	72.25±10.539	3.25±.946	1.00±.000	1.00±.577	17.50±8.382	3.00±1.472	1.00±.707	1.00±.600
10:01-11:00	17.00±3.536	4.00±.913	.50±.500	1.00±.408	75.25±4.905	1.75±.250	.00±.000	.50±.500
11:01-12:00	2.50±1.893	.75±.479	.00±.000	.50±.500	95.00±2.915	.75±.750	.00±.000	.50±.500
12:01-13:00	3.00±1.780	3.00±1.732	.25±.250	.25±.250	91.25±3.750	.75±.479	.50±.500	1.00±.408
13:01-14:00	.00±.000	2.50±.957	.25±.250	1.50±.866	93.00±3.512	1.50±.957	.00±.000	1.25±.750
14:01-15:00	33.25±8.596	3.00±.707	1.25±.250	1.00±.408	58.25±9.169	2.50±.645	.25±.250	.50±.289
15:01-16:00	40.25±12.599	3.00±.707	1.00±.707	1.25±.629	50.25±13.798	3.75±1.548	.50±.500	.00±.000
16:01-17:00	85.50±2.986	1.75±.479	.75±.479	.50±.289	3.25±1.974	1.50±.957	6.00±2.000	.75±.479
17:01-18:00	88.75±6.223	.75±.645	.50±.577	.25±.000	.00±.000	1.50±1.225	6.50±3.544	1.75±.707

Percentage of bats performing in each behavior type during the day in May 2011 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Aggression	Mating/Court ship	Maternal care
6:01-7:00	56.00±4.416	19.75±4.479	3.25±.629	2.75±.479	.00±.000	3.00±.408	4.25±1.436	6.25±2.097
7:01-8:00	71.50±3.428	8.00±	3.00±2.121	1.50±.289	.00±.000	3.00±.408	7.00±1.225	5.75±1.601
8:01-9:00	81.75±2.250	4.50±.289	2.50±.866	1.50±.289	.00±.000	1.50±.289	4.75±.479	3.50±1.443
9:01-10:00	89.00±3.873	1.75±.854	1.50±.957	1.25±.750	.00±.000	1.75±.854	1.50±.645	3.25±.854
10:01-11:00	61.75±8.159	6.25±1.181	2.25±1.315	3.75±1.493	18.75±7.364	2.75±.750	1.75±.854	2.75±.750
11:01-12:00	35.50±9.921	5.25±2.250	1.75±.479	3.25±1.109	44.75±10.160	2.50±.500	2.50±.866	4.50±1.323
12:01-13:00	9.75±9.096	6.00±1.780	1.25±.629	3.75±.629	72.50±11.420	3.50±.500	.50±.289	2.75±.629
13:01-14:00	10.50±9.215	4.75±2.323	1.00±.577	2.00±.707	75.50±12.679	4.50±.866	.00±.000	1.75±.750
14:01-15:00	32.25±2.869	4.25±2.869	1.50±2.869	1.50±2.869	51.75±2.869	3.00±2.869	1.75±2.869	4.00±2.869
15:01-16:00	41.50±7.890	4.00±.913	2.25±.629	2.50±.289	42.50±8.372	2.50±.289	1.25±.750	3.50±.866
16:01-17:00	73.25±4.270	4.00±.816	2.00±.577	1.25±.479	11.50±1.555	2.25±.750	3.25±1.250	2.50±1.041
17:01-18:00	95.25±2.810	.75±.479	.00±.000	.00±.000	.00±.000	1.00±.707	3.00±1.780	.00±.000

Percentage of bats performing in each behavior type during the day in June 2011 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Aggression	Mating/Courtship	Maternal care
6:01-7:00	49.25±4.871	31.25±3.351	2.75±.946	3.75±.629	.00±.000	4.75±.854	4.50±1.041	3.75±1.493
7:01-8:00	72.00±2.483	11.50±1.323	3.00±.913	1.25±.250	.00±.000	2.25±.946	6.50±1.500	3.00±1.155
8:01-9:00	75.25±2.016	8.75±1.601	2.25±.479	1.25±.479	.00±.000	3.00±1.291	6.50±1.500	3.00±1.000
9:01-10:00	84.25±4.479	9.25±2.562	2.25±.629	1.25±.946	.00±.000	.50±.289	1.25±.750	1.25±.479
10:01-11:00	92.75±3.772	4.25±2.213	.75±.479	.75±.479	.00±.000	.00±.000	.75±.479	.75±.479
11:01-12:00	62.50±8.986	8.00±1.581	1.50±.645	2.75±1.315	20.50±7.599	2.50±1.041	.00±.000	2.25±.629
12:01-13:00	48.50±5.867	7.25±1.436	1.50±.289	2.00±1.225	34.25±5.677	3.75±.250	.25±.250	2.50±.957
13:01-14:00	33.75±2.626	8.00±1.414	1.25±.479	8.25±2.056	43.50±4.664	2.50±.866	.75±.750	2.00±.577
14:01-15:00	39.25±5.921	6.75±1.031	1.75±.250	3.00±.707	42.00±6.258	4.50±.645	.00±.000	2.75±1.109
15:01-16:00	57.00±4.708	3.00±.577	2.50±.957	2.25±.250	32.75±4.404	1.75±.854	.25±.250	.50±.500
16:01-17:00	96.50±2.021	1.25±.629	.25±.250	.25±.250	.00±.000	.75±.750	1.00±1.000	.00±1.000
17:01-18:00	91.75±3.750	3.50±2.179	.75±.479	.50±.289	.00±.000	.75±.479	1.50±.645	1.25±.750

Percentage of bats performing in each behavior type during the day in July 2011 (Mean±SE)

(data obtained from four observation days)

Time of day	Behavior category							
	Sleeping	Grooming	Wing spreading	Movement	Wing flapping	Aggression	Mating/Courtship	Maternal care
6:01-7:00	58.25±3.473	26.00±3.851	5.00±1.155	4.00±.408	.00±.000	3.50±.866	1.50±.500	.50±.289
7:01-8:00	72.00±1.354	12.00±1.225	4.25±.250	2.50±.500	.00±.000	3.50±.866	4.50±.957	.75±.250
8:01-9:00	76.25±1.315	10.75±1.181	3.00±.000	1.00±.408	.00±.000	3.50±.500	4.00±1.155	1.00±.577
9:01-10:00	88.00±1.732	4.25±1.436	1.75±.250	1.00±.408	.00±.000	2.75±.479	1.75±.250	.75±.250
10:01-11:00	90.00±5.774	2.50±1.443	.50±.289	2.00±1.225	.00±.000	.00±.000	.00±.000	.00±.000
11:01-12:00	38.75±2.926	6.25±.479	1.50±.866	3.50±.645	36.50±2.021	3.25±.750	.50±.500	.50±.289
12:01-13:00	45.75±4.715	5.75±.250	1.25±.479	5.25±2.016	40.00±3.697	1.00±.577	1.00±577	.25±.250
13:01-14:00	41.75±4.837	4.75±.479	2.00±.000	3.25±2.287	37.75±5.105	1.75±.750	.00±.000	.50±.289
14:01-15:00	46.25±2.175	4.75±.479	2.25±.946	2.25±.750	51.00±5.260	2.50±.289	.00±.000	.50±.500
15:01-16:00	86.25±1.750	4.75±1.315	4.00±1.732	1.00±.577	27.50±10.308	.50±.289	.00±.000	.00±.000
16:01-17:00	96.75±3.250	.50±.500	.00±.000	.00±.000	.00±.000	1.00±.000	1.50±1.500	.25±.250
17:01-18:00	96.50±2.021	.50±.289	1.00±.577	.00±.000	.00±.000	1.50±.866	.50±.289	.00±.000

APPENDIX B

Individual emergence

Individual emergence times of Lyle's flying fox in relative to sunset time (Mean±S.E.). The number in parentheses represents the number of individual observed.

Month	Date	Minute after sunset			
		Male	Female	Lactating female	Juvenile
October	28/10/2010	30.5±5.82 (7)	31.88±5.67 (10)	-	34.8±3.56 (6)
October	29/10/2010	34±2 (5)	30.573±7.18 (7)	-	32±1.73 (3)
October	30/10/2010	30.83±6.15 (6)	34±4.16 7)	-	42±7.87 (4)
October	31/10/2010	37.16±5.88 (6)	35.5±4.64 (6)	-	38.6±4.72 (5)
November	10/11/2010	38.83±5.98 (6)	40.5±5.24 (8)	-	35.5±0.71 (2)
November	11/11/2010	34.8±5.81 (5)	38.375±6.82 (5)	-	40.33±1.15 (3)
November	12/11/2010	34.5±4.32 (6)	33±4.85 (5)	-	38.66±4.51 (3)
November	13/11/2010	36.2±4.97 (5)	39.7±4.45 (10)	-	37.66±1.53 (3)
November	14/11/2010	41.8±4.44 (5)	43.72±5.26 (11)	-	46.6±4.51 (5)
November	15/11/2010	42.66±4.76 (6)	37.57±5.71 (7)	-	38.71±4.39 (7)
November	16/11/2010	37.5±1.29 (4)	37.6±6.48 (10)	-	43.66±4.51 (3)
November	17/11/2010	42.5±5.75 (6)	41.14±3.58 (7)	-	37.75±2.99 (4)
December	22/12/2010	39.16±4.62 (6)	42.75±6.25 (8)	-	41.25±2.50 (4)

Month	Date	Minute after sunset			
		Male	Female	Lactating female	Juvenile
December	23/12/2010	42.2±7.76 (5)	43.6±6.79 (10)	-	42.75±2.50 (4)
December	24/12/2010	39.75±8.73 (4)	44.41±6.11 (12)	-	38±3.61 (3)
December	27/12/2010	41.2±8.53 (5)	42.5±5.28 (10)	-	44.4±5.68 (5)
December	26/12/2010	39.57±6.29 (7)	44.27±4.34 (11)	-	43.25±4.46 (8)
December	12/12/2010	43.4±5.32 (5)	39.76±8.40 (13)	-	42.6±6.80 (5)
December	13/12/2010	36.4±4.04 (5)	36.8±4.18 (10)	-	39±4.24 (4)
December	15/12/2010	43.2±3.56 (5)	39.09±7.44 (11)	-	39.8±1.48 (5)
January	19/1/2011	50.75±12.44 (5)	50.66±12.00 (11)	-	45.25±4.40 (4)
January	21/1/2011	43.83±7.27 (4)	47.5±7.78 (12)	-	47.75±13.57 (12)
January	22/1/2011	57.57±19.48 (6)	50.33±10.14 (12)	-	58±5.91 (4)
January	23/1/2011	53.25±7.02 (7)	57.88±3.87 (9)	-	53.55±8.04 (8)
January	24/1/2011	57.57±3.59 (4)	5±4.92 (9)	-	56±3.81 (9)
January	25/1/2011	54.6±5.38 (7)	58.5±7.39 (10)	-	56.5±2.31 (4)
January	26/1/2011	50.8±5.18 (5)	48.09±2.59 (6)	-	49±4.20 (4)
February	3/2/2011	65±6.24 (3)	55.79.17 (10)	-	52±10.10 (4)

Month	Date	Minute after sunset			
		Male	Female	Lactating female	Juvenile
February	4/2/2011	57.83±9.72 (6)	56.58±8.05 (12)	-	50.25±8.14 (4)
February	5/2/2011	55.44±9.21 (9)	60.54±5.84 (11)	-	48.75±13.23 (4)
February	6/2/2011	54.57±10.47 (7)	58.83±5.02 (14)	-	47.75±2.99 (4)
May	17/5/2011	53±10.95 (6)	45.62±8.14 (8)	49.66±16.92 (3)	57±3.37 (4)
May	18/5/2011	33.8±5.07 (5)	37.18±7.11 (11)	52±1.41 (2)	44.5±6.81 (4)
May	20/5/2011	35.2±10.50 (5)	43.5±7.34 (6)	43.57±8.99 (7)	48±11.17 (4)
May	21/5/2011	37.8±8.32 (5)	36.4±7.67 (5)	53.5±0.71 (2)	40.25±3.69 (4)
June	1/6/2011	27.62±6.91 (8)	25±3.16 (4)	29.6±3.71 (5)	31.16±4.36 (6)
June	2/6/2011	24.6±5.59 (5)	20.25±2.36 (4)	28.71±3.90 (7)	27.75±4.99 (4)
June	3/6/2011	19.75±2.36 (4)	18±2.65 (3)	23.75±1.71 (4)	22.6±3.51 (5)
June	4/6/2011	25.4±3.29 (5)	23±3.54 (5)	25±2.00 (3)	26.8±2.28 (5)
June	16/6/2011	27.66±10.22 (9)	26±6.91 (8)	22.66±4.59 (6)	28.4±6.88 (10)
June	17/6/2011	25.57±6.85 (7)	21.57±5.91 (7)	25.42±6.29 (7)	26±5.33 (6)
June	18/6/2011	27.75±4.89 (8)	21.71±6.73 (7)	22.66±4.80 (6)	24.5±5.24 (6)
June	30/6/2011	17.33±3.7 (9)	17±3.90 (6)	17.14±1.57 (7)	19.66±3.79 (3)

Month	Date	Minute after sunset			
		Male	Female	Lactating female	Juvenile
July	1/7/2011	22.8±5.55 (10)	21.5±3.92 (10)	25±3.46 (6)	25±5.53 (8)
July	3/7/2011	14±1.41 (2)	30.5±2.38 (4)	-	30.33±4.51 (3)
July	4/7/2011	26±3.49 (11)	23.6±4.93 (10)	24.5±2.38 (4)	25.14±6.28 (7)
July	15/7/2011	18.8±4.49 (5)	21.66±6.66 (6)	28±0 (1)	-
July	17/7/2011	22.625±3.50 (8)	20.09±4.09 (11)	16±0 (1)	20.85±6.01 (7)
July	18/7/2011	16.5±5.09 (6)	18.7±2.16 (10)	24±0 (1)	18.85±7.07 (7)
July	29/7/2011	17.75±6.40 (4)	13.2±5.56 (10)	-	15.66±3.21 (3)
July	31/7/2011	20.6±3.36 (5)	18.57±2.41 (7)	-	19.4±3.85 (5)
August	1/8/2011	15.5±3.39 (6)	14.83±5.60 (6)	-	17.5±3.11 (4)
August	2/8/2011	23.5±3.39 (6)	21.2±8.24 (10)	-	24.62±4.63 (8)
August	13/8/2011	28.33±5.72 (9)	24.3±4.06 (10)	-	28.33±2.16 (6)
August	14/8/2011	21.625±2.67 (8)	19.33±4.06 (9)	-	20.33±2.16 (6)
August	15/8/2011	23±2.00 (4)	21.85±5.21 (7)	-	18±1.87 (5)
August	16/8/2011	23.4±3.51 (5)	22.6±4.20 (10)	-	21±1.41 (2)
August	28/8/2011	19±3.22 (6)	18.71±4.99 (7)	-	20±2.65 (3)

Month	Date	Minute after sunset			
		Male	Female	Lactating female	Juvenile
September	1/9/2011	19.66±3.78 (6)	18.55±4.38 (9)	-	20.66±3.21 (3)
September	2/9/2011	27.66±3.01 (6)	24.2±2.77 (5)	-	24±1.00 (3)
September	12/9/2011	26.2±3.42 (5)	25.22±4.82 (9)	-	22±0 (1)
September	13/9/2011	28±2.92 (5)	23.66±5.35 (6)	-	27.4±5.86 (5)
September	14/9/2011	29.25±2.22 (4)	26.33±4.63 (6)	-	32±4.24 (2)
September	15/9/2011	16.75±4.57 (4)	12.4±2.30 (5)	-	16.5±0.71 (2)
September	29/9/2011	18.5±2.65 (4)	17.25±1.26 (4)	-	21.25±2.87 (4)
September	30/9/2011	19.5±1.55 (4)	18.15±1.24 (4)	-	22.25±1.56 (4)

Month	Date	Minute after sunset			
		Male	Female	Lactating female	Juvenile
March	10/3/2012	70.75±21.73 (4)	56±20.85 (4)	117.45±41.62 (11)	33.67± 4.75 (3)
March	11/3/2012	115.75±33.98 (4)	163.33±28.88 (3)	237.06±34.11 (16)	-
March	12/3/2012	113.5±26.16 (2)	237±0 (1)	240±20.84 (6)	183±9.90 (2)
March	13/3/2012	117±0 (1)	88±0 (1)	217.92±28 (12)	-
March	21/3/2012	164±1.41 (2)	-	198.62±50.39 (13)	-
March	22/3/2012	110.67±3.51 (3)	106±0 (2)	175.7±38.35 (20)	115±0 (1)
March	23/3/2012	107±25.98 (3)	136.5±6.36 (2)	177.4±56.25 (15)	-
March	24/3/2012	76±22.44 (4)	76.2±26.32 (5)	109.82±27.17 (11)	37.6± 1.15 (3)
April	6/4/2012	91±0.00 (1)	50.67±12.50 (3)	93±18.98 (6)	43.67±3.06 (3)
April	7/4/2012	42±6.24 (3)	38±7.11 (5)	65.89±16.22 (9)	-
April	8/4/2012	64±0 (1)	61±11.60 (4)	103.64±21.55 (11)	-
April	9/4/2012	36.25±11.62 (4)	44.29±14.67 (7)	53±6.96 (5)	-
April	20/4/2012	-	49±0 (1)	100.56±16 (9)	-
April	21/4/2012	79±0 (1)	79±15.56 (2)	93.22±14.03 (9)	39±0.82 (4)

BIOGRAPHY

Miss Yupadee Hengjan was born June 14, 1986 in Kanchanaburi Province. She received a Bachelor of Science degree in Biology from the Faculty of Science, Silapakorn University in 2008. Later, she continued her study in Zoology program for Master degree at Department of Biology, Faculty of Science, Chulalongkorn University in 2009 and she completed the program in 2011.

Proceeding

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Abstract

Poster presentation

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