Vertical Stratification in Foraging Activity of the Wrinkle-Lipped Free-Tailed Bat, *Chaerephon plicatus* (Buchanan, 1800) in Central Thailand

Tuan Ngoc Nguyen

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science in Ecology (International Program)

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This is to certify that the work here submitted is the result of the candidate's own investigations. Due acknowledgement has been made of any assistance received.

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I hereby certify that this work has not been accepted in substance for any degree, and is not being currently submitted in candidature for any degree.

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ABSTRACT

The Wrinkle-lipped free-tailed bat, *Chaerephon plicatus*, widely distributes in South and Southeast Asia. The species roost in large colony with the estimated number up to several million individuals. *Chaerephon plicatus* also provides important guano resource**.** Previous studies have shown the species as important pest suppression agents which predated on rice pests such as White-backed planthopper, *Sogatella furcifera*, and Brown planthopper, *Nilaparvata lugens*. It is also suggested that *C. plicatus* forage at high altitude since substantial number of brown planthopper, a high altitude migratory insects, found in bat diet while no brown planthopper capture in the ground. Yet there is any direct evidence found to confirm this hypothesis.

This study concentrates on the foraging activity of *C. plicatus* on vertical dimension. The bat activity was measured by acoustic sampling using bat detectors mounted on a 3×3m obsolete helium kite balloon. Three altitudinal levels were measured simultaneously including 2m, 100m and 200m. Foraging activity of *C. plicatus* was highly stratified in vertical dimension. Number of call recorded aloft (100m and 200m) was significantly higher than at the ground. Nocturnal boundary layer was typically formed at the nights when the data were collected. The level of 100m might have been the top of nocturnal boundary layer which is known at the layer of high migratory insect density. The high number of calls recorded at 100m and 200m showed a link between foraging activity of *C. plicatus* and migratory insects. However, the altitudinal level of high activity of bats, which ca. 100m is also in the swept-area of wind turbine blade. The construction of wind turbine farms in the areas of high number of *C. plicatus* could be harmful to the species.

The vertical stratification in foraging activity of *C. plicatus* might also reveal a niche partitioning between open space bats in vertical dimension. This study revealed a clue in a shift in whole-night activity pattern of *C. plicatus*. Whole night pattern at the ground has a peak in the early part of the night, however, gradually decrease until morning. The biomass of insects near ground level also showed at gradual decrease trend during the course of night. Meanwhile, an increasing in activity found at high altitudes after midnight. *Chaerephon plicatus* might take advantage by foraging near ground level when the insects swarm shortly after dusk. However, as the number of insects decrease, *C. plicatus* shift their activity to higher altitude to avoid interspecific competition with other edge-open space bats such as *Myotis* sp. However, this remains a hypothesis and needs to be investigated in more detail since a few data are available in the area. Future study can be conducted to test this hypothesis.

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Tuan Ngoc Nguyen

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ABBREVIATIONS

ABL: Atmospheric Boundary Layer

AGL: Above Ground Level

LLJ: Low Level Jet

NBL: Nocturnal Boundary Layer

PBL: Planetary Boundary Layer

SBL: Stable Boundary Layer

CHAPTER 1

GENERAL INTRODUCTION

1.1 Background and rational

To be survived and successful passing genes to the next generation, animals first need to fulfill the requirement of energy obtaining from foods. Foraging thence one of the most important process in animal ecology. Since the very first men, hunters and gatherer, set food on Earth, they probably applied their "ecological knowledge" to answer where and when to find the animals. Yet, the distribution of animals is determined by the distribution of their resources (WallisDeVries, 1996). Resources, in their turn, are determined by physical factors of the environment which vary in spatial and temporal scale (Soberón, 2007). As the only owning the capability of flying, second highest number of species in the class of mammal, foraging ecology of bats contains various aspects of ecology and even multi disciplines of biology to be explained. When first imagine about bats, people might probably think about the dark, as Chiroptera has evolved to be fully nocturnal. The hypotheses have been proposed either to avoid the predation and competition by birds (Rydell and Speakman, 1995) or to avoid hyperthermia during the high daylight temperature (Thomas et al., 1991). Whatever the fact was, the nocturnal activity of bats making it both difficult and fascinating for the researchers to understand bat foraging ecology.

Insectivorous bats hunt on the wings as their foraging activity are mostly aloft. It has been widely accepted to divide bats into foraging guild based on the habitat a bat species uses including clutter, edge-space, and open space bats (Schnitzler et al., 2003) (see also Denzinger and Schnizler (2013) for a finerscale category). However, this "guild-definition" is a ground based definition since the core concept is whether bats are adapted to fly in the habitat with or without the presence of vegetation. Numerous bats, has been found in their routine activity, foraging or commuting, far higher than the vegetation structure near the ground (Voigt et al., 2018). A recent attempt to define the airspace as a habitat (Dieh, 2013) has opened a new frontier in ecology. This breakthrough definition also brings a formal recognition to the vertical dimension in foraging activity of bats. The lowest part of troposphere comprises multiple layers which physical traits vary by time, day-night cycle and season, and location. And some of the first attempt has proposed to define layers within the low troposphere as the framework for future studies (Davy et al., 2017; Voigt et al., 2018). For many decades, researches have searched to answer how bats vary their activity in different habitats and why. The same question could now be asked for the habitat air as how bats vary their foraging activity in different altitudes and why they do so.

The wrinkle-lipped free tailed bat *Chaerephon plicatus* (Bunchanan, 1800) (synonym *Tadarida plicata*) is widely distributed through South Asia and Southeast Asia (Csorba et al., 2014). This species is a member of free-tailed bat, family Mollosidae, with average body mass 15.4g (for male) or 15.5g (for female, and forearm length 46-49mm (Thong, 2014). *Chaerephon plicatus* forms large colonies which up to 2-3 million bats in a single cave (Hillman, 1999; Thong, 2014). In mainland Southeast Asia, *C. plicatus* reproduces two times per years (Furey et al., 2018).

As other mollosid species, *C. plicatus* is classified as open space, fast flying bats (Norberg 1988), with an estimated foraging range ca. 27km in diameter from roosting cave. The species is an ecosystem engineer species since owning large number of individuals and high insect consumption rate (up to 50% body mass per night) (Leelapaibul et al., 2005). It is also reported as potential pest control agent as the species stably consume large amount of insect pest such as the white-back planthopper (*Sogatella furcifera*) (Leelapaibul et al., 2005) and the brown planthopper (*Nilaparvata lugens*) (Srilopan et al., 2018). The species also provides the income source from guano for the local people surrounding the caves.

Recent dietary researches posed a question about the foraging ecology of *C. plicatus* since a stable amount of migratory pests, *S. furcifera* and *N. lugens*, found in bat diet while no insects capture found in the bat habitat. It is known that *S. furcifera* and *N. lugens* are migratory insects that could climb up to the altitude 150-2000m for migration (Qi et al., 2014). This led to a hypothesis whether *C. plicatus* acquire those insects by high flying forage which mean the species foraging range is not limited to a few tens meter above ground level. Thence, this present study aimed to investigate the foraging ecology of *C. plicatus* in the vertical dimension, the habitat air.

1.2 Objectives

- To identify if foraging activity of *C. plicatus* is stratified in vertical dimension.
- To determine if there is any variation in nightly foraging activity of the species (i.e. whether the species shift their whole-night activity pattern in between altitudinal levels?)

1.3 Literature review

1.3.1 Monitoring bat activities by echolocation

1.3.1.1 Echolocation

Echolocation, or bio-sonar, is a process to locate objects by emitting and receiving echoes which is used by bats and other animals such as cetaceans, swiftlets. Living in the dark and pursuing small size preys making observing by vision become very challenge, in order to adapt insectivorous bats have evolved their echolocation making the bat operate independently to light condition. Bats use echolocation to perceive dimensional images about surrounding environment (Simmons et al., 1995).

Bats own the ability to hunt the moving preys and avoiding obstacles simultaneously (Griffin et al., 1965; Simmons, 1989; Schmidt, 1992). Echolocation also gives bat the ability to identify their prey targets in a dense clutter (Kalko, 1995) and discriminate preys by size (Jones, 1990). Echolocation is used as communication tools in bats. In the case, echolocation help bats avoid collision or jamming when emerge with the large number from the roosting site (Ulannovsly et al., 2004; Ibáñez et al., 2004).

To scientists, bat echolocation provides various information that could further our understanding on many aspects about bats. Every species of bats own their specific echolocation signal, this unique information can be used as a tool for species identification (Fenton and Bell, 1981), many cryptic species have been identified based on the differences in their echolocation (Jones et al., 1993; Kingston et al., 2001). Echolocation also provides information on sex, age, and individual quality (Siemers et al., 2005) and their activities (Fenton, 1970).

1.3.1.2 Monitoring bat activities

Bats activity can be measured by estimating the number of bats being caught in a certain area (O'Farrell and Gannon, 1999). However, this method has two main limitations: (1) causing disturbance to bat community, (2) cannot apply with bats which active in open space and high altitude. Fenton (1970) first introduced a new method for monitoring bats activity by recording their ultrasonic sound and converting to audible "clicks". Single bat was recognized by a chain of "clicks" considered as "bat passes". However, measuring bat activities based on bat passes cannot discriminate between bat individuals and species of bats. Broders (2003) gave a new method for quantifying bat activities based on file size "bytes", the file size of recording bat echolocation could be used as "unit" of bat activities.

While foraging, insectivorous bats emit feeding buzz. Feeding buzz comprises high frequency calls which help bats quickly determine the prey position. The feeding buzz represents for foraging activity of insectivorous bats. A study of foraging behavior in the two species of bats, *Lasiurus borealis* and *Lasiurus cinereus*, showed bats emit longer feeding buzz in associated with bigger preys (Acharya and Fenton, 1992).

However, the bat detectors can only record the bat echolocation ca.30m because of the strong absorption of the air to high frequency sound (Griffin, 1971). Therefore most of the studies were about bat activities at the altitude below 30m above ground level (AGL) whilst many insectivorous bats are open foragers and they forage in the altitudes much more than 30m, maybe up to more than 1,100m AGL in the case of *Tadarida brasiliensis* (McCracken et al., 2008).

Griffin and Thompson (1982) firstly introduced the new technique that permitted them to record bat activity up to 300m AGL. They used a radio-microphone, which comprise a microphone, and a bat detector, and FM transmitter, attached to a balloon. The recorded echolocation was transmitted to FM receiver and recorded in the ground. With the same approach, Fenton and Griffin (1997) recorded bat foraging activities up to 600m AGL.

Later on, McCracken et al. (2008) recorded the bat activities up to 1100m AGL, and bat foraging was most concentrated at the level 400-500m AGL, which also the altitudes with the highest nocturnal insect density from 100-1000m AGL (McCracken et al., 2008). The insect density data was estimated from X-band radar.

However, the three studies on high altitude activity of bats were mostly about *Tadarida brasiliensis* (Griffin and Thompson, 1982; Fenton and Griffin, 1997; McCracken et al., 2008). Many species of bats belong to family Molossidae which are unique for their high wing aspect ratio, which means they can fly up to several hundred meters AGL. The information about the vertical stratification of these bats is still unknown.

1.3.2 Layer of troposphere

Troposphere is the lowest part of the Earth's atmosphere and this is also the place where most weather conditions happen (UCAR, 2011). Troposphere thickness varies in different areas of the world, 18km for tropic regions, 17km for middle latitude regions, and 6km for polar region (UCAR, 2011). Troposphere is composed of various sub-layers. The lowest part of troposphere called Planetary Boundary Layer (PBL), or Atmospheric Boundary Layer (ABL), is the place where the friction between atmosphere and the Earth's surface happens. The PBL thickness varies from several hundred meters up to two kilometers depending on landscape and time of the day (Stull, 1988).

Since PBL is directly contacted by the Earth's surface, this layer of troposphere is characterized by the surface to which it contacts. There are two typical types of PBL: Convective boundary layer and Stably stratified planetary boundary layer, or Stable boundary layer (SBL) (Stull, 1988). In tropical and mid-latitude regions, the Convective boundary layer is usually formed during day time. On the other hand, SBL is usually formed at night when the Earth surface losing heat due to loss of radiation. SBL is characterized by statistically stable air with weak and sporadic turbulence (Stull, 1988). The top of SBL, however, is poorly defined as it smoothly blends into the layer of atmosphere above (Stull, 1988). The vertical profile of temperature can be used to identify the height of SBL (Beyrich and Weill, 1993). The temperature of SBL usually increases up to SBL top and stays almost constant above it (Alappatu et al., 2009).

Temperature inversion layer

One of the most important characteristic of troposphere is the decreasing of temperature as increasing altitude. In general, temperature in troposphere drops 6.5^{o}C for every increase 1000m in altitude. However, under specific condition, a layer of called temperature inversion, in which the temperature increases when it comes to higher altitude, is formed. Temperature inversion is the process commonly found in the Stable Boundary layer (SBL), when the temperature at higher altitude is warmer than the air near the ground level (Stull, 1988).

Nocturnal low level jet

Nocturnal low level jet or low level jet (LLJ) is the strongest wind, 10-30m/s, in the vertical profile which formed at top of stable boundary layer (Stull, 1988).

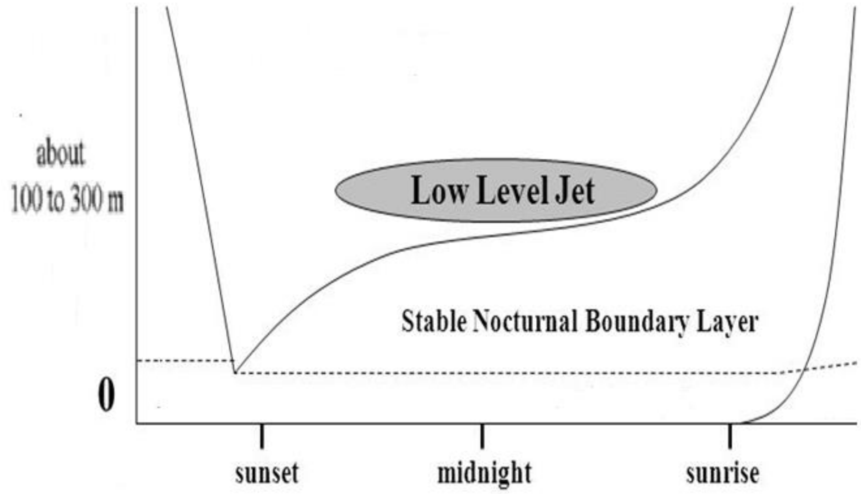

Figure 1.1 The Stable boundary layer at night.

1.3.3 Aerial insects

High flying migratory insects tend to form horizontal layers in different altitudes and these layers depend on certain meteorological conditions (Drake and Farrow, 1984; Wood et al., 2010). A substantial researches showed firmly evidence that temperature keep the main role in forming heterogeneity altitudinal insect layers. Brown plant hopper takes off at dawn and dusk and form layers where temperature is more than 15^{o}C (Rosenberg and Magor, 1983; Qi et al., 2014). Radar observation of insect summer migration in southern U.K showed that the highest density concentrated at 400m AGL where the temperature was highest in horizontal scale (Chapman et al., 2004; Wood et al., 2010). In tropical areas, migratory insects are also found in the layer of temperature inversion at high altitude (Riley et al., 1995). However, it is suggested large aggregate of insects found at high altitude is caused by strong wind condition rather than warm temperature (Feng et al., 2004). Insects may concentrate in top of surface inversion where the wind maxima, LLJ, usually form. In India, the brown planthopper (*N. lugens*) and other migratory insects are found at the top of inversion layer, around 150m AGL, where the wind reaches highest velocity in vertical profile up to 1000m. In Southeast Asia, *N. lugens* are expected to migrate at high altitude, as found by studies in China (Qi et al., 2014). Large numbers of *N. lugens* migrate from Southeast Asia to China and vice versa annually (Hu et al., 2017). However, till now, no research has been conducted in Southeast Asia to confirm the presence of *N. lugens* at high altitude and also the conditions which result the formation of large amount of *N. lugens* at altitude.

1.3.4 Bat detector

Bat detector is the device that turns the ultrasonic sound emitted by bats to audible sound. There are three basic types of bat detector that commonly used – heterodyne, frequency division, and time expansion. There are two methods for analyzing bat calls in detectors, depending on types and commercial brands, devices apply one of the two systems – zero-crossing and Fourier analysis or full spectra analysis. Each type of detectors and analysis methods has certain advantages and limitations concerning three main factors: sensitivity, ultrasonic sound recording and processing capacity, and providing parameter for species identification (Brigham et al., 2004).

Time expansion is the method used by bat detectors to detect bat echolocation which is based on the inverse relationship between time and frequency. When increasing time duration of a signal by a ratio its frequency is decreased at the same ratio. Insectivorous bats emit high-frequency calls, 10-250kHz, which are mostly higher than hearing range of human, 0.02kHz to 20kHz. With an appropriate ratio, time expansion function of a bat detector can extend the duration of a particular bat call and by doing that it also decreases the call frequency to the hearing range of human. The commercial bat detectors in the market like Pettersson D240x (Pettersson Elektronik AB, Uppsala, Sweden), with time expansion ratio which can be adjusted at 10× or 20×, can extend call duration, and also decrease call frequency, as a ratio of 10× or 20×, respectively. For example, a 40kHz and 0.02s duration call is being recorded by a time expansion bat detector at a ratio of 10×, the output call will have a frequency of 4kHz and 0.2s in duration.

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CHAPTER 2

Vertical Stratification in Foraging Activity of *Chaerephon plicatus* (Molossidae, Chiroptera) in Central Thailand

This chapter was submitted to Mammalian Biology

Vertical Stratification in Foraging Activity of *Chaerephon plicatus* (Molossidae, Chiroptera) in Central Thailand

Abstract

Studies of bat activity mostly concentrate at ground level while some open space bats may forage at higher altitudes. This study investigated the stratification in foraging activity of *Chaerephon plicatus* from near ground level up to 200m above ground by using a helium kite-balloon. The activity of *C. plicatus* aloft (100m and 200m) on average was significantly higher than that close to the ground. Peak activity corresponded with the top of the nocturnal stable boundary layer which is also the layer of maximum temperature and wind speed. Brown plant hoppers (*Nilaparvata lugens*) found at the height of peak activity suggested that *C. plicatus* actively followed the migratory insects in the air. However, the height of peak activity also corresponded with the area swept by wind turbine blades, thus such turbines installed in areas with large colonies of *C. plicatus* may pose a serious threat to the species.

Keywords: foraging ecology; high altitude; migratory insects; stable boundary layer; wind turbine.

2.1 Introduction

Foraging is the process by which animals search for and acquire food. Foraging activity of most terrestrial animals is usually considered in the horizontal dimension. Bats, however, spend most of their foraging time in the airspace, commuting and feeding aloft, and are able to change their echolocation patterns in vertical gradients to capture insects (Ratcliff and Dawson, 2003; Gillam et al., 2009, Krauel et al., 2018). Recording echolocation by various techniques has allowed researchers to monitor bat activity effectively in various habitat types for the last four decades (Fenton, 1971; Fenton, 1977; Fenton, 1980; Grindal et al., 1999; Frey-Ehrenbold, 2013). However, most of these studies concentrated on bat activities at a height below 30m above ground level (AGL). Few studies investigated bats flying higher than >100m and these studies concentrated on *Tadarida brasiliensis*. Fenton and Griffin (1995) used a radio-microphone attached to a balloon and recorded bat activities up to 600m AGL. Foraging activity of *T. brasiliensis* was recorded up to nearly 1,000m AGL (McCracken et al., 2008), although it was estimated to forage up to 3,000m AGL (William et al., 1973). Other molossid bats probably also forage in high altitudes like *T. brasiliensis* (Griffin and Thompson, 1982).

The wrinkle-lipped free-tailed bat, *Chaerephon plicatus*, is widely distributed throughout Southeast Asia. They usually roost in large colonies which could be up to 2.6 million individuals as in Central Thailand (Hillman, 1999). Diet studies showed that *C. plicatus* consumed a substantial number of both white backed planthoppers (Leelapaibul et al., 2005) and brown planthoppers (Srilopan et al., 2018) whichever is common in the area. In Thailand, *C. plicatus* helps to protect rice plants from white backed planthopper, a service worth 1.2 million USD each year, and equivalent to enough rice to provide a meal for more than 26,000 people annually (Wanger et al., 2014). A colony of 280,000 individuals of *C. plicatus* in Sabah, Malaysia could consume nearly 930 metric tons of insects annually over a 270km^2 area based on their foraging range (McFarlane et al., 2015).

Migratory insects represent the biggest biomass movement at a global scale (Hu et al., 2016). Many long distance migratory insects are carried by wind (Drake and Gatehouse, 1997). Insect migration assisted by wind results in serious damage to agricultural production since the wind can carry the insect pests for several hundred kilometers, as in the migration of the corn earworm moth (*Helicoverpa zea*) up to 1400km in Texas, USA (Westbrook et al., 1993). Under certain favorable meteorological conditions, migratory insects could form layers with large concentrations in the air column. Planthoppers are considered to be one of the most dangerous pests of rice and their migration also relies on wind (Drake and Gatehouse, 1997). Brown plant hoppers (*Nilaparvata lugens*) could migrate as far as 750km (Rosenberg and Magor, 1987), from Central Vietnam to South China (Hu et al., 2017). During the night, the dissipation of heat from the earth into the atmosphere forms an inversion layer of temperature (i.e. colder air remains close to the surface of the earth while warm air is at higher altitude) creating the nocturnal boundary layer (NBL) or stable boundary layer (SBL). At the top of SBL, a strong and fast moving airstream is typically formed, namely the low level jet stream (LLJ). In tropical areas, the formation of LLJ at night is suitable for insects to migrate (Drake and Farrow, 1988) and *N. lugens* was found to migrate in this layer (Riley et al., 1995a).

Chaerephon plicatus has narrow wings with a high aspect ratio, characteristic of open space foragers (Norberg and Rayner, 1987). However, its actual foraging behavior has never been documented. Particular insect groups rarely found at ground traps are substantially present in the diet of *C. plicatus*. This has led researchers to propose that *C. plicatus* may forage at high altitude on migratory insects (Leelapaibul et al., 2005; Srilopan et al., 2018). However, till date, there is no direct evidence on high altitude activity of *C. plicatus*. Therefore, this study aims at investigating the vertical stratification in foraging activity of *C. plicatus*. It is hypothesized that *C. plicatus* concentrates its foraging at high altitude. The understanding of vertical activity of *C. plicatus* has an implication for its ecosystem services. High altitude foraging which is appropriate for following migratory insect pests would suggest that its pest-suppression service occurs over a large landscape scale.

2.2 Materials and methods

2.2.1 Study area

This study was conducted in Ban Mi District (15.057^{o}N, 100.5313^{o}E, 35.70±7.02m above sea level), Lopburi Province, Thailand. Two colonies of *C. plicatus* are known in the area: Khao Wongkot Cave (15.018^{o}N, 100.545^{o}E; ca. 500,000 bats) and Dongdueng Cave (15.144^{o}N, 100.614^{o}E; ca. 100,000 bats). In Khao Wongkot, the landscape is dominated by rice paddy fields (70% within 20 km from caves), sugarcane and other crops (10%). In Dongdeung Cave, the landscape is dominated by field crop (60% within 20 km from caves), rice paddy fields (35%). There are three seasons: wet (May to October), dry cool (November to January) and dry hot seasons (February to April). Annual rainfall is 1,100mm which mostly falls during July to September. Wind is much stronger during the dry cool season.

2.2.2 Acoustic sampling

Data were collected in 12 nights during February 4th-17th 2018. Echolocation was recorded with Pettersson D240x bat detectors (Pettersson Elektronik AB, Uppsala, Sweden, 170g including battery) connected to a Zoom H2 recorder (ZOOM Corporation). The time-expansion function of Pettersson D240x provided high quality calls with full spectrum (10-120kHz). The bat detector was powered by a 9V-alkaline battery which could allow 12-16 hours in continuous operation. Record duration was set to 0.1 and 1.7second.

Bat activity was recorded at three heights: (1) 2m above ground level (“ground level”), (2) 100m above ground level and (3) 200m above ground level. A bat detector and one recorder were placed in a waterproof box (25x7x5cm). At 100 and 200m, boxes were suspended with a 3m x 3m helium-filled kite aerial oblate spheroid balloon (©Tichuan International Co., Ltd, China), at least 10m below the set height. A piece of microphone sponge was placed in front of the microphone of a bat detector to alleviate wind noise.

Altitude of bat detectors to the ground level were estimated by the formula $h = 0.9L\sin(\alpha)$ (Griffin and Thompson, 1982); with (h) is the relative elevation of a bat detector to the ground, (L) is the length of the line that was paid out and (α) is the angle of the line. A GPS transmitter was also attached to the balloon. The transmitter continuously sent the altitude and GPS coordination of the balloon to a laptop on the ground every second.

Each night, the three levels (ground, 100m and 200m) were monitored simultaneously. A data logger (TM-305U, Tenmars Electronics Co., Ltd, Taiwan) was also deployed at each level to record the humidity and temperature. The balloon was ascended at 18h00 (local time) and mostly descended at midnight or up to 07h00 next morning, but only data until midnight was used for further analysis. A whole night recording on Feb7th revealed more than 80% of calls of *C. plicatus* occur before midnight, while no activity was recorded after midnight at ground level. There was no recording at nights when the weather condition was not suitable to launch the balloon such as rain and strong wind (> 30km/h). Such conditions would deteriorate the sampling results, as well as harming our equipment.

A total of ten sites were chosen to launch the balloon. Sampling was conducted one night per site, except for the first site where data was collected for three consecutive nights. Site selection criteria include large open areas with no or very few high trees, far from power lines, and accessible with a truck. Selected sites were fallowed rice fields or other crop plantations located 2-10km from the nearest colony of *C. plicatus*. Sites were at least 2km apart.

Flight schedule and GPS coordination were informed to Kok Kratium military air base, also, a flashing light was attached to the balloon for aviation safety. Balloon launching followed the regulations of the air base.

2.2.3 Aerial insect sampling

Insects were collected by sticky traps in 12 nights. Plastic sheets were attached with sticky glue and folded to form 20×30cm-cylindrical-sticky traps. Each sampling night, a sticky trap was attached at each altitude, a few meters below bat detector. This method was adopted from Petkliang et al. (2017) and Fritz et al. (2011). Captured insects were kept at $4^{o}C$ and identified to order. Insect biomass was calculated from measurements of body length (Lumsden and Bennett, 2005).

2.2.4 Call analysis

Bat calls were analyzed using BatSound® software, version 4.2.1 (Petterson Elektronik AB, Uppsala, Sweden). Call identification of *C. plicatus* followed descriptions in previous studies (Utthammachai et al., 2008) and a reference collection made during the study. In the study area, *C. plicatus* has quasi-constant frequency calls with various peak energy frequency ranging mostly from 17-27kHz which, however, are distinctive from other known species whose calls are characterized by higher peak energy frequency.

2.2.5 Data analysis

Bat passes per minute was used to evaluate bat activity. A bat pass was defined as a sequence of calls with at least 2 sweeps within 1s. On average, bat activity was counted from 19h00 to 00h00 for each night, except two nights when the balloon was launched later because of weather and technical problems. For a site where sampling was done for three nights, data was averaged prior further analysis.

The Shapiro-Wilk test was applied to test if data followed a normal distribution. Square root transformation was used to normalise the data. One way ANOVA was used to examine the difference of bat activity at three altitude levels. Tukey’s post-hoc test was applied once there was a significant difference. In case data did not follow normal distribution, Kruskal-Wallis test was applied. Post-hoc Dunn’s test with Bonferroni correction was applied if there was a significant difference found after the Kruskal-Wallis test. The outlier was eliminated from the analysis. In one site where it was treated as an outlier, the number of feeding buzzes collected from the ground was exceptionally high. This site, in contrast to others which have no trees, was a fallow rice field next to a patch of madras thorn (*Pithecellobium dulce*) and earleaf acacia (*Acacia auriculiformis*) plantation. This acacia often in attract insects when in flower.

All statistical analyses were performed in R statistical software, version 3.5.0 (R core team) and RStudio, version 1.1.453 (RStudio, Inc). The level of significance for all tests is 0.05.

2.3 Results

During the course of field work, 12 nights of data collection were obtained. A total of 145.63h of recording at all three levels were analyzed with 2,633 recognizable passes of *C. plicatus* (Table 2.1).

There was a significant difference in the activity of *C. plicatus* between levels (Kruskal-Wallis test, $\chi^2 = 20.09$, d.f. = 2, p = 0.000). Number of recorded calls at ground level was significantly lower than aloft ($p < 0.01$). There was no statistical difference in bat activity between at 100m and 200m (post hoc Dunn's test with Bonferroni correction, p = 0.126). Temperature was significantly different between levels (ANOVA, $F_{2, 35} = 22.02$, $p < 0.001$). Temperature at the ground was significantly lower than at 100m and 200m (Tukey HSD test, $p < 0.001$), and there was no significant difference between 100m and 200m (Tukey HSD test, p = 0.682).

Humidity was also significantly different between the three levels (Kruskal-Wallis test, $\chi^2 = 15.649$, d.f. = 2, $p < 0.001$). Humidity at the ground level was higher than at 100m (post hoc Dunn's test with Bonferroni correction, p = 0.0048) and 200m (post hoc Dunn's test with Bonferroni correction, p = 0.0003). There was no significant difference found between 100m and 200m (post hoc Dunn's test with Bonferroni correction, p = 0.6245)

The number of feeding buzzes per minute was significantly different between the three levels (Kruskal-Wallis test, $\chi^2 = 16.019$, d.f. = 2, $p < 0.001$). The feeding buzz rate was highest at 100m, followed by 200m, and the lowest at the ground. However, there was no significant difference in feeding buzz per minute between ground level and at 200m (Dunn test with Bonferroni's correction, p = 0.2735).

Table 2.1 Total recording time (MEAN±SE), number of passes (MEAN±SE), average passes per minute (MEAN±SE), temperature (MEAN±SE), and relative humidity (MEAN±SE) in three altitude levels over 10 sites in Lopburi Province during February 2018. Different superscript letters indicate a significant difference among different altitudes.

	Total recording time (min)	**Average time per night (min)**	**Total bat passes**	**Number of bat pass per minute**	**Number of nights**	**Total feeding buzz**	**Number of feeding buzz per minute**	**Temperature (^{o}C)**	**Relative humidity (%)**
200m	2680	220 ± 20	876	0.30±0.06^{b}	10	10	0.0031±0.0013^{a}	28.35±0.54^{b}	48.68±2.27^{b}
100m	2780	230 ± 18	1619	0.62±0.11^{b}	10	96	0.0364±0.0148^{b}	27.68±0.60^{b}	52.51±2.92^{b}
Ground	3278	267 ± 16	138	0.05±0.02^{a}	10	1	0.0003±NA^{a}	23.46±0.56^{a}	69.16±2.69^{a}

The result from sticky traps showed that the highest biomass captured per night was at ground level (111.27±76.78 mg), followed by 100m (9.96±1.95 mg), and 200m (7.38±2.09 mg). The highest proportion of total insect biomass captured at the ground belonged to Isoptera, followed by Diptera, Homoptera, Coleoptera, Ephemeroptera, others, and Lepidoptera. At 100m level, Ephemeroptera was the order with highest percentage of biomass, followed by Homoptera, Isoptera, Diptera, Coleoptera, Lepidoptera. At 200m level, Diptera was the order with highest percentage of biomass, followed by Homoptera, Isoptera, Coleoptera, others, and Lepidoptera (Table 2.2).

Table 2.2 Percentage of insect biomass by orders in three altitude levels over 10 sites in Lopburi Province during February 2018. Column "Others" means various orders of insects which were found in the sticky traps including Odonata, Orthoptera or unidentified.

	Diptera	**Homoptera**	**Coleoptera**	**Isoptera**	**Ephemeroptera**	**Lepidoptera**	**Others**
200m	32.09	20.29	14.72	16.93	0	4.67	11.30
100m	12.91	22.47	11.57	16.71	25.95	10.38	0
ground	11.41	1.83	0.45	85.26	0.37	0.31	0.37

2.4 Discussion

The present study demonstrated for the first time the vertical stratification in activity of *C. plicatus*, an open space bat from Southeast Asia. The activity of *C. plicatus* was not distributed uniformly in the vertical dimension. Bat activity was lowest near ground level while the number of bat passes recorded aloft (100 and 200m) was nearly ten times higher. A pilot study conducted in rainy season 2017 showed that activity of *C. plicatus* at 100m was 3 times higher than near the ground (Nguyen and Bumrungsri, 2017). Griffin and Thompson (1982) also found activity of molossid bats, *Chaerephon jobensis* and *Mormopterus beccarri*, at 200m was 2-2.5 times higher than near the ground. A handful of bat species have been found foraging routinely at high altitude such as *Lasiurus cinereus* (Peaurach, 2003), *Nyctalus noctula* (Roeleke et al., 2016), *Tadarida tenotis* (Wellig et al., 2018), and *Taphozous theobaldi* (Roeleke et al., 2018). *Chaerophon plicatus* may have higher foraging activity at altitudes above 200m as found in the another mollosid bat, *T. brasiliensis* (McCracken et al. 2008). However, due to the regulation of the authority for flight safety, a balloon cannot be launched higher than 250m. From the evidence of *C. plicatus* foraging at height, activity monitoring studies of *C. plicatus* solely at ground level might provide an ambiguous insight into this species.

The higher number of passes and feeding buzzes recorded at high altitude may result from higher insect density at that level which is a consequence of the temperature inversion layer formed at night in the altitude of ~100 to 200m. The presence of a temperature inversion layer at this layer was confirmed by the evidence that the temperature at that altitude was on average 4.20^{o}C higher than at ground level while temperature difference was only 0.6^{o}C between 100m and 200m. The altitude of 100m might be the top of the SBL as there was no significant difference of temperature within a layer (i.e. from 100m to 200m) (Allappatu et al., 2009). The reason for insect layering and thus high bat activity may be maximum wind speed within inversion layer (Feng et al., 2004). The top of the SBL is usually associated with strong winds known as low level jets which are suitable for insect migration (Drake and Farrow, 1988; Riley et al., 1995b).

McCracken et al. (2008) mentioned that peak insect density corresponded with the altitude of the low level jet. In northeast India, an aerial netting study revealed a mass flow of insects, especially the brown plant hopper *N. lugens*, migrating at elevations between 130-180m (Reynold et al., 1999). In the present study, the presence of brown plant hoppers (*N. lugens*) at around 100-150m altitude was confirmed from sticky trap captures, while no *N. lugens* was found at ground level. This evidence supports the hypothesis that *C. plicatus* feeds on migratory *N. lugens* at high altitudes as the authors found evidence of *N. lugens* in the diet of *C. plicatus* in the dry season when there was no active rice field within the foraging range (Srilopan et al., 2018). McCracken et al. (2008) suggested a link between high altitude foraging of *T. brasiliensis* and migratory insects as both reached peaks at the same altitude. In addition, it is also reasonable to assume that bats are capable of changing altitude to follow the food resources. It has been established that *T. brasiliensis* track preys by changing foraging altitude in association with aerial insect distribution (Krauel et al., 2017). Previous radar studies have shown the presence of large *N. lugens* migration from 130 up to 2000m (Seino et al., 1987; Riley et al., 1995a). With the staple content of *N. lugens* in diet of *C. plicatus*, it can be hypothesized that *C. plicatus* forages both at 100-200m altitude as well as those much higher to follow the insect distribution in the air. This bat may also adjust their echolocation calls at different altitudes to increase foraging efficiency as found in *T. brasiliensis* (Gilliam et al., 2009; Krauel et al., 2018)

A study conducted by Srilopan et al. (2018) at the same area showed that Homoptera, Coleoptera, and Diptera together accounted for 75% of the diet of *C. plicatus*. It is remarkable to note that the sticky traps in the present study revealed that these three insect orders together represented 46.95% and 67.10% insect biomass at 100m and 200m, respectively. The ground level owned the highest biomass captured by sticky traps, however, nearly 90%of biomass were Isoptera, which seems not to be found in the diet of *C. plicatus*.

Increasing number of wind farms may increase the mortality risk of aerial bats such as *C. plicatus*. For wind turbines, the LLJ formed at the top of SBL is a major source of energy (Gurtierrez et al., 2017). Most newly installed two-megawatt wind turbines have blades which sweep from 60-120m in height which coincides with the altitude of highest activity of *C. plicatus* in this study. Bat species active at the altitude coinciding with the swept area of wind turbine blades are likely to be killed by barotrauma as found in the cases of *N. noctula* (Roeleke et al., 2016) and *T. teniotis* (Wellig et al., 2018) in Europe. In Asia, very few studies on the impact of wind turbines on bats has been conducted (Chou et al., 2017) despite the fact that it has the highest development rate of wind energy. As the trend for renewable resource continues, more wind farms are expected to be built. Locations proposed for wind turbine projects need to be surveyed both in vertical and horizontal dimensions to minimize the negative effect on bat communities. Awareness of the scientific community for the conservation of open airspace gradually increases (Davy et al., 2017), however, there are still many aspects remains unknown about the biology and behavior of open space bats (Voigt et al., 2018). It is known that *C. plicatus* moves between the roosting sites (Furey et al., 2018) and therefore between countries. As large number of *C. plicatus* aggregate and also possibly migrate, the understanding about altitude and landscape in the movement path at the 3D scale is needed to avoid the constructing or operating artificial objects hindering or harmful to the species.

Our finding supports the idea that airspace is also a habitat (Diehl, 2013). Bats, especially open space guilds, may perceive the vertical dimension as important as horizontal ones. Recent findings suggest insect migration represent mass nutrients moving between terrestrial ecosystems. The ability of flight means that insectivorous bats play a vital role in ecosystems. The stratification in foraging activity in the airspace implies *C. plicatus* play an important role in insect pests control and nutrient flux fixation not only in the area they inhabit of their presence but also at the landscape scale. Thus, conservation of this bat population will secure pest control services at a much larger scale. Unfortunately, a recent study in central Thailand found a dramatic decline in population of this bat (Binlasoi et al., unpublished data), for reasons yet unknown, and this could have a serious negative impact to food crop in the region.

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CHAPTER 3

Temporal Variation in Whole-Night Activity of an Open Space, High Flying Bat, *Chaerephon plicatus* (Buchanan, 1800) During Rainy Season

Temporal Variation in Whole-Night Activity of an Open Space, High Flying Bat, *Chaerephon plicatus* (Buchanan, 1800) During Rainy Season

Abstract

Foraging activity of *Chaerephon plicatus* was monitored for 104 hours in three levels from near the ground to 200m above ground level. The whole night activity pattern of *C. plicatus* in each level showed a high variation in different parts of the night. In addition, *C. plicatus* showed different patterns of nightly temporal variation between levels. All three levels showed the high activity of bats in the early part of the night. However, the activity of *C. plicatus* near the ground was gradually decreased until dawn. In contrast, the levels of 100m and 200m both showed a second peak of activity after midnight. The second peak of activity of 100m was from 01h00-03h00 and the second peak of 200m was from 04h00-05h00. Insect biomass collected from 2-15m near the ground level showed a gradual decrease from dusk to dawn which might have resulted in the decline in activity pattern of *C. plicatus*. Differences in whole night activity pattern of *C. plicatus* between levels might have been a result of shifting foraging activity in the vertical dimension to cope with changes in insect biomass and physical condition of the airspace.

Keywords: Aeroecology; vertical stratification; niche partitioning; migratory insects; nocturnal variation

3.1 Introduction

Spatial and temporal variation in activity patterns of organism reveals importance aspects in their ecology. Both diurnal and nocturnal animals are known to change their activity pattern for foraging or avoiding predation. The evolution of order Chiroptera, bats, were hypothesized that the group shift their activity to nocturnal to exploiting niche left by birds and reduce the risk of being predated (Thomas et al., 1991; Rydell and Speakman, 1995). Variation in whole night activity of bats was found in various groups of insectivorous bats (Kunz, 1973) and fruit bats (Zeppelini et al., 2017).

Previous studies suggested vertical stratification on bat activity in different levels of forest canopy (Hayes and Gruver, 2000; Plank et al., 2012). Clear stratification patterns were found profoundly in tropical forests rather than the temperate ones may be due to the distinction of forest strata in tropical regions (Plank et al., 2012). Therefore, a stratify habitat could be expected to result in the stratification in bat activity. Airspace is also a habitat with heterogeneity in physical conditions and resource distributions (Diehl, 2013). The vertical variation in these physical conditions and resource distributions may lead to the vertical variation in activity of open space bats. However, the stratification of open space bats occurs when considering in the airspace much higher than the vegetation structure.

The understanding of nocturnal rhythm of chiropterans in currently limited to understory bats, little is known if high altitude, open space bats vary their activity over space and time. Bats are opportunistic foragers, the high demand for food and highly mobile capacity would provide them highly dynamic in hunting for insects. Various researches have shown the shifting in activity of open space bats in accordance to insect abundance by season (Kelm et al., 2014; Roeleke et al. 2018). Kalcounis et al. (1999) suggested the temporal variation in bat activity recorded at the ground level might be a result in activity shifting of bats in vertical dimension. It is reasonable to expect the same model hold true for open space bats. Previous studies show that *T. brasiliensis* (McCracken et al. 2008), *T. teniotis* (Wellig et al., 2018), *C. plicatus* (Nguyen et al. submitted) concentrate their foraging activity at high altitude. The study in dry season suggested that peak activity of *C. plicatus* corresponded with top of stable boundary layer which is also the layer with high density of insects (Nguyen et al., submitted). Recent studies suggested that *T. brasiliensis* change their foraging altitude in accordance with insect density in the air column (Krauel et al., 2018a; Krauel et al., 2018b). Lee and McCracken (2005) found the difference in diet composition found between evening and morning foraging bats which suggest that *T. brasiliensis* change foraging altitude between two periods. Currently, there is, still no direct evidence found for a shifting in foraging patterns between altitudes. Thus, this present study aimed to answer if *C. plicatus* show temporal variation in vertical activity pattern.

3.2 Materials and methods

This study was conducted in Ban Mi District (15.057^{o}N, 100.5313^{o}E), Lopburi Province, Thailand. Khao Wong Kot Cave located in the study area is home of nearly half a million wrinkle lipped-free tailed bats. The surrounding landscape is dominated by paddy fields (Figure 3.1).

3.2.1 Bat activity sampling

Data were collected in six nights during May 29th to June 6th 2017. To record bat echolocation, we used two Pettersson D240x bat detectors (Pettersson Elektronik AB), each weights 170g including battery. Each detector was set at Time expansion mode (0.1, 1.7second in length) and connected to a Zoom H2 recorder to store the echolocative calls. Recoding files were set at *wav format, 44.1 kHz sampling rate. The bat detector was powered by a 9V-alkalin battery which could allow 12-16 hours in continuous operation.

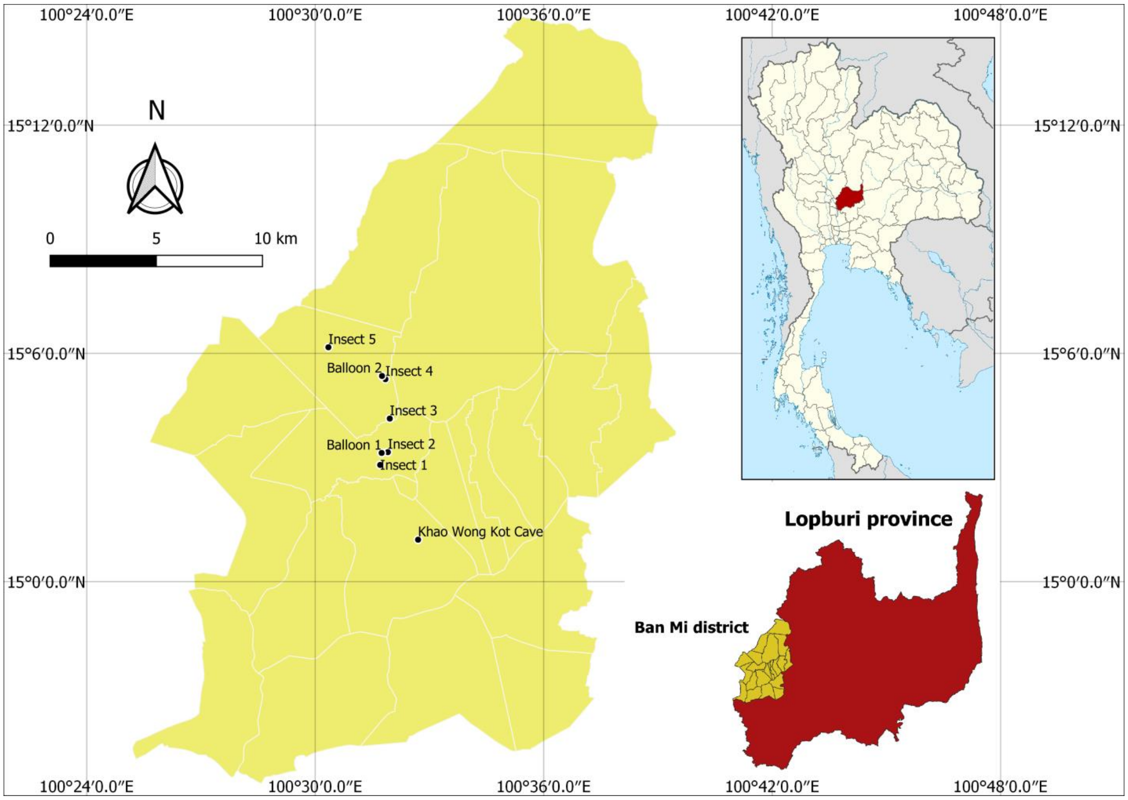

Figure 3.1 Map of the study area and distribution of sampling sites (Insect 1-6: Sites where insects were collected; Balloon 1-2: Sites where balloon was launched).

We placed one bat detector and one recorder in a waterproof box with a dimension of 25×7×5cm. A piece of microphone sponge was placed in front of microphone of each detector to alleviate wind noise. Mentioned boxes of equipment were suspended at least10m below a 3mx3m kite aerial oblate spheroid balloon (©Tichuan International Co., Ltd, China). Bat activity was recorded in three levels: (1) 2m above ground level (ground level), 100m above ground level and (3) 200m above ground level. Each night, two of the three mentioned levels were randomly recorded simultaneously. The balloon was ascended at 19h00 (local time) and descended at 07h00 in the next morning. There was no recording at nights when the condition were not favor for recording bats and launching balloon such as rain and strong wind (>30km/h), such conditions would deteriorate the sampling results, also be harmful to our equipment.

Altitude of bat detectors to the ground level were estimated by the formula h = 0.9Lsin(α) (Griffin and Thompson 1982); with (h) is the relative altitude of a bat detector to the ground, (L) is the length of the line was paid out and (α) is the angle of the line.

Sunset time was 18h45 local time and sunrise was 05h45 local time. We divided night into 20^{th} percentile (Hayes, 1997). Each percentile contains 33minutes time duration (Table 3.1).

Table 3.1 Time and percentile of the night.

Time	**Percentile**
18h45-19h17	5^{th}
19h18-19h50	10^{th}
19h51-20h23	15^{th}
20h24-20h56	20^{th}
20h57-21h29	25^{th}
21h30-22h02	30^{th}
22h03-22h35	35^{th}
22h36-23h08	40^{th}
23h09-23h41	45^{th}
23h42-0h14	50^{th}
00h15-00h47	55^{th}
00h48-01h20	60^{th}
01h21-01h53	65^{th}
01h54-02h26	70^{th}
02h27-02h59	75^{th}
03h00-03h32	80^{th}
03h33-04h05	85^{th}
04h06-04h38	90^{th}
04h39-05h11	95^{th}
05h12-05h44	100^{th}

Flight schedule and GPS coordination were informed to Kok Kratium military air base, also, a flashlight was attached to the balloon for aviation safety. Balloon launching was followed the regulations of the air base.

3.2.2 Call analysis

Bat calls were analysis by BatSound software, version 4.2.1 (Petterson Elektronik AB). Call determination of *C. plicatus* were followed descriptions by previous studies (Utthammachai et al., 2008) and the references from this study collection.

3.2.3 Insect sampling

Aerial insects were collected at five sites each distant 1-3km from the closet one at three heights above the rice canopy: 1-2m, 6-8m, and 12-15m. We applied the method as described by Petkliang et al. (2017) which a pole was set to hang six 20×30cm-cylindrical-sticky traps, two sticky traps per height. A battery-powered light was also set as each height to lure insects. Collecting insects simultaneously at the same spot allowing insects to be trapped in their currently height rather than collecting each individual height at different spots (Intachat and Hollway, 2000).

Insects were collected 2-3 consecutive nights, whenever possible, at each site when not raining and calm wind (< 16km/h). Arthropods were sampled from 18h00 to 6h00. The traps were removed at a three-hourly interval, thus, on average, each sampling night contained four consecutive periods: 18h00-21h00, 21h00-00h00, 00h00-03h00, and 03h00-06h00. Temperature (^{o}C) and relative humidity (%) were recorded every 10mins by a datalogger TM-305U (Temars Electronics Co., Ltd).

Samples were stored in refrigerators at 4^{o}C and identified to order or family using a compound microscope at the Small Mammal, Bird, and Spider Research Unit lab, Department of Biology, Prince of Songkla University.

3.2.4 Data analyses

All statistical analysis was performed by R statistical software, version 3.4.1 (R core team) and RStudio, version 0.99.489 (RStudio, Inc). Level of significance for all tests is 0.05.

Bat activity

Kruskal-Wallis test was applied to test if there was any difference in activity between three levels. Post-hoc Dunn's test would be applied if there was a significant difference found in Kruskal-Wallis test.

Kolomogorov-Smirnov two-sample test was applied to check if the activity of three levels followed the same distribution. In case null hypothesis rejected, the conclusion that bat activity was significantly difference between levels of testing could be given.

Insect biomass

Barlett's test of homogeneity of variances ($\alpha = 0.05$) was used to test if the data were normal distribution. Kruskal-Wallis test ($\alpha = 0.05$) and post-hoc Dunn's test (with Bonferroni correction, $\alpha = 0.025$) were used to check if there was a difference in the four periods within one night.

3.3 Results

3.3.1 Bat activity

A total of 104 hours of recording was collected and selected for data analysis, including 41 hours, 32 hours and 29 hours of recording at the ground, 100m and 200m level, respectively.

Kolmogorov-Smirnov two-sample test showed that the pattern of bat activity at the ground was statistically different that at 100m ($p = 0.002$) and 200m ($p = 0.022$). Meanwhile, no statistical difference was found in the activity pattern at 100m and 200m, although the value of p was marginal ($p = 0.057$) (Table 3.2).

Table 3.2 Result from Kolmogorov-Smirnov two-sample test comparing activity pattern between ground, 100m, and 200m (*-p < 0.05, **-p < 0.01).

Level	Ground	100m
Ground	-	0.002**
200m	0.022*	0.057

Bat activity at the ground was peak in the early part of the night till 45th percentile, 23h41 local time, 70% of activity concentrated in this period. The activity at the ground level showed a gradually decreasing trend through the course of the night (Figure 3.2A). This trend could be clearly seen when whole night activity was divided into 4 parts including 18h45h-21h29, 21h30-00h14, 00h15-02h59, and 03h00-05h44 (Figure 3.4B). The Kruskal-Wallis test showed significant different found in activity of *C. plicatus* at night between four parts (Kruskal-Wallis test, χ^2 = 8.563, d.f. = 3, p = 0.035). Post hoc Dunn test with no correction showed that activity at the first part of the night was significantly different from the third (p = 0.011) and fourth part (p = 0.007) (Table 3.3).

Table 3.3 Foraging activity of *C. plicatus* at the ground during four time period. Difference letters indicates statistical difference (Post-hoc Dunn test, p<0.05). Different superscript letters indicate a significant difference among different time periods.

	Bat pass per minute recorded in four time periods			
Time	18h45-21h29	21h30-00h14	00h15-02h59	03h00-05h44
Pass per minute (±SE)	0.72±0.26^{a}	0.31±0.14^{ab}	0.11±0.02^{b}	0.02±NA^{b}

Whole-night activity pattern of *C. plicatus* was similar at 100m and 200m level with 2 peaks, first peak was at early part of the night followed by a flat duration in activity and the second peak came after. However, the relative difference of two peaks was also difference between two levels. At 100m, the first peak was from early of the night until 40th percentile (23h0h), and the second peak was smaller than the first one with duration from 60th till 75th percentile (from 00h48 to 02h59). Meanwhile, the 200m showed an opposite trend with the first peak, from early to 30th percentile of night, was relatively smaller than the second peak near the dawn, 75th until 95th percentile of the night (Figure 3.2B, Figure 3.2C).

3.3.2 Insect biomass

Nightly insect catches were obtained from 13 sampling nights, 2.60 ± 0.24 nights per site. A total of 17,735 insects were captured from 2-15m above ground level. There were 12 orders of insects found during the study, the highest number of insects belonged to order Homoptera (Figure 3.3A), 4,442 catches. Family Delphacidae and Cicilidae were the highest proportion among captured Homopterans (Figure 3.3B), as respectively, 55.76% and 27.13%.

Insect biomass showed a gradual decrease during the night (Kruskal-Walliss test, $p < 0.0001$) (Figure 3.4A), with the highest biomass obtained at 18h00-21h00 (16.00 ± 0.58 mg/3 hours), following by 21h00-00h00 (6.22 ± 0.71 mg/3hours), 00h00-03h00 (3.62 ± 0.55 mg/3hours), and 03h00-06h00 (2.45 ± 0.24 mg/3hours) respectively (Dunn's test with Bonferroni correction, $p < 0.0003$). However, there was no significant difference found between 00h00-03h00 and 03h00-06h00.

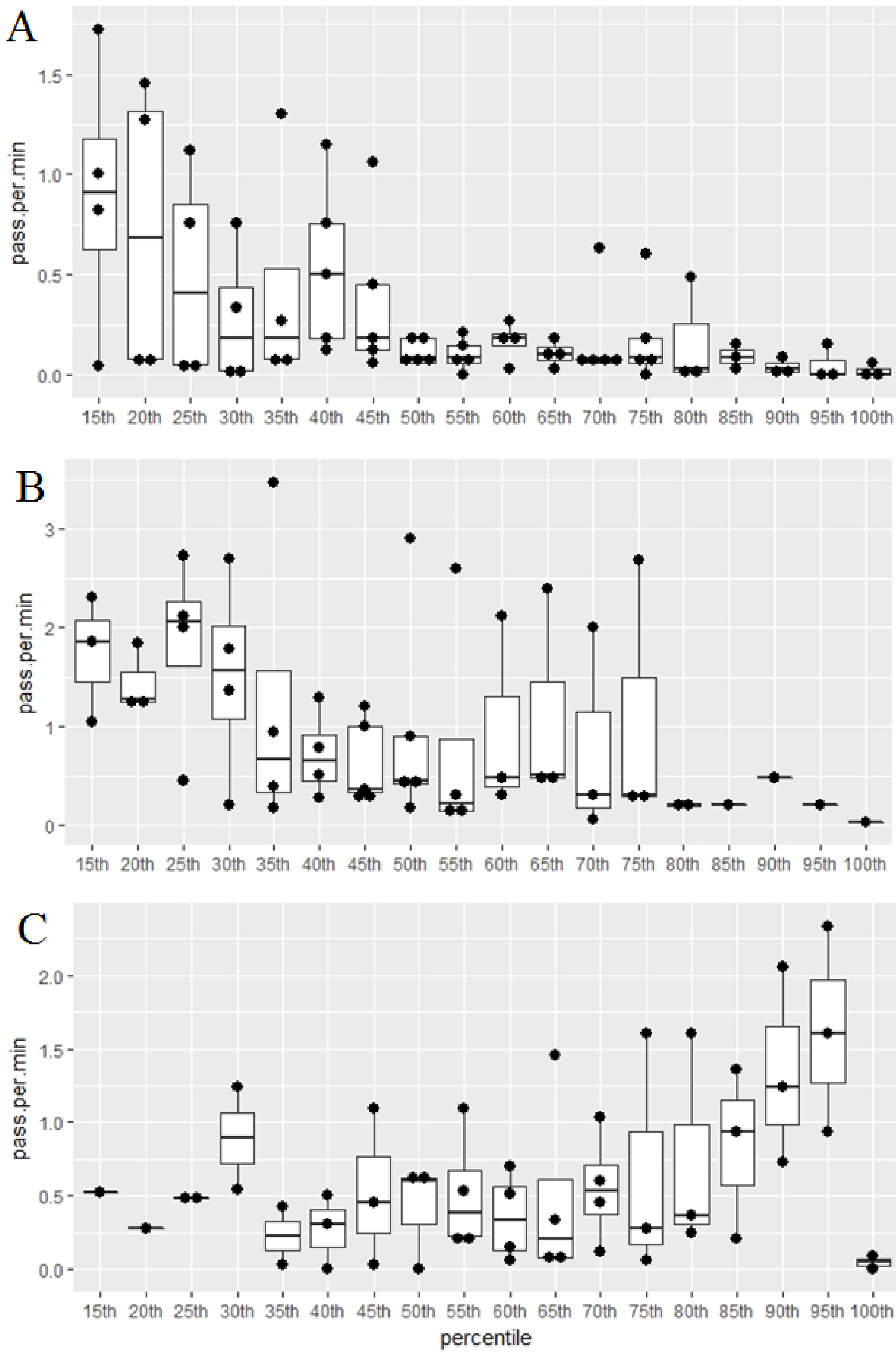

Figure 3.2 Temporal distribution of activity of *C. plicatus* for each studied level. (A) Ground level, (B) 100m, (C) 200m.

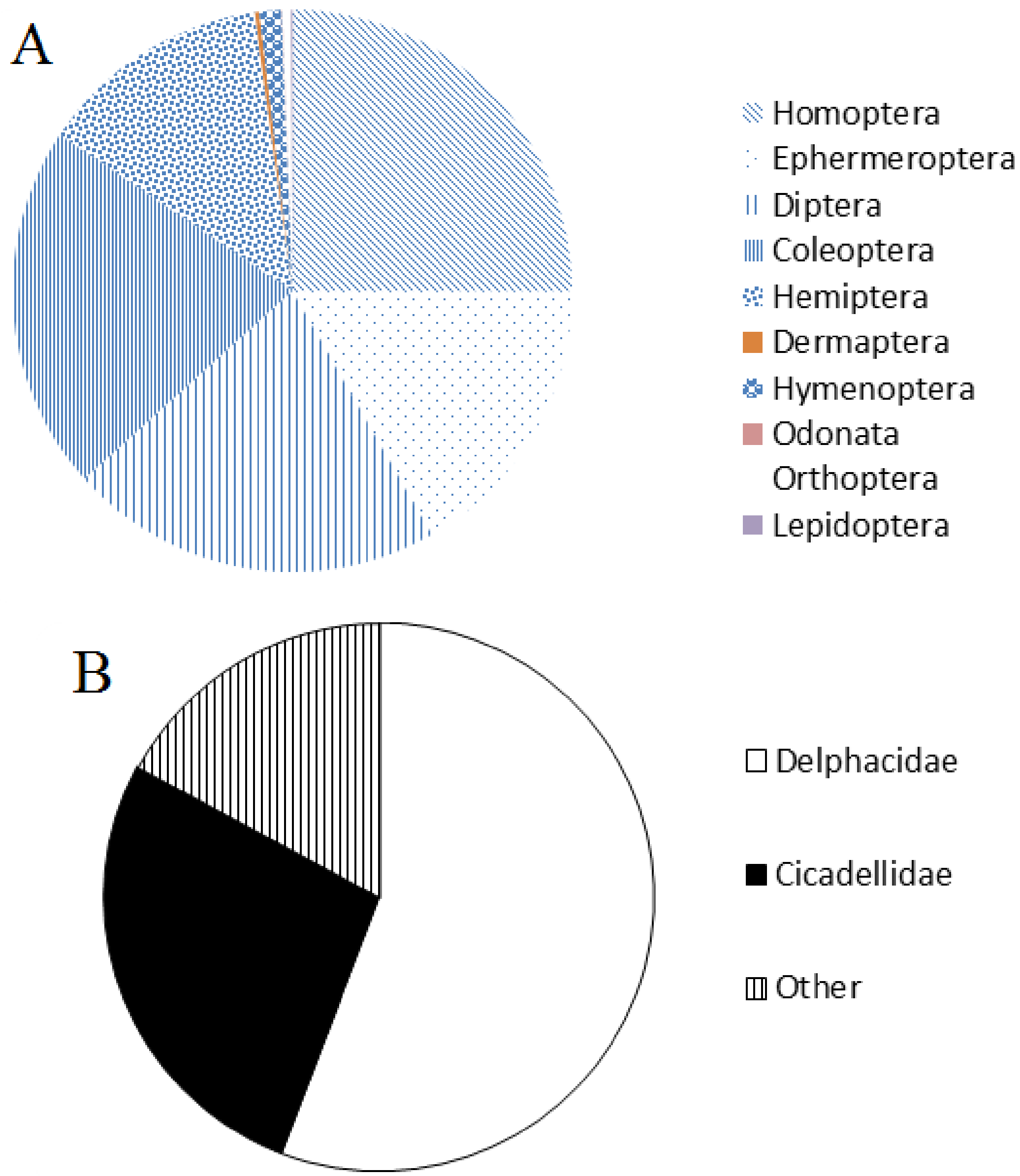

Figure 3.3 (A) Propotion of total number of captured insect orders (Total catches: 17,735). (B) Propotion of Homopteran.

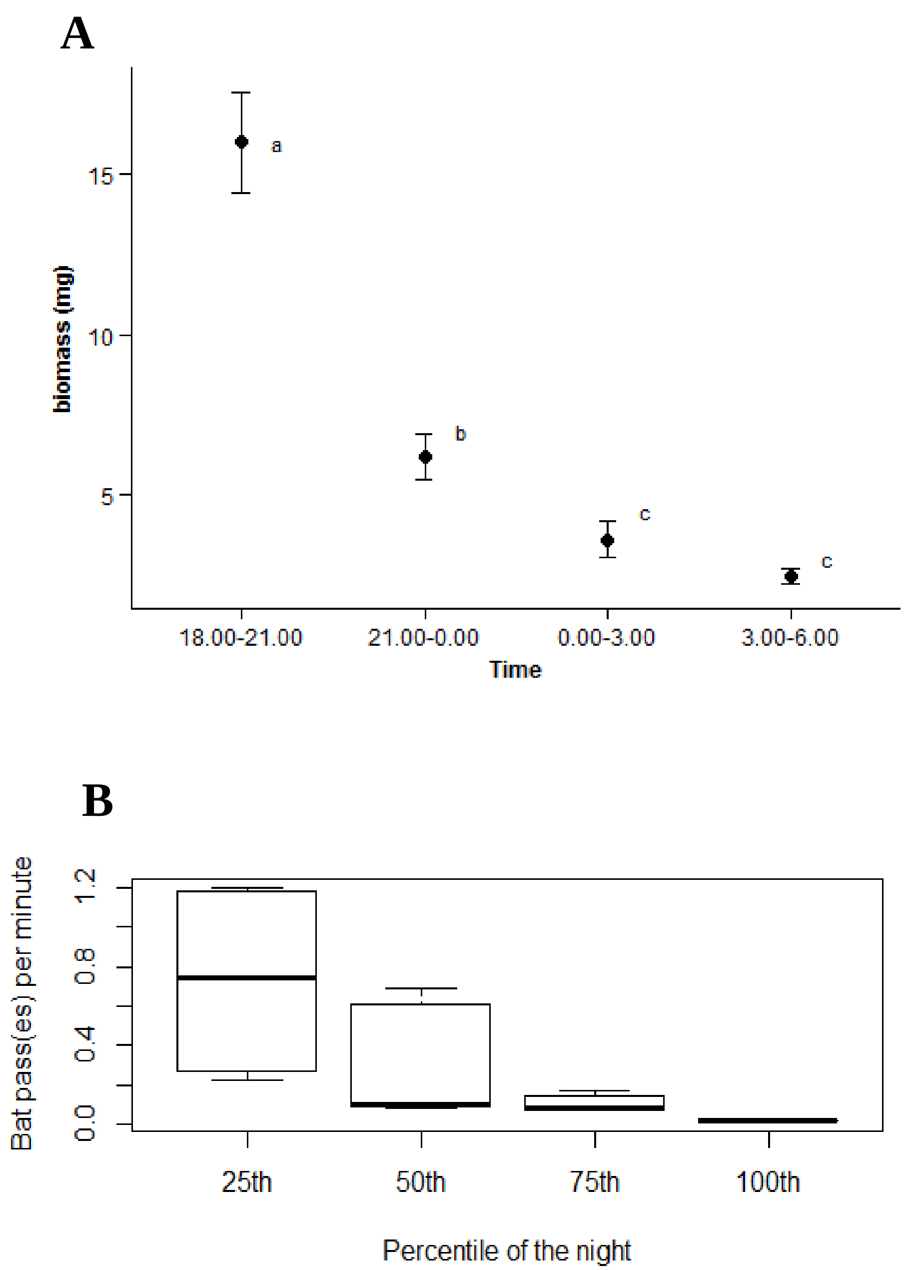

Figure 3.4 (A) Total insect biomass in four time period. Error bars represent the standard error of the mean. The annotate letters denoted a significant differences performed by Dunn's test, with Bonferroni correction (significant level = 0.025). (B) Number of bat passes near ground level (2m) in four parts of the night. Different superscript letters indicate a significant difference among different parts of the night.

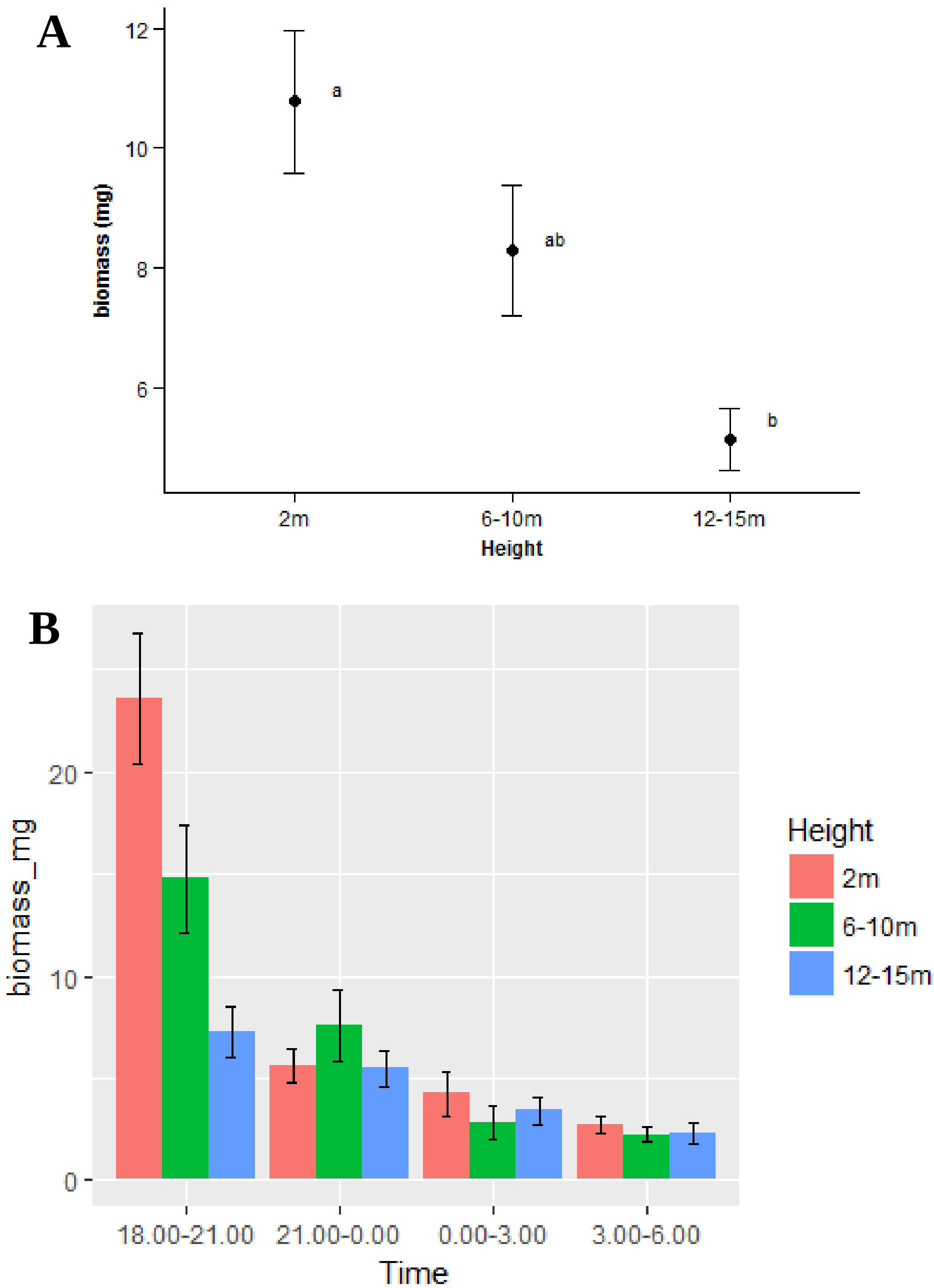

Figure 3.5 Insect biomass in different heights. (A) Average nightly insect biomass in different heights. (B) Insect biomass in different heights at different parts of the night. Different superscript letters indicate a significant difference among different parts of the night.

The height of traps also affected the number of captured insect biomass (Kruskal-Wallis test, $p < 0.0001$) (Figure 3.5A). The 2m-trap and 6-8m-trap showed a similar number of biomass which were, respectively, 11.01 ± 1.35 mg and 8.05 ± 1.97 mg (Dunn's test with Bonferroni correction, $p = 0.3$). Meanwhile, the capture at 12-15m was 4.90 ± 0.72 mg, which were significantly lower than 2m (Dunn's test with Bonferroni correction, $p < 0.0001$).

3.4 Discussion

In this chapter, we propose a temporal variation in activity of *C. plicatus*, an open space bats. The activity of *C. plicatus* was not distributed uniformly from the dusk to dawn at three levels. Since the limitation in our data collection, we would like to acknowledge this chapter as a hypothesis that can be further examined in future studies.

Nightly activity of *C. plicatus* showed highly temporal variation when considering each set stratum. Variation in nightly activity pattern between forest strata was found in Myotis bats in a temperate forest (Hayes and Gruver, 2000). The reverse trend among three height levels might be a result of shifting activity of bats in vertical dimension (Kalcounis et al., 1999). In this present study, the gradually decreasing trend found at the ground can be explained by the decline in insect biomass during the course of the night as previous studies also found bat activity related with insect abundance (Wickramasinghe et al., 2003; Phommexay et al., 2011). Most insects swarmed at the first three hours of the night. Planthoppers are known to begin their migration at the early evening (Riley et al., 1987). Previous studies showed the capture of migratory planthoppers from 130-2,000m above ground level (Riley et al., 1995; Qi et al., 2014). The study at the dry season in the area showed migration insects such as brown plant hoppers captured at the altitude from 100-150m (Nguyen et al., submitted). This trend also was the trend of Homopterans as the insects were the main diet of *C. plicatus* with 43% volume (Srilopan et al., 2018). High altitude foraging activity of *T. braziliensis* revealed a link with the aerial insect density (McCracken et al., 2008). In this study, we could not acquire data of aerial insect abundance in the air at high altitude. However, high insect density at level 100 to 200m might also have resulted on high activity of *C. plicatus* at 100m and 200m above ground level.

It is worth mentioning that the difference in activity pattern of the 100m and 200m level, although showed no significant difference, hidden an interesting fact about the ecology of fauna in the evolution of air column. The study in dry season revealed evidence that 100m altitude might have been the top of the stable boundary layer (Nguyen et al., submitted) at least until midnight. At the progress of the night, the warm air column rise its altitude leading the top of stable boundary layer moving up to the higher altitude (Day et al., 2010). It could be hypothesized that the evolution in air column led to the rise of peak activity of *C. plicatus* at 200m near the dawn. Numerous studies have concluded that aerial insects tend to form large aggregate at top of stable boundary layer where they could find the favorable conditions for migration such as shear wind with high velocity (Drake and Farrow, 1988). The only case known in bats was proposed by McCracken et al. (2008), which showed a link between peak activity of *T. brasiliensis* and the low level jet winds that formed at top of stable boundary layer. A second explanation for the very high activity recorded at 200m near the dawn is that bats raised their activity to fly back roosting sites. Observation at the roosting sites showed that when returning early morning, bats tended to aggregate around 200m height, ca. 0.5-1km from cave entrance, and dived to the roost with high speed (Bumrungsri pers. obs.). Bats raised altitude possibly to take advantage of high wind speed and avoid contact to objects near the ground in their hurry-home flights. An alternative hypothesis for increase in activity at higher altitude is a temporal influx of migrating insects in the early morning at high altitude. In North America, studies on the high flying bats, *Tadarida brasiliensis*, suggested that the species changed their foraging altitude to exploit the migratory insects at high altitude near the dawn (Lee and McCracken, 2005; McCracken et al., 2012).

Lack of empirical data about aerial insect fauna and physical conditions of the aero-habitat in this study making the explanation for the vertical stratification of *C. plicatus* remain ambiguous. Future studies focus on higher altitudes and nature of aerial resources and conditions are needed to uncover great number of conceal aspects of *C. plicatus* as well as other aspects of aero-ecology.

Spatial and temporal variation in foraging activity of animals may reveal the partitioning of resource in a community. Kunz (1973) showed that differences in temporal and spatial activity patterns of different bat species in central Iowa, USA was a result of reducing resource competition. The temporal variation in vertical scale of *C. plicatus* that we found in this study suggests a spatial partition in the third dimension. In studied site, we found seven species of bats actively foraging at the ground level including: *Myotis horsfieldii, M. muricula, Scotophilus kuhlii, S. heathii, Taphozous melanopogon, Taphozous* sp., *and C. plicatus.* However, at the altitude of 100m and 200m above ground level, most calls recorded belonged to *C. plicatus*, and few calls of *T. melanopogon*, and *T.* sp. To *C. plicatus*, low frequency and high intensity echolocation call which suffer less atmospheric attenuation is an adaptation to open space foraging. However, the ground level with higher clutter structures and vegetation require a different echolocation structure with higher frequency, shorter call duration, and broader bandwidth (Gillam et al., 2009), by which *Myotis* sp. and *Scotophilus* sp. are more fit than *C. plicatus*. In addition, Voigt and Holderied (2012) proposed that Molossid bats are adapted to forage in open space since high cost of manoeuvring at the edge or near tree top areas. The high activity of *C. plicatus* at early part of the night at ground level may have explained by the high density of insect swarming after sunset. *C. plicatus* takes advantage from the burst of swarming insects near ground at dusk. The high cost of manoeuvring flight near the ground can be compensated by high insect yields. Especially, the insect biomass at 2m, below tree canopy, is significantly higher than that of 15m, also the height of tree top in the area of study (Fig. 3.5A). However, later at night, especially after midnight, the density of insects drastically decrease forcing *C. plicatus* to shift their activity to higher altitude since the high paid off in energy expenditure. Meanwhile, the other open-edge species like *Scotophilus* sp. and *Myotis* sp. are more efficient to exploit habitat near the ground with lower energy expenditure. A previous study showed that *Myotis horsfieldii* accounted for the highest proportion of bat passes recorded near the ground in the area of study with 40% of all species (Suksai and Bumrungsri, submitted.). When insects are abundance, interspecific competition is not serious, multiple bat species can exploit the resource at the same spatial scale. However, when the resource abundance reduce, species with less hunting efficiency are forced to shift their activity to reduce interspecific competition as shown in case of *Nyctalus noctula* and *Pipistrellus nathusii* (Roeleke et al., 2018). Niche overlapping of *C. plicatus* and other insectivorous bats in horizontal dimension might be a reasonable explanation for the shift in activity of this species in vertical dimension.

3.5 Conclusion and suggestion

This present study highlights highly time-dependent variation activity pattern of *C. plicatus* in three studied strata from the ground level to the altitude of 200m. These differences may come from the shift in vertical dimension of *C. plicatus*.

Although revealing the stratification in vertical lane of *C. plicatus,* this study could only reach the altitude of 200m since the limitation of air-traffic-safety regulations in the study area. It is reasonable to suggest that *C. plicatus* could climb far-higher than 200m. The lowest part of troposphere is highly stratified with high dynamic in spatial and temporal scale. This may pose a suggestion about the dynamic of its fauna. Bats are opportunistic foragers which are attracted by large aggregate of insects. It is still unknown how high flying bats species such as Molossids could navigate to find the prey in a non-boundary habitat air. How high flying bats exploit the complex and dynamic structure of the vertical dimension will reveal new insight about the ecology and evolution of Chiropterans.

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CHAPTER 4

GENERAL DISSCUSION AND CONCLUSION

Vertical stratification in foraging activity of *Chaerephon plicatus* in Lopburi province, Central Thailand was investigated by comparing the activity of bats between ground level and aloft (100m and 200m). In addition, comparison of whole-night activity patterns between altitudinal levels was conducted to further clarify the stratification of the species in the air column. These prospects will be discussed and concluded with implication revealed for conservation and future studies.

4.1 Vertical stratification in foraging activity of *Chaerephon plicatus*, a potential of specialization in exploiting layering nature of the airspace

This study highlighted the importance of vertical dimension to the ecology of a high flying open space bat species, *C. plicatus*. As the species is found to forage on migratory insects and exhibited a high activity in Stable boundary layer, it is possibly a potential specialization of *C. plicatus* to exploit the layering nature of the lowest part of the troposphere.

There has been suggested a general link between migratory insects and bat activity in high altitude (Rydell et al., 2010). However, it has been known for decades that nocturnal migratory insects aggregate in layers which are well defined by special atmospheric condition such as strong wind or warm air (Drake and Farrow, 1988; Wood et al., 2010). In tropical area, it is proposed that the layers of strong wind are more important for the formation of large aggregate of insects in the air (Feng et al., 2004). A recent study suggested that bats can assess the weather condition such as wind speed, wind direction and air pressure for their migration flight (Dechmann et al., 2017). It means bats can possibly probe the air for layers with suitable atmospheric conditions which promise to have high insect density. Therefore a link between bat activity and migratory insects suggested before may have indeed been a link between bats and layering nature of troposphere. As many bats are known to exploit high altitude for their daily tasks, the specialization to exploit layer of airspace may possibly be common among them.

4.2 Variation in whole-night activity of *Chaerephon plicatus* in vertical dimension

This is the first study has tried to describe the whole-night activity patterns of *C. plicatus*, a tropical aerial-hawking bat, from near the ground up to 200m above ground level. Although a small sampling size, we proposed that *C. plicatus* exhibited different whole night activity pattern between altitudinal levels. *C. plicatus* can shift their activity in different parts of the night in order to seek vertical dimension as seeking for large aggregate of insects which provide bats with the highest profit. Previous studies suggested a shift in foraging behavior of bat in different seasons (Kronwitter, 1988), or different meteorological conditions such as the arrival of cold front (Krauel et al. 2018). In this case, the bats might change their altitude of foraging in different parts of the night. The composition of insects at different altitude can be different, if the bats do shift their activity in vertical dimension, we can predict some differences in diet composition between the early night and early morning feeding bout as the bats forage at different altitudes with different insect compositions.

4.3 Implication for conservation

This study showed the evidence of high altitude foraging activity in *C. plicatus* for the first time. However, the altitude with highest activity of *C. plicatus* is also the range of the two-megawatt wind turbine blade, which from 40-120m. Wind energy installed in the area with large colony of *C. plictus* might harm the species as increase fatality by collision. A decrease in *C. plicatu*s population is also equal to economic loss to the rice farmers in the area of bats, since the species is an effective bio-control agent to rice pests.

Traditional approaches in monitoring bats suggest intense monitoring in different habitats to investigate the habitat use of bat species. However, open-space bats could fly far higher than the canopy layer of vegetation, monitoring at the ground might create insufficient data. Bats vary their activity three dimensionally.

From the evidences obtained in this study, we strongly suggest that projects for monitoring bats considering obtaining data both at different habitats near the ground (horizontal dimension) and different altitudes above ground (vertical dimension).

4.4 Limitation of this study and recommendation for future studies

This study highlights the vertical stratification in vertical dimension from near ground level to 200m above the ground level in population level. We suggest that the *C. plicatus* might probably forage higher than 200m. Future studies could uncover the foraging activity of the species in higher altitude and the relationship with insect distribution in the air column. With the upgrade and evolution of technology, lighter transmitter that fitted to *C. plicatus* body weight, 15.4 g, are expected to be built. Thence, we suggest further researches on individual levels to see how sex and body condition affect the high altitude foraging of the bats.

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APPENDIX

Appendix 1 Budget for research items

Item (Type)	Company (or origin)	Unit	Price (in THB)
Helium-filled kite aerial oblate spheroid balloon (3x3m)	Tichuan International Co., Ltd, China	2	27,700
Helium gas	Local providers	21 cubic meter	18,000
Dyneema tether 450kg test	http://www.winchline.nl/index.php	1000m	5,600
12 V Electric Winch	Allsopp Helikites Ltd	1	49,500
GPS-microclimates transmitter	Custom-made by Asst. Prof. Dr. Annop Ruangwiset	1	8,000
Pettersson D240x bat detector	Pettersson Elektronik AB, Uppsala, Sweden	3	97,800
Zoom H2 (or H2n) recorder	ZOOM Corporation	3	19,500
Data logger TM-305U	Tenmars Electronics Co., Ltd, Taiwan	3	11,310
Harris Single Stage Regulator	©Harris Products Group	1	3,500
Total			**240,910**

Appendix 2 Some notes on technical details

1. The most important issue for this balloon project is the strength of the tether line. The line is needed to be strong enough to withstand the tension since the wind at high altitude could reach up to 10-30m/s. I would suggest using the Dyneema line, 450kg-test, for a 3m×3m balloon.
2. The tail of the balloon plays a vital role in its dynamic and stable during operation. It is recommended to check the tail carefully before ascending.
3. Using an electric winch could save a lot of effort for researchers and helpers. However, the operation of the winch to ascend and descend the balloon is needed to be aware of in term of speed. Ascending or descending the balloon too fast and continuously would result overheat the winch and therefore the balloon line. Dyneema tether is not heat-resistant, the strength of Dyneema is drastically decreased in higher temperature, particularly over 50^{o}C.
4. A 3m×3m balloon as used in this thesis can be transported by using a standard pick-up truck. However, the transportation process poses a high risk for the balloon. In this thesis, two balloons were damaged during transportation.
5. It is important to fill gas and check the balloon daily. Therefore, it is necessary to have a reserve helium tank in the field.
6. The wind condition might be very unpredictable. Researchers can frequently check the tension of the balloon line to decide when to descend the balloon, a lot of efforts can be saved.
7. A suitable type of glove will be very useful for researchers and helpers

Appendix 3 Inflating and setting balloon

1. Put the balloon on a tarpaulin

2. Install a regulator to helium tank

3. Pump helium gas to the balloon

4. Keep pumping until the balloon is fully inflated

The links below are videos, which I posted on Youtube, demonstrating how to inflate and ascend the balloon.

https://www.youtube.com/watch?v=hTIDk-QrND0
https://www.youtube.com/watch?v=dHWsE0BFwJg

5. Install the tail for the balloon

6. Nail the balloon on the ground

7. A thunderstorm is coming

Appendix 4 Setting equipment, transporting the balloon and others

1. A box contains bat detector and recorder

2. The box is mounted to the balloon line

3. GPS transmitter

4. Data logger

5. Ascend the balloon with a tow net

6. Sticky traps

7. Use a car as an “anchor”

8. Monitor altitude of the balloon

9. Transport the balloon by a normal pick-up

10.Transport the balloon by a truck

11. Damage caused by transportation
(The first balloon was totally damaged)

12. Damage caused by transportation
(This is the second balloon)

13. Luckily, we could seal the holes and continued the campaign

14. Pupils of Nong Krabueang School came to see the balloon before going to school

15. A picture with Khun Piroj Nasing (right), and his wife (left)

16. A taste of Lopburi after the field campaign (the last day of King Narai Festival)

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