The Relationship between the Proportion of Moths in Diet and Call Frequency of Bats in Superfamily Rhinolophoidea in Bala Forest, Hala-Bala Wildlife Sanctuary, Narathiwat Province

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ชื่อวิทยานิพนธ์	ความสัมพันธ์ระหว่างสัดส่วนผีเสื้อกลางคืนในอาหารกับคลื่นความถี่เสียงของค้างคาวในวงศ์ค้างคาวมงกุฎ และวงศ์ค้างคาวหน้ายักษ์ ในป่าบาลา เขตรักษาพันธุ์สัตว์ป่าฮาลา บาลา จังหวัดนราธิวาส
ผู้เขียน	นายอมร ประจักษ์จิตร
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บทคัดย่อ

จากการศึกษาความสัมพันธ์ระหว่างสัดส่วนของผีเสื้อกลางคืนในอาหารกับคลื่นความถี่เสียงของค้างคาวในวงศ์หน้ายักษ์และค้างคาววงศ์มงกุฎ ในป่าฮาลาบาลาจังหวัดนราธิวาส เพื่อทดสอบความสามารถของคลื่นเสียงที่ใช้ของค้างคาวในสองกลุ่มดังกล่าวต่อการล่าเหยื่อในกลุ่มผีเสื้อกลางคืน (ตามข้อสมมุติฐาน Allotonic Frequency Hypothesis (AFH) ที่กล่าวว่า ค้างคาวที่ใช้คลื่นความถี่เสียงสูงหรือต่ำกว่าเสียงที่ผีเสื้อกลางคืนส่วนใหญ่ได้ยิน (20 - 60 กิโลเฮิร์ต) จะสามารถล่าเหยื่อในกลุ่มผีเสื้อกลางคืนได้ดีกว่าค้างคาวที่ใช้ช่วงความถี่เสียงในช่วงความถี่เสียงที่ผีเสื้อกลางคืนส่วนใหญ่ได้ยิน) โดยมีข้อสมมุติฐานในการทดสอบหลักสองข้อ คือ หนึ่ง ค้างคาวที่ใช้คลื่นความถี่เสียงต่ำกว่า 100 กิโลเฮิร์ต จะมีความสัมพันธ์ของสัดส่วนผีเสื้อกลางคืนในอาหารในเชิงบวกกับคลื่นเสียงที่เพิ่มขึ้น สอง สำหรับค้างคาวที่ใช้คลื่นความถี่เสียงมากกว่า 100 กิโลเฮิร์ตขึ้นไปสัดส่วนผีเสื้อกลางคืนในอาหารน่าจะผันแปรเชิงบวกกับลักษณะของความสามารถในการบิน

จากค้างคาวที่จับได้จำนวน 87 ตัว จาก 6 ชนิด ในวงศ์ค้างคาวมงกุฎ และ 71 ตัว จาก 6 ชนิด ของค้างคาวในวงศ์หน้ายักษ์ โดยทดสอบแยกเป็นกลุ่มๆ ตามคลื่นความถี่เสียงคือ กลุ่มค้างคาวที่ใช้คลื่นความถี่เสียงน้อยกว่า 100 กิโลเฮิร์ต กลุ่มค้างคาวที่ใช้คลื่นความถี่เสียงมากกว่า 100 กิโลเฮิร์ต และกลุ่มที่รวมค้างคาวทั้งสองกลุ่มเข้าด้วยกัน พบว่าค่าสัดส่วนเปอร์เซ็นต์เชิงปริมาณเฉลี่ยของผีเสื้อกลางคืนที่พบในมูล มีความสัมพันธ์เชิงบวกกับคลื่นความถี่เสียงอย่างมีนัยสำคัญ ทั้งสามกลุ่ม ซึ่งเป็นไปตามข้อสมมุติฐานข้อแรก แต่ไม่พบความสัมพันธ์ของระหว่างค่าสัดส่วนเฉลี่ยของผีเสื้อกลางคืนในอาหารกับค่าลักษณะของความสามารถในการบินค้างคาวในกลุ่มที่ใช้คลื่นความถี่เสียงมากกว่า 100 กิโลเฮิร์ต ตามสมมุติฐานข้อสอง นอกจากนี้ยังพบว่าค้างคาวหน้ายักษ์และค้างคาวมงกุฎในป่าบาลามีความยาวคลื่นเสียงเฉลี่ยแตกต่างกันอย่างมีนัยสำคัญ และมีโครงสร้างคลื่นเสียงสะท้อนต่างกัน เมื่อแยกทดสอบเฉพาะกลุ่มค้างคาวหน้ายักษ์และค้างคาวมงกุฎพบว่าค่า

สัดส่วนของเฉลี่ยผีเสื้อกลางคืนที่ปรากฏอาหารของค้างคาวมงกุฎมีความสัมพันธ์เชิงลบกับค่าความ
ยาวคลื่นเสียงเฉลี่ยอย่างมีนัยสำคัญ แต่ในกลุ่มค้างคาววงศ์หน้ายักษ์ค่าสัดส่วนของเฉลี่ยผีเสื้อ
กลางคืนที่ปรากฏอาหารมีความสัมพันธ์เชิงบวกกับคลื่นความถี่เสียงอย่างมีนัยสำคัญ โดยความ
แตกต่างของโครงสร้างและความยาวคลื่นเสียงดังกล่าว เมื่อเปรียบเทียบในกลุ่มค้างคาวมงกุฎพบว่า
ค้างคาวที่มีค่าการรับน้ำหนักของปีกที่แตกต่างกันมีค่าสัดส่วนผีเสื้อกลางคืนในอาหารแตกต่างกัน
อย่างมีนัยสำคัญโดยมีค่ามากขึ้นตามคลื่นเสียงที่มากขึ้น แต่ในกลุ่มค้างคาวหน้ายักษ์พบว่าค้างคาวที่
มีค่าการรับน้ำหนักของปีกที่แตกต่างกันมีค่าสัดส่วนผีเสื้อกลางคืนในอาหารค่ามากขึ้นตามคลื่นเสียง
ที่มากขึ้น นอกจากนี้ยังพบว่าค้างคาวหน้ายักษ์บางชนิดกับค้างคาวมงกุฎบางชนิดที่มีค่าการรับ
น้ำหนักของปีกใกล้เคียงกัน พบว่ามีค่าค่าสัดส่วนเฉลี่ยของผีเสื้อกลางคืนที่ปรากฏอาหาร ไม่แตกต่าง
อย่างมีนัยสำคัญ

เนื่องด้วยความแตกต่างของลักษณะ โครงสร้างคลื่นเสียงและความสามารถในการ
บินของค้างคาวทั้งสองกลุ่ม จึงไม่ควรรวมค้างคาวทั้งสองกลุ่มเพื่อหาความสัมพันธ์ของคลื่นความถี่
กับค่าสัดส่วนของผีเสื้อกลางคืนที่ปรากฏในอาหาร

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ABSTRACT

        The relationship between the proportion of moths in diet and call frequency of bats in superfamily Rhinolophiodea was investigated in Bala tropical rain forest. The allotonic frequencies hypothesis predicts that the frequency dominating the echolocation calls of bats should be correlated with the evidence of moths in their diet. 87 individuals from six species rhinolophids and 71 individuals from six species of hipposiderid bats were collected. Only 6 species of rhinolophids and and 6 species of hipposiderids were analyzed. An analysis of twelve bats in these superfamily showed that the relationship between moth consumption (% volume) and echolocation call frequency (kHz) was statistically significant. When an analysis was carried out separately, only the bat species using echolocation was dominated by sound lower than100 kHz and over 100 kHz, the relationship was statistically positive for both bat groups. Although the relationship was shown, but the present percentage of Lepidoptera in diet of all bats was lower than what is predicted by the AFH, there should be effect from other factors influencing the attention or efficiency of bats hunting moths, such as some moths in the area were found to respond the high call frequency (146 kHz) of bat, and the abundance of insects (Coleopteran, Isopteran, Hymenopteran) which should be more easily preyed than moths.

        The echolocation call structure of rhinolophid and hipposiderid bats are different, under the same conditions of wing loading, rhinolophid bats used lower frequency than hiposiderid bats to reach in the same proportion of moths in diet. When

separated analyzed by bat group, hipposiderid and rhinlophid bats. The incident of percentage volume of moths in diet of rhinolophid bats was significantly related to mean call duration, but for the hipposiderid bats moths in diet was significantly related to peak call frequency. There is not only echolocation call frequency help bat to win the mechanism of moth ear defense, their wing ability and call structure with exert on the efficiency hunting on moths.

To test the AFH, these bats could not be included together or with other bats due to the difference in their wing ability and call structure design which made them different in an ability to prey on moths.

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Finally, owe my deepest appreciation to my mom, Mrs. Anong Prajaktitr, for her love and care and incessant encouragement throughout my life.

Amorn Prajakjitr

CONTENTS

CONTENTS (Continued)

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

CHAPTER 1

INTRODUCTION

The co-evolution of predator and prey has been indicated in many animals. Predator tries to capture prey, at the same time, prey evolves strategies to avoid or to escape. Insectivorous bats and their insect prey are an example of predator-prey co-evolution in a nocturnal setting. Insectivorous bats locate and capture insects by echolocation calls. However, many nocturnal insects such as moths, lacewings, beetles and praying mantises have evolved ears as a defend mechanism against echolocating bats (Roeder, 1967; Miller, 1983; Fullard, 1987; Surlykke, 1988). With the evolution of moth defense, some groups of bats anti-defend eared moth by using a call frequency range out of moth hearing range, called an allotonic frequency (Novick, 1977; Fenton and Fullard, 1979). This co-evolution may be an event that exerts on food partitioning, which determines species composition in bats communities.

Tympanate moths are most sensitive to frequencies between 20 and 60 kHz, coinciding with the peak-frequency range of most echolocating bats (Fullard, 1987; Fenton *et al*., 1998). Eared moths can hear the echolocation calls of an approaching bat and respond by either flying away from the bat or executing a series of complex flight maneuvers (Jacob, 2000). Hearing combined with a complex suite of evasive flight maneuvers allows tympanate moths to be 40% more successful at evading bat predation than non-tympanate moths (Roeder, 1967; Rydell, 1992; Acharya and Fenton, 1999). Moth ears appear to have no function other than to detect approaching bats (Roeder, 1975; Bailey, 1991; Fullard and Yack, 1993). Fullard *et al*. (1997), Fullard *et al*. (2001) and Surlykke *et al*. (1998) have shown that day-flying moths no longer subjected to bat-predation, display advanced auditory degeneration.

The allotonic frequency hypothesis (AFH) predicts that the incidence of eared insect should be highest in the diet of bats whose echolocation calls are dominated by frequencies outside the 20-60 kHz range. This hypothesis was tested and supported by several previous studies (Pavey and Burwell, 1998; Jacobs, 2000;

Schoeman *et al.*, 2003). For example, Pavey and Burwell (1998) studied three sympatric bat species using constant frequency (CF) calls; Jacobs (2000) tested on a single bat community in north-eastern South Africa which is dominated by bats using CF calls; and Schoeman *et al.* (2003) studied bats in the Western Cape Province, South Africa which is dominated by species using frequency modulated (FM) calls. In these studies, dietary and echolocation data were collected at the same time. All studies showed that, as predicted by the AFH, echolocation frequency positively relates to the proportion of moths in the diet of bats which used a frequency above 50 kHz. The diet studies in *Tadarida teniotis* (11-12 kHz) also support the AFH for bats that use a call frequency below the most sensitive hearing range of tympanate insects (Rydell and Arlettaz, 1994). Bogdanovicz *et al.* (1999) suggested that for bats whose echolocation calls are dominated by a frequency <100 kHz, the relationship between moth consumption (% volume or % frequency) and echolocation call frequency was parabolic-like dependency. Schoeman and Jacobs (2003) suggested that prey defense might mediate other factors structuring bat communities such as competition. Competition may be reduced for those species of bat that can circumvent prey defense. The echolocation frequency may be better used in the prediction of diet than forearm length or wing area (Schoeman and Jacobs, 2003). Therefore, the selection pressure exerted by moth hearing might have acted directly on call frequency and secondarily on body size and wing morphology, as part of the same adaptive complex.

However, the previous study of the AFH is still controversial for bats in the superfamily Rhinolophoidea (Hipposideridae and Rhinolophidae). For example, in a study on the diet of desert insectivorous bats in Isarael, Feldman *et al.* (2000) found the diet of *Rhinolophus clivosus* (92 kHz) dominated by Coleoptera and Lepidoptera which are different from the study carried out by Schoeman *et al.* (2003), that the diet of this bat was dominated by Lepidoptera. Jones (1992) compared published echolocation and dietary data from around the world on bats belonging to the family Hipposideridae and Rhinolophidae which their calls are dominated by a single frequency [constant frequency (CF) calls]. He found a positive relationship between call frequency and the proportion of moths in the diet of these bats and negative relationship between call frequency and the proportion of beetles (i.e. non-tympanate insects). Bogdanowicz *et al.* (1999) studied the relationship between

echolocation calls, morphology and diet in 62 species of insectivorous bats. They found that support for the allotonic frequency hypothesis was not clear for rhinolophid and hippoposiderid bats (25 species) whose echolocation calls are dominated by sounds > 100 kHz because the incidence of moths in their diets was variable. They suggested that morphological characteristics rather than echolocation call frequency might limit the range of potential prey items. However, in this study, the data of diets was not collected in the same time and place.

There are many factors that could influence hunting efficiency of insectivorous bats. These are internal factors such as the morphology (body size, body mass, wing loading, wing area and aspect ratio) and echolocation call, and the external factors including competition and prey defense. Both factors may determine food niche of bats.

For body size, generally small bat can feed on small preys while the large-size bat can feed on small to large preys (Aldridge and Rautenbach, 1987). However, largest bat may like to feed on large prey, as suggested by optimization. Wing morphology of bat may indirectly influence prey availability as this character permits different bats to use difference micro-habitat, and thus feed on different prey items (McKenzie *et al*., 1995; Aldridge and Rautenbach, 1987; Fleming, 1982; McKenzie and Rolfe, 1986). Aldridge and Rautenbach (1987) suggested that bats with high wing loading and fast flying, fed on the flying insects in open areas, while bats with low wing loading, resulting in high maneuverability and able to forage in cluttered space and feed on resting or the surface-walking insects. A number of studies supported that bat morphology has influenced feeding strategies and determine their diet.

Bat echolocation calls usually relate to morphology (Aldridge and Rautenbach, 1987). Bats feed in cluttered space use the high frequency, while the bat using low frequencies tend to feed in open space. The low frequency calls are unsuitable for the detection of small prey, and low repetition rates may limit prey detection rates (Waters *et. al*., 1995; Jones, 1999).

For reducing pressure from competition, bats in the Rhinolophoidea may have to partition resource in existing area. The mechanisms of resource partitioning may not be predicted based on either the morphological characters or echolocation (Arlettaz, 1999). These may effect on the moth proportion on diet of bats in this group. Perhaps this may explain the high variability in proportion of moth for rhinolophoidid bat who use echolocation >100 kHz. Whether wing morphology explains the diet variability of bat with frequency >100 kHz, while the diet of those bats with lower frequencies (<100 kHz) could be predicted by AFH, are merit for further investigation.

Bala Forest supports a great diversity of bats in Thailand. About 50 species of bats have been found, twelve are species of fruit bat (Pteropodidae) and the others are insectivorous bats (with seven families; Vespertilionidae, Rhinolophidae, Hipposideridae, Emballonuridae, Nycteridae, Megadermatidae, and Molossidae) (Thong-aree, pers. comm.; Bumrungsri, pers. comm.). This makes up about 40% of bat fauna in Thailand (from 112 species, Pumiparkpun, 2002). Bats in the family Rhinolophidae and Hipposideridae are mostly found at the understorey level, and their calls range from 40-150 kHz, (Bumrungsri, pers. comm.). They both belong to the superfamily Rhinolophoidea, thus these bats are from the same adaptive group where they are generally similar in the morphology and types of echolocation call. The coexistence of this group of species is quite interesting, because 12 species in this area appear to vary slightly in size and call frequency. The great diversity of moth fauna has been documented here. There are at least 129 species in the Geometridae (Pramual, 2004), a tympanate moth which is found throughout the year. Such a high diversity of bats and tympanate moths make Bala Forest is a very interesting place to examine bat-moth interaction, as the AFH have never been tested on a large group of Rhinolophoidea in the same community bat. In addition, it is very interesting to investigate on the relationship between both wing morphology and echolocation call to the proportion of moths in the diet.

The objective of this study was to examine the relationship between the proportion of moth in the diet and call frequency of bats in the superfamily Rhinolophoidea in Bala Forest. For bat with call frequencies over than 30 kHz, according to AFH, it is predicted that the proportion of moth in their diet is positively

related to call frequency. For bat using frequencies higher than 100 kHz, it is hypothesized that their diet variation are explained by wing morphology.

CHAPTER 2

MATERIALS AND METHODS

Study area

This study was carried out in Bala Forest ($5° 44' – 5° 57'$ N, $101° 46' – 101° 51'$ E), Hala-Bala Wildlife Sanctuary, which is located in Narathiwat and Yala Provinces, southern Thailand (Figure 1). This reserve area is divided into two parts, the larger area is Hala Forest and the smaller one is Bala Forest. Bala Forest is located in Waeng District, Narathiwat Province. The area is about 105,700 Rai (169.1 hectare), characterized by old growth tropical rain forest and surrounded by rubber plantations, orchards and villages. The southern part is connected to rubber plantations and oil palm plantations in the State of Kelantan, Malaysia. Bala Forest was selectively logged 20-30 years ago.
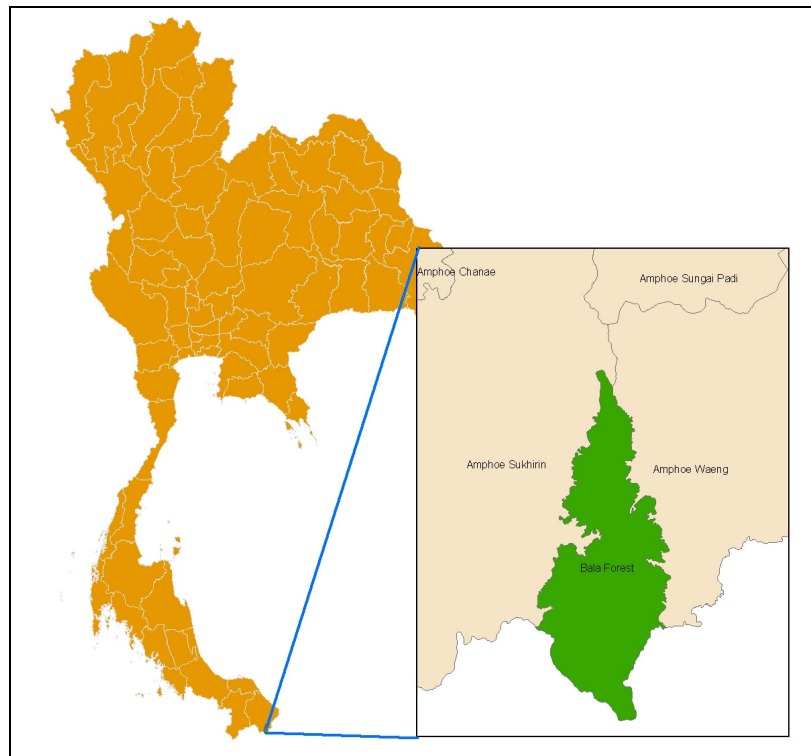
Figure 1. Study area, Bala Forest, Narathiwat Province.

Vegetation is characterized with the Malayan-type tropical rain forest (Niyomtham, 2000) (Figure 2). The top canopy is dominated by *Shorea curtisii* Dyer ex King, *S. assamica* Dyer*, S. leprosula* Miq., *S. singkawang* Miq., *Neobalanocarpus heimii* (King) P.S. Ashton. The understorey varies from sparse to dense, and consists of seedlings and saplings of canopy and subcanopy trees, fern, rattans, and climbing rattans (*Calamus* sp.). This forest is the catchment area of Ko-Lok River. The plant community can be categorized into three major communities (Niyomtham, 2000) as follows:

1. Tropical Lowland Rain Forest, which can be classified according to altitude level.
    1.1 Dipterocarp and Palm Community at the altitude lower than 600 meters MSL.
    1.2 Shorea-Eugeissona and Johannesteijsmannia Community at the altitude between 600-1000 meters MSL.
2. Lower Montane Rain Forest which can be classified according to altitude level.
    2.1 Fagaceae and Illicium Community at the altitude between 600-1000 meters MSL.
    2.2 Podocarpaceae-Ericaceae and Laurel Community at the altitude over 1400 meters MSL.
3. Ericaceae and Dacrydium Community over limestone hills.

Figure 2. Bala tropical rain forest, Narathiwat Province, characterizes with the Malayan tropical rain forest type, which is dominated by dipterocarps.

Climate

There are generally two seasons: dry and rainy season. The average rainfall is 2,500 mm annually. The relative humidity is over 60% and average temperature is about 28 C°. There are many river channels, ditches and drainage paths between the hills in the area.

Topography

The topographic level ranges from 50-900 meters MSL. The area is dominated mainly by high steep hills, deep valleys, and interspersed with low terrains. There are small patches of plains between the ravines of the hills, with some containing patches of swampy areas.

Trapping Area

Trapping sites were selected along natural, research, tourist recreation, and man-made trails. These trails are used for scientific research, and for travelling to collect non-timber forest products by villagers. All trapping sites were located in Dipterocarp and Palms Community, at the elevation under 600 meters above MSL The trapping sites were placed on various habitat including plains between hills, foot of the hill near streams, areas mid-way up the hill, hill tops, and patches of swampy areas located within small valleys. Trapping sites are dominated by Dipterocarpaceae, Myristicaceae, Apocynaceae, Anacadiaceae and rattans.

Bat trapping

Field work was carried out between August 2004 - July 2005. Bats were collecting with four-bank harp traps (Francis, 1989) (Figure 3). In each sampling night, two harp-traps were set in the same area, at the narrowest sections of forest trails. The trapping locations were chosen based on some typical features; the presence of tree cover that hangs low, to reduce the gap beside and over the traps. Each trap was set in different trails or at different junctions of the same trail. Traps were opened from 18.00 h to 23.00 h with an assistant present at all times. Captured bats were removed from traps and put into cotton labeled bags. Bats were kept for at least one hour or until all measurement were completed. Calls were recorded and feces were collected. Trapping was set until 23.00 h on nights without rain, and in the unexpected event of rain, traps were closed only during severe rain. Bats were released in the same area where they were captured. Released bats were marked by fur clipping on its back to avoid sampling the same bat twice. Bat sampling was continuously operated until at least 80% of recorded hipposiderid and rhinolophid bats were documented since rare species are unlikely to be captured.

Figure 3. Harp trap was set at understorey level, across a research trail.

Bat Measurement

After capture, bats were aged, sexed and reproductive status were examined. Morphology measurements were undertaken in adult bats only. Captured bats were weighed (Figure 4) to the nearest 0.5 g with a 100 g Pesola spring balance. Bats are first put in a plastic bag to reduce movement, which could affect the accuracy of weight measurements. Body measurements were made for forearm length, ear, and tail (to the nearest 0.1 mm) length using dial calipers.

Figure 4. Bats were put in a plastic bag to reduce movement, and weighed.

Bats Wing drawing

Only the extended left wing of captured bats was used (which bat position was facing up), and its outline traced onto a sheet paper (Figure 5) for wing calculation. Again juveniles, pregnant, and lactating bats were exempted. Wing loading was calculated, based on the length of wingspan, b (m), wing area, S (m^2), including body area without the head, and the area of the uropatagium (Norberg and Rayner, 1987). Wing loading (WL) = Mg/S where M is total weight in kg, g is gravitational acceleration in ms^{-2} and S is wing area in m^2. Aspect ratio (AR) = b^2/S; (Norberg and Rayner, 1987).

Figure 5. Left wing of captured bats were extended, and its outline was traced onto a sheet paper.

Bats Feces collection

A minimum of five fecal pellets was collected from each individual. The feces of each individual were collected from bags and kept in a small labeled eppendoft tube. The fecal pellets were dried under a 100 W. lamp or under sunlight at least 6 hours during the next day, before being kept again for further analysis.

Species identification of bats

The identification of bat species was followed Lekagul and McNeely (1977), Payne and Francis (1985), Corbet and Hill (1992) and Ingle and Heaney (1992), then it was confirmed by sound analysis.

Bat call recording

Echolocation calls were recorded from bagged bats (i. e. bat was kept in a cotton bag) using 32x time expansion Transquility II connected directly to a notebook computer. Recording and call analysing was performed on a notebook computer with BatSound Pro software (version 3.2, Pettersson Elektronik AB, Upsala, Sweden).

Insect sampling

Insects from the study area were collected by black-light traps at the same night as bat sampling. Two traps were set at the ground level (1.5-2.5 m height), and at least 30 m from harp traps. A black-light trap consists of the fluorescent lamp (10 W.), a 50 cm diameter plastic container and 12v 7.5 Amp. battery. A container contained 10% detergent solution in water at one third of its height. The detergent solution was used to increase a tension of surface water for more efficiency in trapping insects. Trapped insects were weighed, and 1/3 of each trapped insects were preserved in 70% ethanol, and was identified to order.

Diet Analysis

Feces analyses were done under 32x stereoscope (Olympus) multiply by 2x converter lens. Each feces was put on glass slide (Sedgwick-Rafter Cell), and softened with drops of 70% ethanol. The fragments of arthropod (e.g., legs, wings, antennae, scales, claws, mandibles or reproductive organs) were identified to order follow Borror *et al*. (1989), Pinratana (1990), Inove *et al.* (1996), and insect reference collection from the capture site. Percentage frequency and percentage volume of each diet item were quantified. Percentage volume is the visual estimate (compare to other insects order under the scale of Sedgwick-Rafter slide) of percent volume of identifiable fragments from each insect order in a sample (Whitaker, 1988). Percentage volume of the prey taxa was given as estimated percentage volume in all fecal pellets (total = 100%) for each species. Percentage frequency was the number of occurrence of taxon (i.e. the number of pellets contain), divided by the total number of occurrence, multiplied by 100 (McAney *et al*., 1991).

Wing area calculation

The wing drawing pictures were scanned by HP printer and scanner at a resolution of 200 dpi. Adobe Photoshop programs were used for wing area calculation. The areas of wing tracing, including body area without the head, and the area of the uropatagium, were selected by magic wand, and measure by counting dot pixel (set at 200 dpi) in histogram window, the total pixel were transformed to square centimeter (divided by pixel per square centimeters (78.74^2)).

Echolocation call analysis

Bat call were analysed using BatSound Pro software (version 3.20, Pettersson Elektronik, Uppsala, Sweden) on an Acer TravelMate 240 notebook computer, using a sampling rate of 22,050 Hz (8 bits, mono) and a threshold of 15, time expansion 32, to measuring peak call frequency of dominant harmonic of a single high-quality call (i.e., high signal to noise ratio) from each individual bat, from the Hanning window, FFT power spectrum (size 1024) and measuring call duration from the Hanning window, FFT spectrogram (size 512) .

Insect identification

Trapped insects from each night were identified to order follow Borror *et al*. (1989). Insect in each order were counted in each trap night. After counting, only moth was sent to the expert to identify into family as possible. Percentage frequency of each individual of insect order was quantified as the occurred of individual in each order divided by the total number of individual in each trap night multiplied by 100.

Statistical Analysis

The bivariate correlation (Spearman's rho, two tailed) were used to determine the relationship between percentage volume of moth or other insect order in diet and call parameter (call frequency, call duration), body parameter (forearm length, weigh), and wing parameter (wing loading, wing area and aspect ratio). Only species which feces were successfully collected from at least 2 individuals were included in the analysis.

CHAPTER 3

RESULTS

Bats species collected

As a result of rain and avoiding the pregnant and lactating period of bats, bat trapping was carried out in two periods. The first was undertaken between November 2004 to April 2005, and the second was performed in late August to the end of September 2005. From October to the middle of February was a period of heavy rain; it rains continuously for several days. Between April to late August was the pregnant and lactating period of most of insectivorous bats in Bala Forest. Trapping were stopped in many nights due to heavy rain. No Rhinolophoidea bats were captured in many nights in this period, although the traps were set in the same location as the other month. The information gained from a bat detector consistently showed that no sound of understorey bats was detected in the trapping area during that period.

Over 300 individual bats were captured under the efforts of 528 trapping hours over 45 nights. More than 190 individuals of mature Rhinolophoidea bats were trapped. There were six species of hipposiderid bats (i.e., *Hipposideros bicolor*, *Hipposideros* sp.*, *Hipposideros sabanus*, *Hipposideros cineraceus*, *Hipposideros dayacorum*, *Hipposideros diaderma*) and seven species of rhinolophid bats (*Rhinolophus acuminatus*, *Rhinolophus affinis*, *Rhinolophus lepidus*, *Rhinolophus robinsoni*, *Rhinolophus stheno*, *Rhinolophus trifoliatus*) (Figure 6)**.** However both feces and calls can be collected and detected from only 71 and 88 individuals of adult hipposiderid and rhinolophid bats respectively.

Figure 6. Twelve bat species of Rhinolophoidea bats caught at Bala Forest; (A) *Rhinolophus luctus*, (B) *Rhinolophus trifoliatus*, (C) *Hipposideros diaderma*, (D) *R. robinsoni*, (E) *R. affinis*, (F) *R. steno* (G) *R. acuminatus*, (H) *R. lepidus*, (I) *H. bicolor*146, (J) *H. dayacorum*, (K) *H. cineraceuas*, and (L) *H. sabanus*.

Feces of more than 4 individuals can be collected in each of nine bats species (*R. trifoliatus*, *R. acuminatus*, *R. affinis*, *R. lepidus*, *R. robinsoni*, *R. stheno*, *H. bicolor*146, *H. bicolor*131, *H. cineraceus*, *H. dayacorum*) while the other species, the number of captured bats was less than four (*R. luctus*, *H. diadema*, and *H. sabanus*) 0894372862

Four individuals of *R. luctus* were captured in the capture period, but feces could be collected from only one individual. More than ten individuals of *H. sabanus* were captured, but feces were collected from only two. *R. robinsoni*, *H. diaderma* and *H. cineraceus* were rarely captured. Only three species, *H. bicolor*131, *H. bicolor*146 (146 kHz) and *H. dayacorum*, were found through the capturing period except in April and August.

Ten Orders of insects' culled parts were identified from 795 feces pellets of twelve bats species. There were Isoptera, Coleoptera, Hymenoptera, Blatodea, Tricoptera, Homoptera, Lepidoptera, Orthoptera, Hemiptera, Diptera, and unidenstified Orders of insects. Only two Orders, Lepidoptera and Homoptera were found in the diet of all twelve bats species, though not all individuals.

In terms of percentage volume, less than 2% of moth were found in seven bat species, 2 – 5% of moths were found in two bat species, 5 – 10% of moths were found in two bat species, *H. bicolor*146 (146 kHz), *H. cineraceus*, and *R. luctus* had over ten percent; The percentage volume of Isoptera, Coleoptera, and Hymenoptera were relatively high in most species, while the percentage volume of Hemiptera, Homoptera, Diptera were quite low in many bat species (Table 1).

In terms of percentage frequency of occurrence of moths in diet, three species, *R. luctus* (n = 1), *R. stheno* (n = 16), *H. sabanus* (n = 2), had percentage frequency higher than 85%, whereas two species, *R. trifoliatus* (n = 16) and *H. cineraceus* (n = 4), had less than 15%. Percentage frequency of two Orders of insects, Coleoptera and Hymenoptera were relatively high in most bat species, while percentage frequency of Tricoptera, Hemiptera and Othorpera were low in all bat species (Table 2).

From the feces analysis, Isopterans were found in the feces of 22 from 159 bat individuals [(*H. bicolor*146 = 11 bats (n = 31), *H. dayacorum* = 5 bats (n = 29), *R. affinis* = 3 bats (n = 26), *R. trifoliatus* = 2 (n = 16), and *H. cineraceus* = 1 (n =

4)]. Hymenopterans were found in the feces of three individuals of *H. dayacorum* and Isopterans only were found in the feces of an individual of *H. diadema* (from 3 piece of feces).

Analysis of echolocation calls

The call frequency of twelve bat species had its peak between 53-203 kHz. All of rhinolophids had call frequency lower than 100 kHz, meanwhile only one species of hipposiderid bats, *H. dideama* (63 kHz), had call frequency lower than 100 kHz. *H. sabanus* had shown the highest peak of call frequency (203 kHz) and the lowest was *R. luctus* (41 kHz). Only two species, *R. luctus* (41 kHz), and *R. trifoliatus* (53 kHz), have peak call frequency that fall within the range of moth hearing, between 20-60 kHz (Table 3).

Although the calls of both hipposiderid and rhinolophid bats were dominated by constant frequency but search call duration of hipposiderid bats was shorter (Figure 7). Call intensity varied between each species. When detected with a bat detector, the call of hipposiderids is generally fainter than the rhinolophid bat.
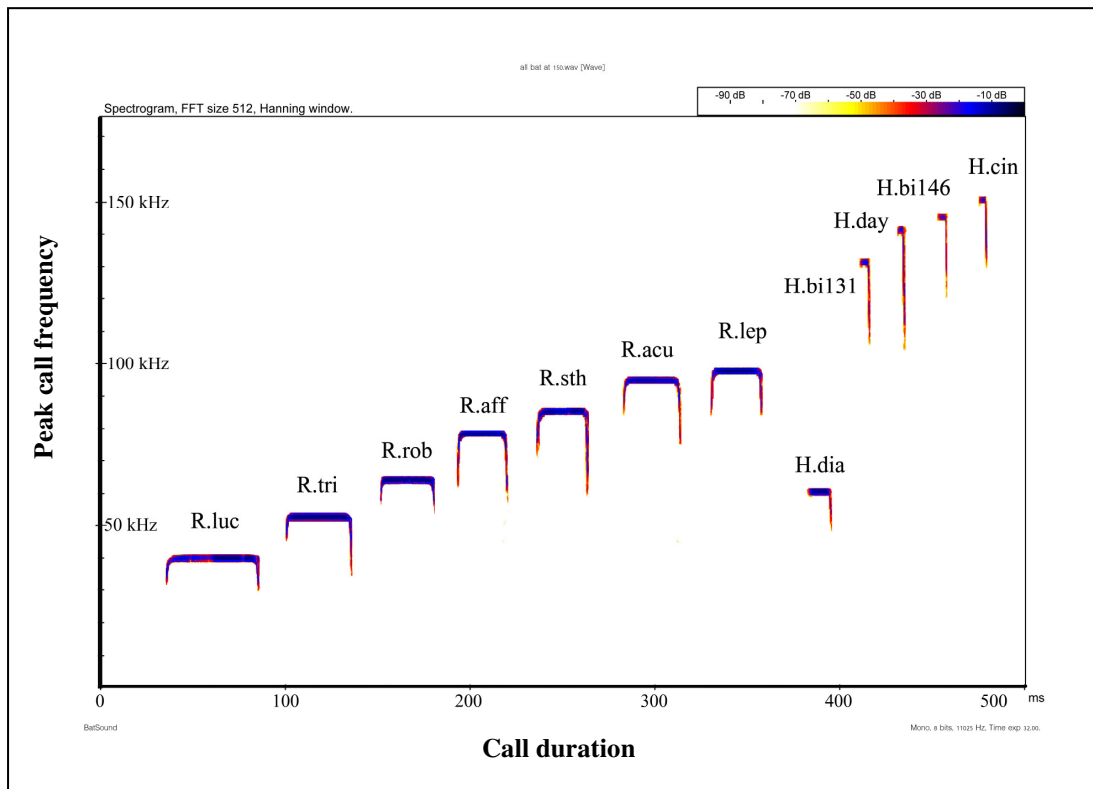
Figure 7. A spectrogram illustration of echolocation call of twelve Rhinolophoidea bats, caught in Bala Forest (without call of *H. sabanus* which highly peak call frequency than other): abbreviations of name as in Table 1.

Table 1. Mean ± SD percent volume of prey categories in the feces of thirteen Rhinolophoidea bats species caught at Bala Forest: *Rhinolophus trifoliatus* (*R.tri*), *Hipposideros diaderma* (*H.dia*), *R. robinsoni* (*R.rob*), *R. affinis* (*R.aff*), *R. steno* (*R.ste*), *R. acuminatus* (*R.acu*), *R. lepidus* (*R.lep*), *H. bicolor*131. (*H.bi*131) *H .bicolor*146 (*H.bi*146), *H. dayacorum* (*H.day*), *H. cineraceuas* (*H.cin*), and *H. sabanus* (*H.sab*)

Bat species	R.luc	R.tri	H.dia	R.rob	R.aff	R.ste	R.acu	R.lep	H.bi131	H.day	H.bi146	H.cin	H.sab
No. of bats	1	16	3	4	26	16	18	8	6	29	25	4	2
No. of faecal pellets	5	80	15	20	130	80	90	40	30	145	125	20	10
Prey category													
Lepidoptera	41	0.21 ± 0.75	0.67 ± 1.15	1.05 ± 2.10	1.19 ± 3.298	2.60 ± 2.35	0.77 ± 1.62	4.78 ± 7.11	0.47 ± 1.14	0.68 ± 2.68	5.92 ± 12.26	13.8 ± 16.29	8.90 ± 11.74
Isoptera	0	28.06 ± 35.75	30.33 ± 52.54	7.5 ± 15.00	27.02 ± 37.74	0	20.11 ± 32.83	0.13 ± 0.35	56.6 ± 39.61	32.68 ± 39.78	46.12 ± 46.20	39.50 ± 44.61	15.50 ± 21.92
Coleoptera	2	28.44 ± 25.03	61.67 ± 53.46	34.25 ± 43.61	28.89 ± 23.88	22.38 ± 12.56	19.92 ± 22.57	7.63 ± 5.82	12.67 ± 31.03	16.72 ± 26.51	8.75 ± 16.55	0	8.30 ± 10.89
Hymenoptera	0	15.6 ± 19.59	0	29.25 ± 25.62	9.27 ± 13.17	9.01 ± 9.92	26.39 ± 28.91	38.00 ± 26.53	13.27 ± 17.71	34.62 ± 34.27	2.32 ± 5.23	5.75 ± 7.23	18.00 ± 25.46
Blattodea	3	14.85 ± 16.57	0	18.25 ± 34.53	16.68 ± 22.82	8.14 ± 15.05	9.07 ± 15.13	14.50 ± 17.73	3.60 ± 4.26	1.00 ± 4.52	14.10 ± 23.99	13.00 ± 26.00	10.00 ± 14.14
Homoptera	35	4.69 ± 8.55	0.47 ± 0.81	3.15 ± 3.65	4.82 ± 6.61	22.08 ± 14.56	5.82 ± 10.32	13.33 ± 14.72	0.50 ± 1.22	1.36 ± 3.13	3.8 ± 10.22	11.00 ± 22.00	3.00 ± 4.24
Tricoptera	0	0	0	0	0.29 ± 1.08	0.04 ± 0.15	5.67 ± 14.36	0.13 ± 0.35	0	0	0.03 ± 0.16	0	17.60 ± 4.24
Hemiptera	0	0	0	0	0	2.65 ± 4.48	0.06 ± 0.24	0	0	0.03 ± 0.19	0.04 ± 0.14	0	0
Orthoptera	0	0	0	0	0	0.06 ± 0.25	0	0	0.83 ± 1.60	0	5.26 ± 12.87	2.25 ± 4.50	4.30 ± 6.08
Diptera	0	0.18 ± 0.53	0.13 ± 2.31	0	1.81 ± 6.67	4.05 ± 9.70	0.06 ± 0.24	3.70 ± 3.07	0	0.26 ± 0.99	0.13 ± 0.44	0	0.10 ± 0.14
Unknow	19	7.97 ± 4.43	6.73 ± 1.80	6.55 ± 0.64	10.03 ± 5.08	29.00 ± 14.19	12.14 ± 5.43	17.82 ± 3.92	12.07 ± 10.22	12.64 ± 12.43	13.51 ± 15.93	14.7 ± 8.53	14.30 ± 4.38

Table 2. Percent frequency of occurrence, prey categories exist in diet of thirteen Rhinolophoidea bats species caught at Bala Forest: abbreviations of name as in Table 1.

Bat species	*R.luc*	*R.tri*	*H.dia*	*R.rob*	*R.aff*	*R.ste*	*R.acu*	*R.lep*	*H.bi*131	*H.day*	*H.bi*146	*H.cin*	*H.sab*
No. of bats	1	16	3	4	26	16	18	8	6	29	25	4	2
No. of faecal pellets	5	80	15	20	130	80	90	40	30	145	125	20	10
Insect Order	Percentage Volume												
Lepidoptera	100	12.5	33.33	25	34.6	87.5	27.8	75	16.7	10.3	32	75	100
Isoptera	0	56.2	33.33	25	50	0	33.3	12.5	83.3	69	56	75	50
Coleoptera	100	68.7	66.67	50	76.9	100	72.2	87.5	16.7	48.3	36	0	100
Hymenoptera	0	56.2	0	100	61.5	75	77.8	87.5	50	72.4	20	50	50
Blattodea	100	62.5	0	50	61.5	42.5	66.7	87.5	50	6.9	44	25	50
Homoptera	100	37.5	33.33	50	50	100	72.2	100	16.7	24.1	28	25	50
Tricoptera	0	0	0	0	15.4	6.3	33.3	12.5	0	0	4	0	100
Hemiptera	0	0	0	0	0	37.5	5.6	0	0	3.4	4	0	0
Orthoptera	0	0	0	0	0	6.3	0	0	33.3	0	20	25	50
Diptera	0	12.5	33.33	0	26.9	25	5.6	87.5	0	6.9	16	0	50

Table 3. Mean ± SD echolocation, body and wing parameter of the thirteen species of Rhinolopoidea bats caught at Bala Forest: abbreviations of name as in Table 1.

Bat species	R.luc	R.tri	H.dia	R.rob	R.aff	R.ste	R.acu	R.lep	H.bi131	H.day	H.bi146	H.cin	H.sab
No. of bats	1	16	3	4	26	16	18	8	6	29	25	4	2
Echolocation parameter													
Peak frequency (kHz)	41	53.38 ± 1.32	60.63 ± 0.45	64.88 ± 2.65	78.82 ± 1.08	85.09 ± .89	91.45 ± 3.15	97.18 ± 1.02	131.83 + 1.83	140.56 ± 1.97	146.06 + 3.55	152.43 ± 2.14	202.95 ± 0.07
Body parameter													
Weigh (g)	24	15.02 ± 5.61	40.5 ± 1.47	8.63 ± 0.24	13.22 ± 1.20	8.36 ± 0.48	12.56 ± 1.58	6.15 ± 0.83	8.73 + 0.90	7.32 + 0.76	9.15 + 1.09	4.13 ± 0.75	5.10 ± 0.85
Forearm length (cm)	63.7	51.38 ± 1.78	84.83 ± 2.22	45.04 ± 2.96	50.26 ± 1	45.67 ± 0.66	47.53 ± 1.04	40.56 ± 1.07	45.52 + 0.95	43.76 + 0.90	44.20 + 0.91	34.83 ± 1.20	38.45 ± 0.35
Wing parameter													
Wing area (cm^2)	246.12	174.72 ± 12.97	348.87 ± 15.17	110.32 ± 8.66	139.03 ± 8.67	110.71 ± 3.55	129.71 ± 10.12	86.01 ± 9.85	121.99 + 0.95	98.89 ± 4.26	117.29 ± 6.70	77.34 ± 5.14	88.07 ± 7.70
Wing loading (Nm^{-2})	9.75	8.54 ± 3.72	11.40 ± 0.56	7.71 ± 0.73	9.35 ± 0.91	7.41 ± 0.43	9.51 ± 1.07	7.05 ± 0.99	7.08 + 1.12	7.27 ± 0.80	7.66 ± 0.85	5.27 ± 1.10	5.66 ± 0.45
Aspect ratio	5.11	4.85 ± 0.28	6.01 ± 0.18	5.74 ± 0.30	5.62 ± 0.32	5.67 ± 0.32	5.40 ± 0.37	5.28 ± 0.13	5.37 + 0.27	5.82 ± 0.35	5.10 + 0.37	5.14 ± 0.35	5.12 ± 0.30

Insect abundance

Fifteen insect Orders were trapped. The percentage frequency of body count of six Orders was relatively high (Lepidoptera, Coleoptera, Hymenoptera, Tricoptera, Hemiptera and Diptera) (Figure 8). An actual body mass in four Orders was relatively high (Hymenoptera, Lepidoptera, Coleoptera, and Orthoptera) (Figure 9). When the average body mass of individual insects was compared: total body mass divided by total body count, average body of three insect Orders (Odonata, Orthoptera and Isopteran) was relatively heavy, while the lightest was Diptera (Figure 10). Most of insects were small (< 10 mm body length). About 80% of captured dipterans has body length smaller than 1.5 mm. About 80% of Coleoptera and Hymenoptera were small (< 7 mm body length). In some night, swarming insects were trapped. For example, 100 – 2,400 individuals of a particular species of Hymenoptera, and Coleoptera were found in some trapping nights.

When separated into two seasons, rainy (after middle of May to January) and dry (Fabuary to the middle of May) seasons, the difference of the most insect mass between seasons was not statistically significant (Mann-Whitney Test; Lepidoptera ($Z = -1.165$, p> 0.5), Isoptera ($Z = -0.091$, p> 0.5), Coleoptera ($Z = -1.347$, p> 0.5), Hymenoptera ($Z = -1.755$, p> 0.5), Blattodea ($Z = -0.483$, p> 0.5), Homoptera ($Z = -0.600$, p> 0.5), Tricoptera ($Z = -1.514$, p> 0.5), Orthoptera ($Z = -0.421$, p> 0.5), Diptera ($Z = -0.253$, p> 0.5), Plecoptera ($Z = -0.065$, p> 0.5), Ephimeroptera ($Z = -1.105$, p> 0.5), Odonata ($Z = -1.312$, p> 0.5), Psocoptera ($Z = -0.447$, p> 0.5), Thysanoptera ($Z = -0.447$, p> 0.5), except for Hemiptera ($Z = -2.156$, p< 0.5). In the dry season, the insect has more mass than that in the rainy season. For insect frequency abundance of individuals, most insect frequency in each order was not statically significant difference between season (Mann-Whitney Test; Lepidoptera ($Z = -0.177$, p> 0.5), Isoptera ($Z = -1.099$, p> 0.5), Coleoptera ($Z = -0.978$, p> 0.5), Blattodea ($Z = -0.176$, p> 0.5), Homoptera ($Z = -0.761$, p> 0.5), Tricoptera ($Z = -1.301$, p> 0.5), Hemiptera ($Z = -0.950$, p> 0.5), Orthoptera ($Z = -0.347$, p> 0.5), Diptera ($Z = -0.308$, p> 0.5), Plecoptera ($Z = -0.127$, p> 0.5), Ephimeroptera ($Z = -1.468$, p> 0.5), Odonata ($Z = -0.763$, p> 0.5), Psocoptera ($Z = -0.535$, p> 0.5), Thysanoptera ($Z = -0.535$, p> 0.5), except for Hymenoptera ($Z = -2.279$, p< 0.5) which in the rainy season was more abundant than that of the dry season.

During the lunar cycle which is divided into three periods, i) light period (day 11th from the waning moon to day 5th of the waxing moon, ii) middle period (day 6th from the waxing moon to day 10th of the waxing moon, and day 6th from the waning moon to day 10th of the waning moon, and iii) dark period (day 11th from the waxing moon to day 5th of the waning moon). Only catches of Lepidopterans were statistically different (Mann-Withney Test, $Z = -2.701$, $p < 0.01$) in the frequency abundance of individuals between the light period and the dark period; the catch during the light period was less abundant than the dark period. Only Hymenoptera was statistically different (Mann-Withney Test, $Z = -2.701$, $p < 0.01$) in the frequency abundance of individuals between middle period and dark period, which dark period was more abundant than middle period. For insect mass, only two insect orders, Lepidoptera and hymenoptera that has difference in mass between Luna period. The Lepidoptera which were statistically difference in mass between light period and middle period (Mann-Withney Test, $Z = -2.134$, $p < 0.01$), and light period and dark period (Mann-Withney Test, $Z = -2.639$, $p < 0.01$), which light period was less in mass than middle and dark period. The mass of Hymenoptera was statistically difference (Mann-Withney Test, $Z = -2.879$, $p < 0.01$) between light period and dark period, which in the dark period was more mass than light period.

Due to damage to body part such as wing, scale, leg, antenna or ocelli, only some moths can be classified into family. Of 20 families of 10 super family were found including Psychidae (Tineodea), Yponomeutidae (Yponomeutidea), Plutellidae, (Pyraloidea), Drepanidae, Uraniidae, Geometridae, Sphingidae (Geometridea), Ooenosandridae, Notodontidae, Noctuoidae, Acronictinae (Noctuoidea), mimalonidae (Mimallonoidea), Lasiocampidae (Lasiocampoidea), Bombycidae, Endromidae, Mirinidae (Bombycoidea). On five family of 3 super family which were known as ear moth (Swinton 1877; Scoble's 1992) There are Pyraloidae (Pyraloidea), Uraniidae, Geometridae (Geometridea), Notodontidae, Noctuoidae (Noctuoidea).

The body size of moths was approximated by eye, about 35% were smaller than 8 mm, about 1% was larger than 30 mm, and about 30% were between 12 – 25 mm.
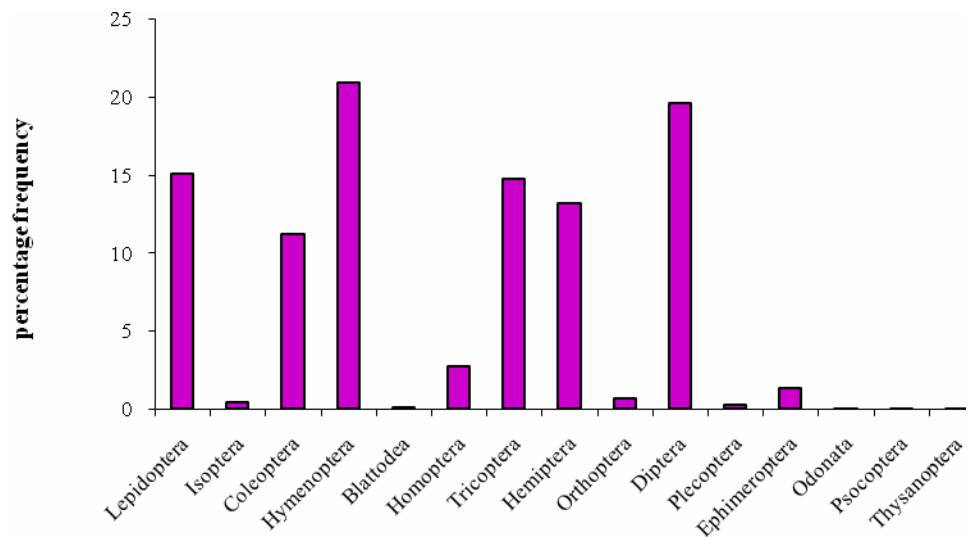
Figure 8. Percentage frequency of insects order from 54 trapped, during November 2003 to April 2004, August to September 2004, and October 2004 to middle February 2005.
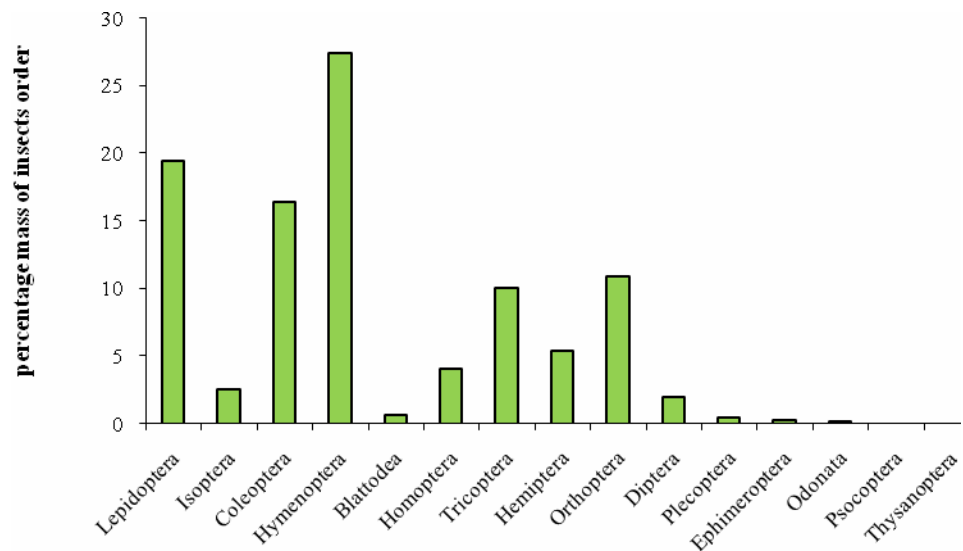
Figure 9. Percentage mass (ca. percent volume) of insects order from 54 trapped, during November 2003 to April 2004, August to September 2005, and October 2004 to mid February 2005.
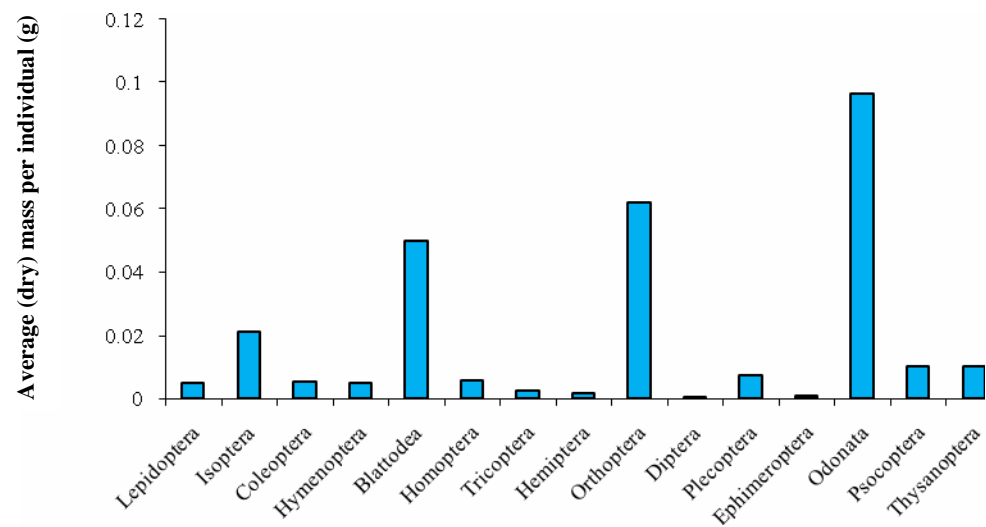
Figure 10. Average mass of insects per individual (g) from 54 trapped nights.

Moths in diet and peak call frequency

        The scatter plot (Figure 11) and bivariate correlations of twelve bats species (peak call frequency between 53 – 202 kHz) has show significant association ($r = 0.664$, $p < 0.05$) between the percentage volume of moths in diet and peak echolocation call frequency. Moreover, bivariate correlations has show significant association correlations ($r = 0.786$, $p < 0.05$) between the percentage volume of moths in diet and peak echolocation call frequency of bats whose peak call frequency <100 kHz (Figure 12). However, for the bat whose peak call frequency >100 kHz (hipposiderid bats only), these was significantly ($r = 0.900$, $p < 0.05$) positive relation between percentage volume of moths in diet and peak echolocation call frequency (Figure 13) (Table 4). The bat that use peak call frequency higher than 100 kHz consisted of four hipposiderid bats (*H. bicolor*131, *H. bicolor*146, *H. dayacurum*, *H. cineraceaus*).

        For only rhinolophid bats species, the incident of percentage volume of moths in diet was not significantly ($r = 0.675$, $p > 0.156$) related to peak call frequency (Figure 14). For only hipposiderid bats species whose peak call frequency

between 60-202 kHz, the incident of percentage volume of moths in diet was positively (r = 0.886, p < 0.05) related to peak call frequency (Figure 15) (Table 4).

The bat that use peak call frequency higher than 100 kHz consisted of four hipposiderid bats (*H. bicolor131*, *H. bicolor146*, *H. dayacurum*, *H. cineraceaus*), while the bat that use peak call frequency lower than 100 kHz consisted of only rhinolophid bats (*R. trifoliatus*, *R. acuminatus*, *R. affinis*, *R. lepidus*, *R. robinsoni*, *R. steno*).
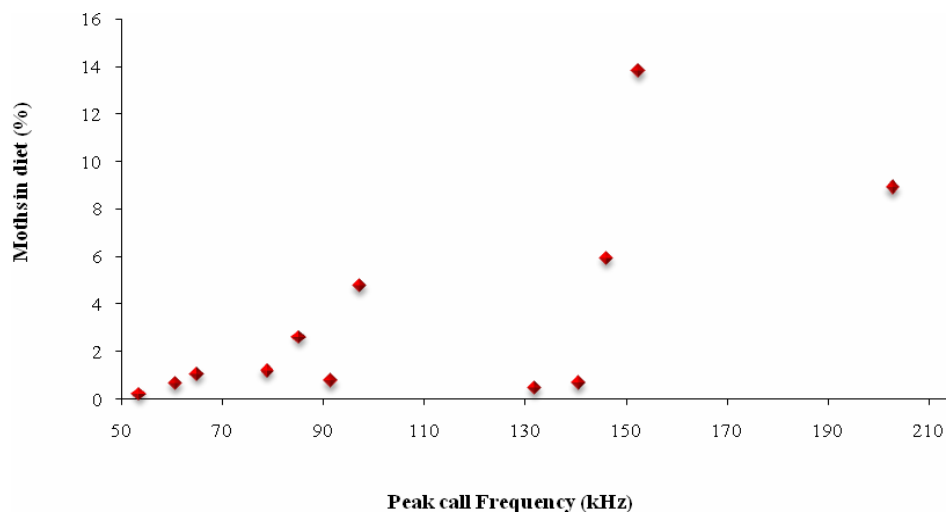
Figure 11. A scatter plot between peak echolocation frequency and the percentage volume of moth in diet of twelve Rhinolophoidea bats species. Bivariate correlation has showed a significant relationship between these two parameter (p < 0.05).
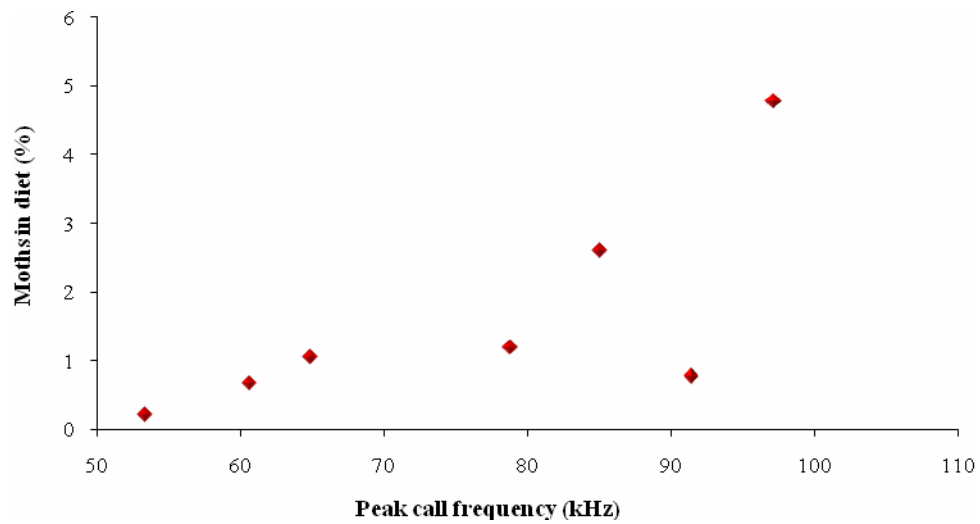
Figure 12. A scatter plot between peak echolocation frequency and the percentage by volume of moths in diets of the bat whose used peak call frequency <100 kHz. Bivariate correlation has showed a positive relationship between these two parameters ($p < 0.05$).
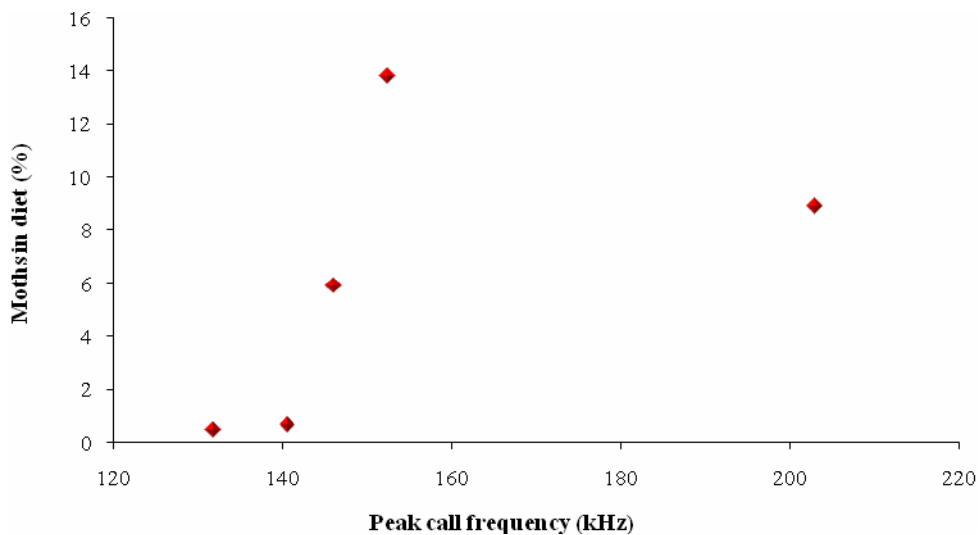
Figure 13. A scatter plot between peak echolocation frequency and the percentage by volume of moths in diets of the bat whose used peak call frequency >100 kHz. Bivariate correlation has showed a positive relationship between these two parameters ($p < 0.05$).
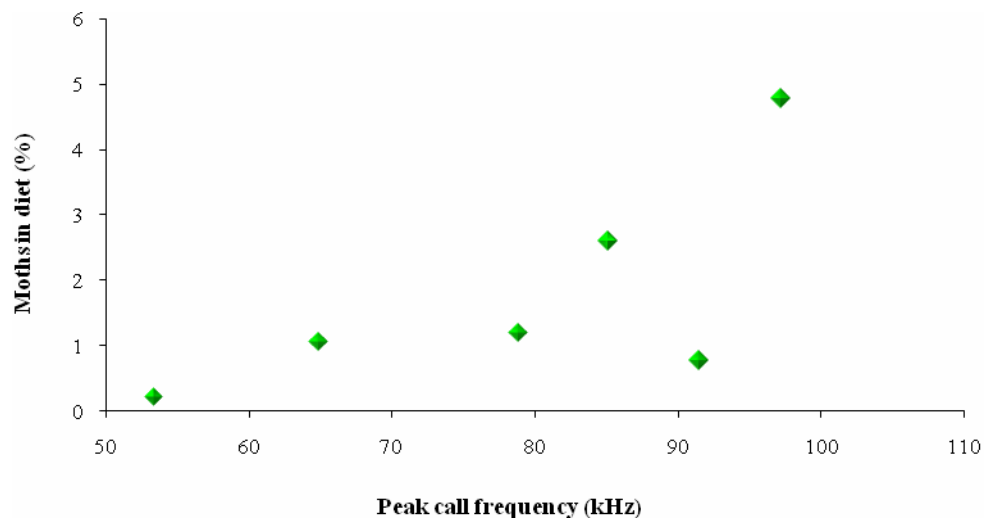
Figure 14. A scatter plot between peak echolocation frequency and the percentage by volume of moths in diets of only the rhinolophid bats whose used peak call frequency between 50 - 100 kHz. Bivariate correlation has showed no significant relationship between these two parameters (p > 0.05).
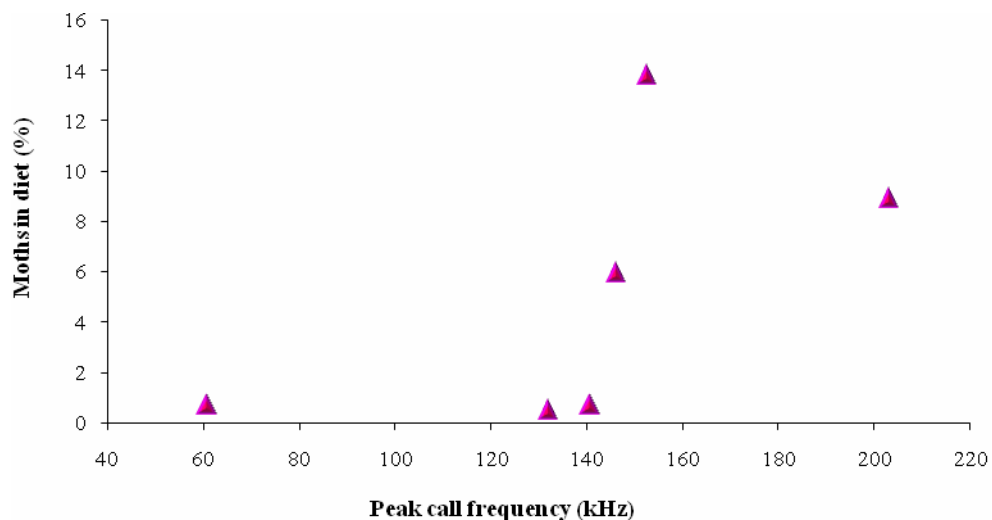
Figure 15. A scatter plot between peak echolocation frequency and the percentage by volume of moths in diets of only the hipposiderid bats whose used peak call frequency between 60 - 202 kHz. Bivariate correlation has showed a positive relationship between these two parameters (p < 0.05).

The relationship between moths in diet, mean call duration and body parameter

The incident of percentage volume of moths in diet of twelve bats species was significantly related to forearm length, weigh, wing area, except mean call duration, wing loading and aspect ratio (Table 4).

For the five bats species whose peak call frequency higher than 100 kHz, the incident of percentage volume of moths in diet was not significantly related to mean call duration and other body and wing parameter (Table 4). For rhinolophid bats species, the incident of percentage volume of moths in diet was negatively related to mean call duration (Figure 16) and weight, but no significantly related to fore- arm length, wing area, wing loading and aspect ratio (Table 4). For hipposiderid bats species whose peak call frequency between 60-202 kHz, the incident of percentage volume of moths in diet was positively related to peak call frequency, mean call duration (Figure 17), forearm length, and wing area, but no significantly related to weight, wing loading and aspect ratio (Table 4).

Table 4. Correlations between peak echolocation call frequency, wing parameter (wing loading and wing area), body parameter (weigh and forearm) and the percentage volume of moths in diet of twelve bats species, rhinolophid bat only, and hipposiderid bats only, and hipoposiderid bats that used call frequency >100 kHz (*H. bicolor*131*, H. bicolor*146, *H. dayacurum*, *H. cineraceaus, H. sabanus*).

| Parameter | % moths in diet | | | | | | | |
| | 12 bats species | | rhinolophid bats | | hipposiderid bats | | > 100 kHz | |
	r	p	r	p	r	p	r	p
peak call frequency	0.664	0.018*	0.657	0.156	0.886	0.019*	0.900	0.037**
mean call duration (ms)	-0.524	0.08	-1.000	0.000**	-0.829	0.042*	-0.800	0.104
Weigth (g)	-0.685	0.014*	-0.829	0.042*	-0.714	0.111	-0.700	0.188
Forearm length (cm)	-0.727	0.007**	-0.714	0.111	-0.886	0.019*	-0.800	0.104
Wing area (cm^2)	-0.713	0.009**	-0.714	0.111	-0.886	0.019*	-0.900	0.037
Wing loading (Nm^{-2})	-0.573	0.051	-0.714	0.111	-0.600	0.208	-0.600	0.285
Aspect ratio	-0.301	0.342	0.371	0.468	-0.600	0.208	-0.500	0.391
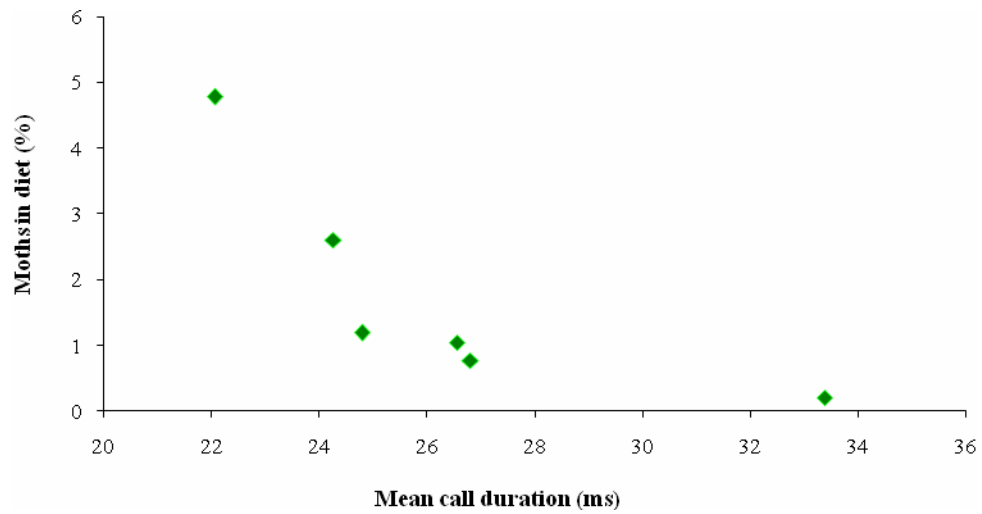
Figure 16. A scatter plot between mean call duration and the percentage volume of moth in diet of six rhinolophid bats species. Bivariate correlation has showed a significant relationship between these two parameter ($p < 0.05$).
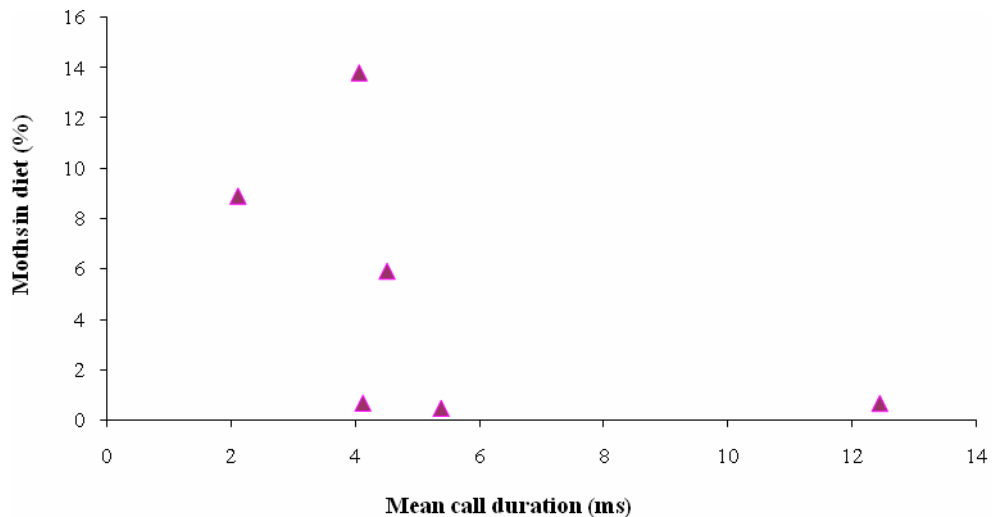

Figure 17. A scatter plot between mean call duration and the percentage volume of moth in diet of six hiposiderid bats species. Bivariate correlation has showed a significant relationship between these two parameter ($p < 0.05$).

The peak call frequency and other body parameters

        The peak call frequency of twelve bats species was negatively related to mean of call duration (Figure 18) and forearm length, and other body and wing parameter (weigh, wing area and wing loading), but was not significantly related to aspect ratio (Table 5).

        For the rhinolophid bats species whose peak call frequency lower than 100 kHz, the peak call frequency was not significantly related to mean call duration (Figure 18) and other body and wing parameter [forearm length, weigh, wing area, and wing loading (Figure 19)] (Table 7). For the hipposiderid bats species that use peak call frequency lower between 60 - 100 kHz, peak call frequency was significantly related to mean call duration (Figure 18), forearm length, wing area, but was not significantly related to weigh, wing loading (Figure 19) and aspect ratio (Table 6).
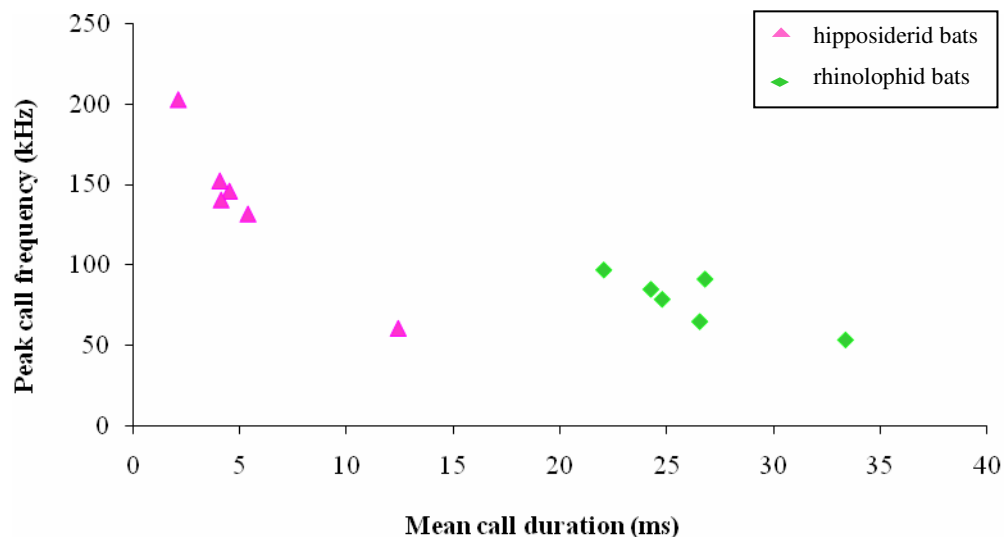
Figure 18. A scatter plot between mean call duration and peak call frequency of rhinolophid and hipposiderid bats species.
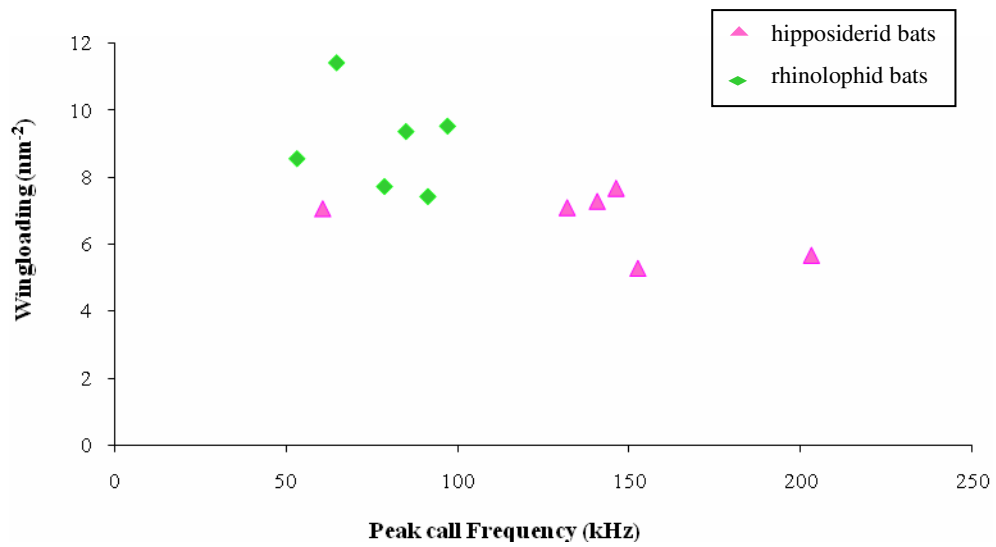
Figure 19. A scatter plot between mean call duration and wing loading of rhinolophidand hipposiderid bats species. There was overlap on wing loading between among rhinolophid and hipposiderid bats.
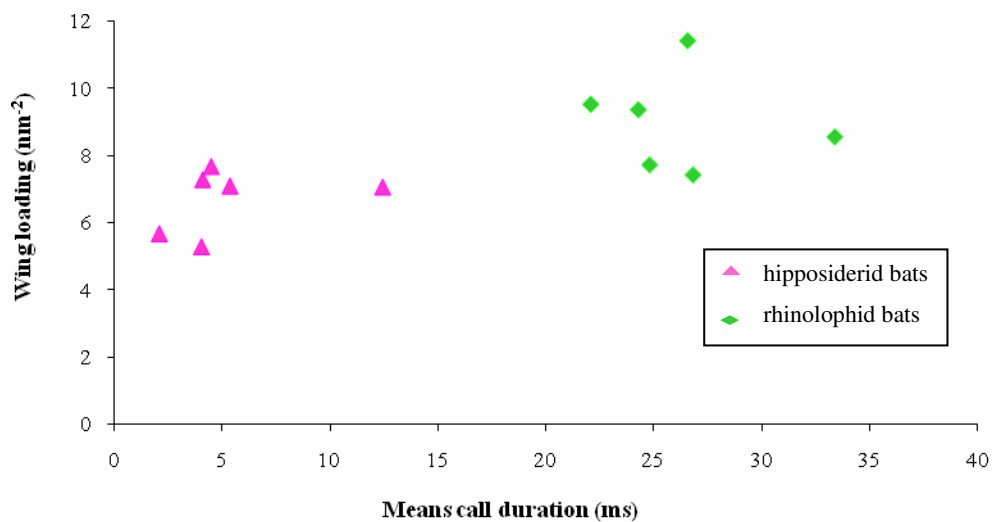
Figure 20. A scatter plot between peak call frequency and wing loading of rhinolophidand hipposiderid bats species.

Table 5. A bivariate correlation of call parameter (call frequency, call duration), body parameter (weight, forearm), wing parameter (wing area, wing loading, aspect ratio) 12 bats species.

	Echolocation parameter		Body parameter				Wing parameter					
	call duration (ms)		Weigh (g)		Forearm length (cm)		Wing area (cm^2)		Wing loading (Nm^{-2})		Aspect ratio	
	r	p	r	p	r	p	r	p	r	p	r	p
Peak frequency (kHz)	-0.846	0.001**	-0.748	0.005**	-0.583	0.000**	-0.713	0.009**	-0.776	0.003**	-0.343	0.276
call duration (ms)			0.629	0.028**	0.713	0.009**	0.580	0.048*	0.699	0.011*	0.091	0.779
Weigh (g)					0.937	0.000**	0.979	0.000**	0.916	0.000**	0.154	0.633
Forearm length (cm)							0.958	0.000**	0.895	0.000**	0.322	0.308
Wing area (cm^2)									0.874	0.000**	0.175	0.587
Wing loading (Nm^{-2})											0.371	0.236

Table 6. A bivariate correlation of call parameter (call frequency, call duration), body parameter (weight, forearm), wing parameter (wing area, wing loading, aspect ratio) of six hiposiderid bats species.

	Echolocation parameter		Body parameter				Wing parameter					
	call duration (ms)		Weigh (g)		Forearm length (cm)		Wing area (cm^2)		Wing loading (Nm^{-2})		Aspect ratio	
	r	p	r	p	r	p	r	p	r	p	r	p
Peak frequency (kHz)	-0.943	0.005**	-0.771	0.072	-0.886	0.019*	-0.886	0.019*	-0.714	0.111	-0.771	0.072
call duration (ms)			0.886	0.019*	0.943	0.005**	0.943	0.005**	0.771	0.072	0.543	0.266
Weigh (g)					0.943	0.005**	0.943	0.005**	0.943	0.005**	0.314	0.544
Forearm length (cm)							1.000	0.000**	0.829	0.042*	0.486	0.329
Wing area (cm^2)									0.829	0.042*	0.486	0.329
Wing loading (Nm^{-2})											0.371	0.486

Table 7. A bivariate correlation of call parameter (call frequency, call duration), body parameter (weight, forearm), wing parameter (wing area, wing loading, aspect ratio) of six rhinolophid bats species.

	Echolocation parameter		Body parameter				Wing parameter					
	call duration (ms)		Weigh (g)		Forearm length (cm)		Wing area (cm^2)		Wing loading (Nm^{-2})		Aspect ratio	
	r	p	r	p	r	p	r	p	r	p	r	p
Peak frequency (kHz)	-0.657	0.156	-0.714	0.111	-0.600	0.208	-0.600	0.208	-0.257	0.623	0.029	0.957
call duration (ms)			0.829	0.042*	0.714	0.111	0.714	0.111	0.714	0.111	-0.371	0.468
Weigh (g)					0.943	0.005**	0.943	0.005**	0.771	0.072	-0.371	0.468
Forearm length (cm)							1.000	0.000**	0.714	0.111	-0.314	0.544
Wing area (cm^2)									0.714	0.111	-0.314	0.544
Wing loading (Nm^{-2})											-0.143	0.787

Relationship between parameter

For twelve bats species the relationship between call duration and wing loading (Figure 20), and other body parameter was significantly related, except aspect ratio (Table 5). For rhinolophid and hipposiderid bats (Table 6 and Table 7).

The relationship between moths in diet and other insects order

The incident of mean percentage volume of moth in diet of rhinolophid was no significantly related to any insect order. For hipposiderid bats, mean percentage volume of moth in diet was negatively related to coleopteran, and positively related to homopteran (Table 8).

Table 8. A bivariate correlation of percentage volume of Lepidoptera and other insect order of rhinolophid and hipposiderid bats.

| | Lepidoptera | | | |
| | Rhino bats | | Hippo bats | |
Insect order	r	p	r	p
Isoptera	-0.771	0.072	-0.314	0.544
Coleoptera	-0.371	0.468	-0.829	0.042*
Hymenoptera	0.086	0.872	0.086	0.872
Blattodea	-0.257	0.623	0.657	0.158
Homoptera	0.657	0.156	0.886	0.019*
Tricoptera	0.203	0.7	0.439	0.383
Hemiptera	0.101	0.848	0.034	0.949
Orthoptera	0.393	0.441	0.58	0.228
Diptera	0.714	0.111	-0.116	0.827

The direct observation of moth-hunting bats

In the study area, direct unexpected observation of the response of an ear moth to bat with high echolocation call (*H. bicolor*146, 146 kHz) was mad. The success in capturing flying moths of this bat was very low (one out of ten was successful)**.** To escape from a continuous attack, the moth changed its flight pattern and finally dropped onto the ground or flied to perch on the wooden crossbeam or pole. The bat then followed and gleaned them. This suggests that some moths in Bala Forest can hear high echolocation frequency (146 kHz). Moreover, *H. bicolor*146 was observed to search for and prey on moths which perched silently on the wall or wooden crossbeam. Furthermore, trapped *H. bicolor*146 were found bitten by the soldier red ant (*Oecophylla smaragina*). This evidence proves that *H. bicolor*146 is a gleaner.

CHAPTER 4

DISCUSSION

In the present study, there was positively significant correlation between the incidence of moths in diet and peak echolocation call frequency of all twelve Rhinolophoidea bats; seven bats used call frequency lower than 100 kHz, and five bats used call frequency higher than 100 kHz. This result agrees with Jones (1992), who compiled published echolocation and dietary data from around the world on bats in the families Hipposideridae and Rhinolophidae and found a positive relationship between incidence of moths in diet and peak echolocation call frequency. This view is also in an agreement with Bogdanowicz *et al.* (1999), who found a relationship between the incorporation of moths in diet and the sound frequency used by bats calling <100 kHz, but does not agree with them for the bats with call frequency higher than 100 kHz. Although the trend of relationship between incidence of moths in diet and peak echolocation call frequency is consistent with the prediction of the AFH, but the percentage of moths in diet of any bats was very low when compared with the previous study, and the scatter plot (Figure 11) has shown that four bats has lower percentage of moths than that of the expected trend line, especially for the bats that used frequency higher than 100 kHz, two of them has very low percentage, and there were not significantly different in the relative proportion of moths in diet between; i) some bats that used call frequency lower and higher than 100 kHz [for example (used Mann-Whitney Test), between; *R. affinis* and *H. bicolor* 131 (Z = -0.705, p> 0.05), *R. stheno* and *H. bicolor* 146 (Z = -1.859, p> 0.05), and *R. acuminatus* and *H. dayacorum* (Z = -1.437, p> 0.05)], ii) between among some bats that used echolocation call frequency lower than 100 kHz [for example; between *R. trifoliatus* and *R. acuminatus* (Z = -1.172, p> 0.05), *R. stheno* and *R. lepidus* (Z = -0.277, p> 0.05)] or higher than 100 kHz [for example; between *H. bicolor* 131, *H. bicolor* 146 and *H. dayacorum* (Krusal-Wallis Test, Chi-Square = 4.781, p> 0.05). This suggests that the proportion of moths in diet

cannot be predicted or explained by echolocation call frequency alone. Nevertheless, the first hypothesis of this study cannot be rejected.

It is not clear for the second hypothesis which predicted that the bats using frequencies higher than 100 kHz, their diet variations are explained by wing morphology, because there was no relationship between the proportion of moths in diet and their wing parameter (Table 4). However, for three bats (*H. bicolor* 131, *H. dayacorum*, and *H. bicolor* 146) that closed in wing loading (Krusal-Wallis Test, Chi-Square = 3.120, p> 0.05), they were not statistically different between the proportion of moths in their diet (Krusal-Wallis Test, Chi-Square = 4.781, p> 0.05), this suggests that wing loading might exert its influence on the relationship between the proportion of moths in diet and call frequency of these high frequency group.

The Rhinolophidea are aerial capturers and some are gleaning bats (*i.e.* glean insects from ground or vegetation) (Shortridge, 1934; Griffin and Simmons, 1974; Schnitzler *et al.*, 1985; Neuweiler *et al.,* 1987; Jones and Rayner, 1989; Mcdonald *et al.,* 1990; Pavey, 1998; Siemers and Ivanova, 2004). The preying ability of these bats allows them to prey on ear or earless night-flying moths or day-flying moths which hold quietly or rest on the tree or leaves. Field personal observation found that *H. bicolor*146 preyed on moths that clinged silently on the wall and wooden crossbeam. This show that they can prey up on earless moths. In northern tropical Australia, *R. megaphyllus* (call 67-71 kHz) eats earless moths (Parvey and Burwell, 1998), and *R. blasii* can glean the fluttering moths on the ground (Siemers and Ivanova, 2004). From direct observation, the response of an ear moth with the high echolocation call bat (*H. bicolor*146, 146 kHz) was seen. The success in aerial feeding on moths of this bat was low (one from over ten times), but from strategy of continuously attacking, the moth changed a flight pattern and finally dropped to the ground or flew to perch on the wooden crossbeam or pole, then the bat followed and gleaned them. This suggests that, firstly; an ear moth can hear bat echolocation call higher than 60 kHz, secondly; there was not only echolocation that helped Rhinolophoidea bats to counteract the mechanism of ear defense in moth.

Wing

The wing morphology is one factor which determines the habitat use by bat (Norberg and Rayner, 1987; Aldridge and Rautenbach, 1987; Stockwell, 2001). The low wing loading and low aspect ratio of these Rhinolophoidea bats in Bala Forest make them highly manoeuvrable, and able to fly through the clutter habitat and reach a narrow space (Norberg and Reyner, 1987). This will increase the success to prey on ear or earless moths. For example, *H. bicolor*146 was found to glean moths immediately when moths escape to the ground or wooden crossbeam. Therefore, wing loading is one of the major constraints for an ability to prey on moths. Moreover, walking or wingless insects, such as blattodea, was present in the diet of most bats except *H. diadema* which has higher wing loading than others, suggesting that most bats in this group can be a gleaner.

Echolocation of rhinolophid and hipposiderid bats

The calls of the Rhinolophoidea bats are specialized, comprising of long constant frequency component and followed by a frequency modulated terminal sweep (CF-FM) (Schnitzler *et al*., 2003). The evolution of echolocation in Rhinolophoidea bats is characterized by two main purposes, first for orientation in a clutter space, and second for prey acquisition rather than specifically hunting on moths (see below for explanations).

The FM signal of short duration and low sound pressure level are used mainly for spatial orientation. A steep FM sweep that precedes or follows the narrowband component is better suited to localize and characterize the background targets (Schnitzler *et al*., 2003). The long CF component of their signal helped to reveal the fluttering insects (Schnitzler, 1983), moreover it might also help them to commute in narrow flyway along landscape contour (Schnitzler *et al*., 2003). Furthermore, in combination with Doppler shift compensation and a specialized hearing system, these bats can recognize echoes from fluttering prey insects modulated in the rhythm of the beating wings between unpopulated background echoes. When combined these echolocation-designs with low wing loading and low

aspect ratio, Rhinolophiodea could be specifically adapted for foraging mainly in clutter habitats.

Difference in phylogenetic of these Rhinolophoidea bats (i.e., *Rhinolophus* and *Hipposideros*), lead them to use different echolocation call designs, and difference in the acoustic fovea of the brain (Neuweiler, 1984), while they overlap in wing loading and aspect ratio. The echolocation may be used to define niche space in bat guild (Jacob *et al.*, 2007; Siemers and Schnitzler, 2004). Call structure of rhinolophid bats clearly consists of a long sweep down frequency modulated (FM) at the front and end of a constant call (FM-CF-FM) (Figure 7), while the long FM component was found at the end of the CF call (CF-FM) in hipposiderid bats. The CF call of rhinolophid bats had a longer duration than the hipposiderid bats (Table 3). Therefore, these call characters can be used to separate between these bat groups. When separated, the efficiency on moths hunting of these two bat groups can be explained as follows.

For Rhinolophid bats, a negative significant association between call duration and proportion of moths in diet was shown suggesting that a shorter call duration of these FM-CF-FM component bats has a higher ability for moth hunting, with the complement of low wing loading (Table 1 and Table 3). For example, *R. affinis* and *R. stheno* or *R. acuminatus* and *R. lepidus*, which were similar in call duration and call frequency, percentage volume of moth in their diet is depended upon their wing loading (Table 1 and Table 3) and partial correlation, showed no significant association (r = -0.789, p = 0.112) between moths and call duration when wing loading was controlled. The rhinolophid bats need to use call frequency lower than hippoiderid bats in order to have the similar efficiency in hunting on moths as hipposiderid bats under the same wing ability condition. For example, *R. lepidus* (call = 97 kHz, wing loading = 7.41) consumes moths in a similar percentage with *H. bicolor*146 (call = 146 kHz, wing loading = 7.66), and *R. robinsoni* (call = 64.8 kHz, wing loading = 7.41).

For hipposiderid bats, a positive significant association between peak call frequency and proportion of moths in diet was found. These bats use short call duration and one long steep FM component, suggesting that the high call frequency increased their ability for moth hunting, and the call higher than 145 kHz was

relatively highly efficient for moth hunting. The high call frequency should allow them to 'see' the picture in a finer scale which helps them separate the small prey from the background. This could explain why this bat tended to use high call frequency and high wing manoeuvres (Table 6), which helped them to reach preys in small hold.

The peak echolocation call of these rhinolophid and hipposiderid bats is not at random (Kruskal Wallis test, chi-Square = 149.238, p <0.01). There exists a separation in frequency bands, and most species have a narrow frequency range (1-6 kHz), representing a standard deviation from the mean for the species less than 5%. This may help facilitate communication.

Under the particular wing morphology and the difference in call structure designs, rhinolophid and hipposiderid bats differ in call frequencies and call structures. These suggest that niche space partitioning of these two bat groups which are in same guild is governed by call design. Due to the effect of difference in call design it should not combine the relationship between moths and call frequency between them.

Habitat and prey

The percentage volume and percentage frequency of occurrence of Lepidoptera in diet were low while relative frequency and percentage mass of trapped Lepiodoptera were high. These may be influenced by two factors; first moth in Bala Forest may hear the high frequency echolocation call, and second the relatively high abundance of prey which are easier to hunt.

From the field observation, moths can hear the high frequency of bat call. Based on the optimum foraging hypothesis, bats will switch from moths when it is hard to prey to swarming termites or beetles which are easier to capture. When Isopterans swarmed, the bats (i.e., *H. diaderma*, *H. bicolor*146, *H. dayacorum*, *R. acuminatus* and *Cheiromeles torquatus*) preyed only on that swarm termite until these insects were finished. The high percentage volume of coleopteran and hymenopteran insects in the diet of many bats corresponded with their abundance in the traps. Jacob *et al.* (2007) found that the percentage of moths in the diet of *R. clivosus* and *R.*

capensis decreases when coleopterans in diet increased. The bats should take advantage of capturing the easier prey insects over the harder individuals.

Although the percentage of moths in diets was high, it is still not possible to elucidate between the percentage of ear moths or earless moths in bat diet. Therefore; if the bats have other tools, except for the call, that help to win the ear-defending mechanism by moths, such as wing manoeuvres, these suggest that the moths in diet tell little about the AFH. In addition, the study on the trend of the AFH by investigating the relationship between moths in bats diet, should be done on at least in the same bats group that has similar foraging ability (e.g., wing loading, aspect ratio, call structure, call type, habitat used or time) except the call frequency.

However, this study was not carried out during the pregnant and lactating period which is an important period for bats. For the further analysis, testing AFH could be done in different seasons. For the rhinolophid and hipposiderid bats, it will be interesting to study the efficiency of echolocation call. This will let us know how they partition resource and their ability in hunting insects. The time when insects were scarce may be suitable for testing the AFH because it may help to verify that echolocation evolved for directly increasing the hunting efficiency on moths, or it is just only a random pattern.

CHAPTER 5

CONCLUSION

The trend of the AFH is valid for this guild due to the wing ability and call structure design are the major factor affected on the ability for moth hunting. For the bats which used frequency call higher than 100 kHz which consist only hipposiderid bats, that likely to be support for the AFH, but for those bats who call < 100 kHz, with consist with only rhinolophid bats, the mean call duration rather than call frequency to limiting ability on hunting moth.

The rhinolophids and hipposiderids are different in call structure-designs. These two bats group tended to have a difference in echolocation ability, especially for moths hunting. Therefore, they could not combine these two bat group together or with other bats species, for test on the trend of the AFH.

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