Chapter 3

Diet, reproductive biology and dawn return patterns of the cave-nectar bat, *Eonycteris spelaea* Dobson (Chiroptera: Pteropodidae) in southern Thailand.

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Abstract

Although *E. spelaea* is exclusive nectarivorous bat, the quantitative contribution of each diet item and its temporal variation is not well understood. The diet of *E. spelaea* was examined from bats captured monthly at the cave entrance between June 2002-May 2003 in Songkhla Province, Thailand. Both faecal analysis and pollen from fur-collected sample were applied to identify plant ingested. From 1,155 diet records of 506 bats' faeces, eleven taxa were identified. *Parkia* spp. (33.85%) and *Musa* spp. (28.05%) have the highest percentage frequency followed by *Eugenia* spp., *Oroxylum indicum* Vent., *Durio zibethinus* Merr., *Ceiba pentrandra* Gaertn. (5-9%), respectively while *Soneratia* spp., Unknown 1 and *Cocos nuciflora* L. made up a minor proportion (<2.5%). Different species of plants were the main diet of *E. spelaea* in different time of the year. In addition to *Parkia* and *Musa* which were the most important in nearly every month, *Durio* spp. has its highest contribution during March-April, and *Eugenia* spp. during November to February, and *C. pentandra* during December to January. Individual bat feed on flowers of up to six species of plant nightly. The results from fur-collected samples contrasted with those from faecal analyses, *Musa* spp. has the greatest percentage frequency (34.29 %), whereas *Parkia* spp. made up 23.22%, while the other items was generally correspondence to faecal analysis. Adult male showed a greater frequency percentage of *Musa* but less *Parkia* than adult female in both sampling techniques, while the other diet items were similar. Sexual variation in the diet was not statistical significantly different. Lactating and late pregnant female *E. spelaea* were found in nearly every month. It appears that there are two periods where higher proportion of lactating female; July –November, and February – May. The morning return pattern differs significantly between sexes. Most mature male returns early the night while most female returns in the morning. This return pattern is similar to foraging pattern during breeding period reported in those polygynous fruit bats that maintaining the harem.

Introduction

In the study on autecology of wild animals, diet is a fundamental information that can reveal the interaction between such animal and its habitat. Specifically, diet of nectarivores can both tell us how such taxa maintains its population, and also suggest its ecological potential of such organism as a pollinator of its visited plants. Such information is ecological and economical importance. In terms of economy, there are increasing global concern on pollination failure of food plants, since some evidence suggested that it is currently happened (Allen *et al.* 1998; Kevan and Phillip, 2001). In addition, since almost all flowering plants (98-99%) in tropical forest rely on animal as its pollinator (Bawa 1990), these animals play a key role in the maintenance of tropical forest structure and/ or restoration of disturbed forest.

Eonycteris spelaea is one amongst three exclusive nectarivorous bats in Thailand. It is the largest one with a forearm length of between 66-78 mm and weighing 40–70 g. Its specialist in nectar feeding is indicated by its long muzzle, and sharply pointed tongue, with well-developed filiform papillae at the tip (Bates and Harrison, 1997). *E. spelaea* is rather common throughout SE Asia and occupies a variety of habitats including primary forest, secondary forest and orchards (Lekagul and McNeely, 1977; Heideman and Heaney, 1989; Kitchener *et al.*, 1990). *E. spelaea* travels up to 38 km each night. Previous studies indicated that this bat feed on plants of 31 species in Malaysia (Start 1974), while Pakarnseree (1986) analysed stomach content of *E. spelaea* indicated that it consumed at least 19 plants species in Thailand. Only Start (1974) that provided quantitatively the contribution of each plant in bat's diet. However, Start (1974) used the proportion of each pollen type to all counted pollen collected from faeces trays set under day roost, which inherently bias toward those plants produced numerous pollen grains. In addition, some pollen type (e.g. *Musa*) is thought to broken down rapidly in guano (Start and Mashall 1976), and therefore, is not represented by this technique. Thus, the actual importance of each food item to E. spelaea is not clear. In the present study, using individual bat as a sampling unit, which is less bias, is applied to study the diet of *E. spelaeae*. In terms of temporal variation, since each plant flowers in different time of the year, as a strategy to avoid pollinator competition, each plant may be varied in time in its contribution to bat's diet. Thus, detail of diet study from interval collection is necessary. For the nondestructive diet study based on individual basis, two common protocols have been used: faecal analysis and fur sample analysis. Both technique may give a different picture from the same sampled bats, and it is suggested that the data on the diet based on fur-collected sample can be detected for longer period especially when grooming is not 100% effective (Thomas 1988). However, no study have been compared the results from both popular techniques, and to test this hypothesis yet.

Sexual variation in diet can be revealed when it differs between sexes in foraging site, or foraging behaviour. Start (1974) indicated that male *E. speleae* were capture frequently in mangrove forest, while females forage inland. In some bats, sexual variation in foraging behaviour during breeding period were reported (Bumrungsri 2002, Balasingh et al. 1995, Kunz et al. 1998). Since it was indicated that this bat is reproductive year round, any sexual difference of foraging behavior can be revealed from capturing bat at the cave entrance is determined.

Material and methods

Study site.

Bat capture was carried out at Khao Kao Cave, Songkhla Province, southern Thailand (6° 42.45' N, 100° 16.64' E, 50 a.s.l.) which situate at the base of limestone hill at the Thailand-Malaysia borders. Within 20km radius from cave, rubber plantations (40%) and tropical lowland forest (30 %) covered most of the area. The large patches of mangrove forest are ca. 19 km from the cave. Surrounding the cave, patches of wild banana (*Musa* sp.) are interspersed in the edge of rubber plantations and recently cleared land. The area, except those in the protected forest, is sparsely inhabited with human settlement, and the closest town is Padang Besar, 30 km from the cave. In villages, plants commonly found in backyard gardens including *Parkia speciosa* Hassk., cultivated banana (*Musa* sp.). The annual rainfall is 2,118mm, and most of the rains are in October- December. Mean temperature and relative humidity is 28.3 °C and 72 percent respectively (Kor Hong Meteorically Station, 2004)

Bat trapping and pollen collecting.

A mistnet (2.6 x 2.6m) was set across cave entrances to capture returned bats. Since the width of cave entrance is about the same as the length of a mistnet, each net pole was hold by assistance in a slight angle (ca. 10 degree) from a vertical plane toward cave interior. A preliminary study in May 2002 suggested that the number of captured male bats were too small when mistnet was set between 0300-0600h, and disturbance to bats appeared to be less when bats were captured for 15 min in every half hour session. Consequently, bats were then captured for 15 minute per half-hour interval from 0130h to 0630h or until the bats stopped returning. This sampling regimen was successful in catching more males and temporal pattern of morning return was revealed. This cave has two entrances, and bats were captured at the lower smaller entrance (2 x 3m) in the first 3 months. Capture site was changed to an upper larger cave entrance (3 x 3 m) after most bats were seen to use that entrance. Video observations revealed that nearly most of the colony still use the upper entrance although net has been set, suggests that disturbance from capture was acceptable.

Bats were captured once a month for a year during June 2002-May 2003. In each month, 39 to 72 bats were caught. From field observation in the early months of study, some bats did not defecate although they were kept in bat bags for a while, consequently, two methods of collecting information on diet were undertaken: diet from faeces and from pollen attached to bat faces and body. The latter was begun one month later than the former, but both methods covered 12 months duration. After bats had flown into the mist nets they were carefully removed. Once removed, a piece of scotch tape was placed on their face, chest, muzzle and head where a large amount of pollen is obvious. The scotch tape sample was put onto a sterile slide with a number corresponding to captured bats. Each captured bat was then kept separately in a clean cotton bag. The individual bat was weighed with a 100 g balance. Sex, age (juvenile or adult) and its reproductive status was noted for female bats (non-reproductive, late pregnant, lactating) following Racey (1988). Pregnancy was detected by palpation, and only that detectable pregnancy was noted. Bats were kept for about two hours or until the sampling period was finished. All bats were released in the cave by 0900h. Sugar syrup was given to most bats before released for save them from too dehydrated. This bat is easily become hyperthermia and become weak or even die shortly when was in sun light, thus they must kept away from the sun. After bat was released, each bag was examined for a faeces sample, when present it was scraped into a labeled eppendorf tube. In case where bat produce very watery faeces and it can not be scraped into a tube, scotch tape was applied to collect faeces and it was put onto sterile labeled slide.

Slide preparation and pollen identification

Faecal analyses

Three slides were made from every faecal sample. A premixed solution of 95% alcohol and ethylene blue was added to the faeces-collected tube until the volume was 1ml. The solution was then thoroughly shaken and faeces were broken up using a jabbing device until faeces had dissolved as much as possible. Using a dropper, three drops of solution were then placed on a sterile slide and the dropper was then washed. Once the alcohol had evaporated off and the faeces sample had dried, a medium-sized drop of PVA (polyvinyl alcohol) was added and a cover slip was placed on top with special care to avoid trapping air bubbles and keep the cover slip straight. Finally, the slide was left in a warm place until completely dry and it was then labeled accordingly. All examination of slides was done using a light microscope at x4, x10 and x40 magnification. Pollen was identified to species if possible by comparing with reference collection and Start (1974). Pollen of any species that was not immediately identifiable was listed as an unknown, with a brief description and sketch along with its coordinates on the slide. Later the unknown was then photographed using an Olympus Digital Camera attached to a light microscope. Photographs were taken at 10x and 40x magnifications for each specimen. These photographs have been kept for further examination.

Once pollen was found, its relative abundance was noted, although relative importance of plant in bat's diet can not be revealed from number of pollen (Thomas 1988). Identified pollen was scored as present/absent. Pollen of any species was categorized as presence if at least two pollen grains were found in any slide prepared from each tube. In case that only one pollen found on a slide, it can be categorized as presence when it was found in at least two from three slides prepared. Thus, with this category, the underrepresenting of plants with small number of pollen will be minimised. Previous researcher used three or more grains as a criterion (Heithaus *et al.* 1975). In addition, pollen from bat bags were identified and this information were complemented the result from faeces collected from bat.

Pollen collected from bat faces and body

Slides with scotch tape attached were carefully examined throughout the slides under light microscopes. In each slide, the area close to the edge was excluded from examination in order to avoid possibly pollen contamination from other sources. Pollen was identified, and their relative abundance was scored. Similar to faecal analysis, taxa with one pollen in each slide were excluded from further analysis.

In both faecal analysis and pollen from bat faces, the contribution of each diet item in the diet was expressed as percentage frequency : the number of occurrences of particular category divided by total occurrences for all categories, multiplied by 100 (McAney *et al.*, 1991).

Statistical Analysis

Intraspecific diet variation was examined with Chi-square contingency test. General linear model was applied to determine sexual variation in return pattern. Data was transformed to meet the assumption of homogeneity of variance. All statistical analyses was performed with SPSS 11.5.

Results

Diet

Diet from faecal analysis

Based on 1,155 diet records from faeces of 506 bats, at least eleven taxa of pollen have been found. Pollen of *Parkia* spp. and *Musa* spp. showed the highest percentage frequency of 33.85% and 28.05% respectively, followed by *Eugenia* spp. (9.44%), *Oroxylum indicum* Vent. (6.41%), *Durio zibethinus* Merr. (6.15%), *Ceiba pentrandra* Gaertn. (5.54%), respectively whilst *Soneratia* spp., Unknown 1 and *Cocos nuciflora* L. made up a minor proportion between 0.26-2.42% (Fig. 1).

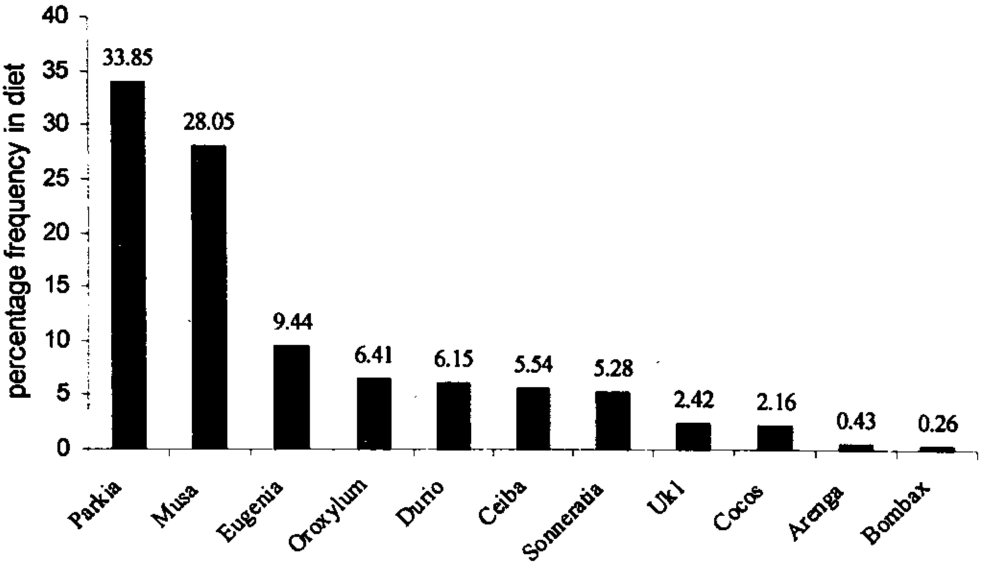

Fig. 1 Percentage frequency of each plant in the diet revealed from faecal analysis of *E. spelaea* during June 2002-May 2003. This is based on the 1,115 diet records of 506 bats.

Temporal variation in diet of E. speleaea

Since overall percentage frequency may obscure the importance of each diet item in particular period, diet in each month was considered. It was found that different species of plants were the main diet of *E. spelaea* in different time of the year. Generally, *Parkia* and *Musa* were the most important in nearly every month. *Parkia* spp. contributed more than half of diet in June–July 2002 and May 2003, and it is generally a main food during rainy season. From field observation, these taxa could be mostly assigned to *P. speciosa* Hassk. which was commonly found flowering during that time. Another species, *P. timoriana* Merr. was in flower during December-January. There could be at least one another species of *Parkia* (*P. streptocarpa* Hance) which is relative rare and could represent in the diet of this bat. However, pollen of these *Parkia* is inseparatable. *Musa* spp. consistently contributes about 17-36% in every month without outstanding peak. Although *Durio* spp., which could be mostly assigned to *D. zibethinus* Merr., was available for short period (March-April), it was the most significant food resource during that time. Likewise, the contribution of *Eugenia* spp. in the diet was greatest during November 2002 to February 2003, and *C. pentandra* was during December 2002 to January 2003 (Table 1). In each night, individual bat could feed on flowers of up to six species of plants (mean ±SD = 2.06 ±

1.21). From faecal analyses, there were 3-9 species of chiropterophilus plant available for this bat in each month. Generally, there was higher diversity of diet items in early to mid dry season compared to rainy season.

Table 1 Percentage frequency of plants in diet of *E. spelaea* in each month. The number of captured bats which faecal analysis based on was indicated.

Month	*Musa*	*Parkia*	*Durio*	*Bombax*	Uk1	*Arenga*	*Cocos*	*Oroxylum*	*Eugenia*	*Ceiba*	*Sonneratia*	*n*
Jun2002	25.00	62.50	0.00	1.79	0.00	1.79	1.79	7.14	0.00	0.00	0.00	46
Jul2002	35.53	50.00	0.00	1.32	1.32	0.00	6.58	3.95	1.32	0.00	0.00	48
Aug2002	35.87	43.48	0.00	0.00	0.00	0.00	6.52	9.78	1.09	0.00	3.26	53
Sep2002	32.43	47.30	0.00	0.00	0.00	1.35	2.70	8.11	8.11	0.00	0.00	48
Oct2002	34.74	36.84	0.00	0.00	0.00	0.00	7.37	18.95	0.00	2.11	0.00	41
Nov2002	26.36	37.27	0.00	0.00	0.91	0.91	0.91	10.00	16.36	3.64	3.64	50
Dec2002	26.39	25.00	0.00	0.00	0.00	0.69	1.39	5.56	15.28	18.06	7.64	62
Jan2003	27.72	16.85	0.00	0.00	0.00	0.54	0.54	4.35	20.11	16.30	13.59	70
Feb2003	28.10	16.53	0.00	0.83	18.18	0.00	0.00	5.79	17.36	1.65	11.57	41
Mar2003	20.59	31.37	39.22	0.00	3.92	0.00	0.00	0.00	0.98	0.00	3.92	41
Apr2003	21.21	33.33	42.42	0.00	0.00	0.00	0.00	0.00	3.03	0.00	0.00	30
May2003	17.14	74.29	8.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28

Diet from fur-collected sample: At least nine taxa of pollen were identified. *Musa* spp. contributed the greatest percentage frequency (34.29 %), while *Parkia* spp. made up 23.22% (Fig. 2). These results contrasted with those from faecal analyses. The contribution of *Eugenia* spp., *C. pentandra*, *Soneratia* spp., *Durio* spp. and *O. indicum* were generally correspondence to the result from faecal analyses. Similar to faecal analyses, there are 1-6 pollen found in each individual (mean ± SD = 2.61 ± 1.28).

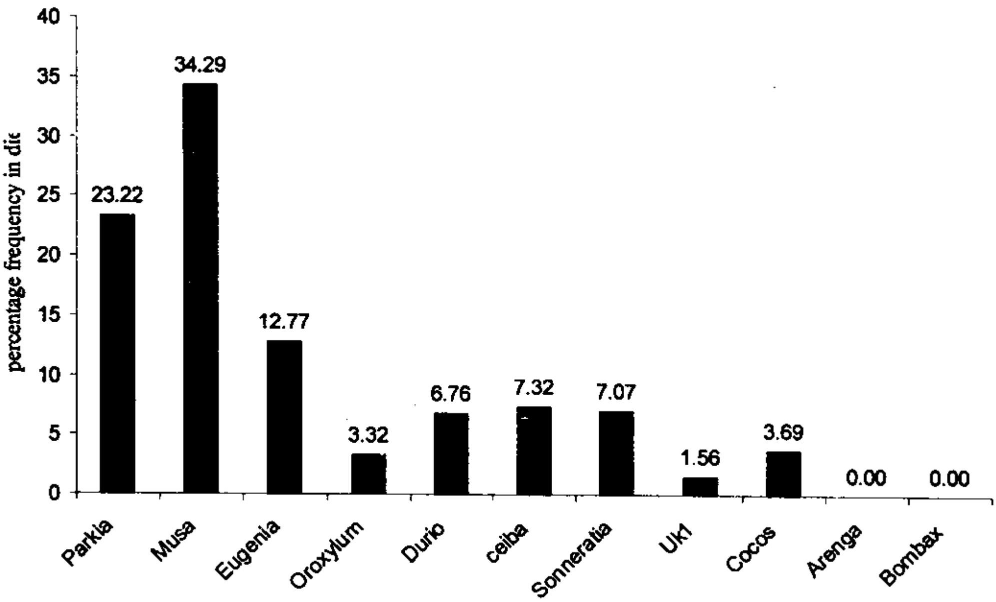

Fig. 2 Percentage frequency of each plant in the diet of *E. spelaea* revealed from fur-collected sample during July 2002-June 2003. This is based on 1,598 diet records of 607 captured bats.

Intraspecific diet variation

Sexual variation in the diet of adult bats was examined. From faecal analyses, adult male showed a greater frequency percentage of *Musa* (30.6/26.6) but less *Parkia* (32/ 37.4) than adult female, while the other diet items were similar. It appears that male showed higher preference to plants normally growing in clump (*Musa, Durio, Soneratia*) while female are more to plant that highly isolated (*Parkia, Oroxylum*). Statistically, the diet of mature males and female was not significantly different (Chi-square = 11.052, df=9, p=0.272) (Fig.3). Consistently, pollen from fur also showed that male has greater percentage frequency of *Musa* (36.1: 33.9) but less *Parkia* (21.9: 25.2) and sexual variation was not significant.

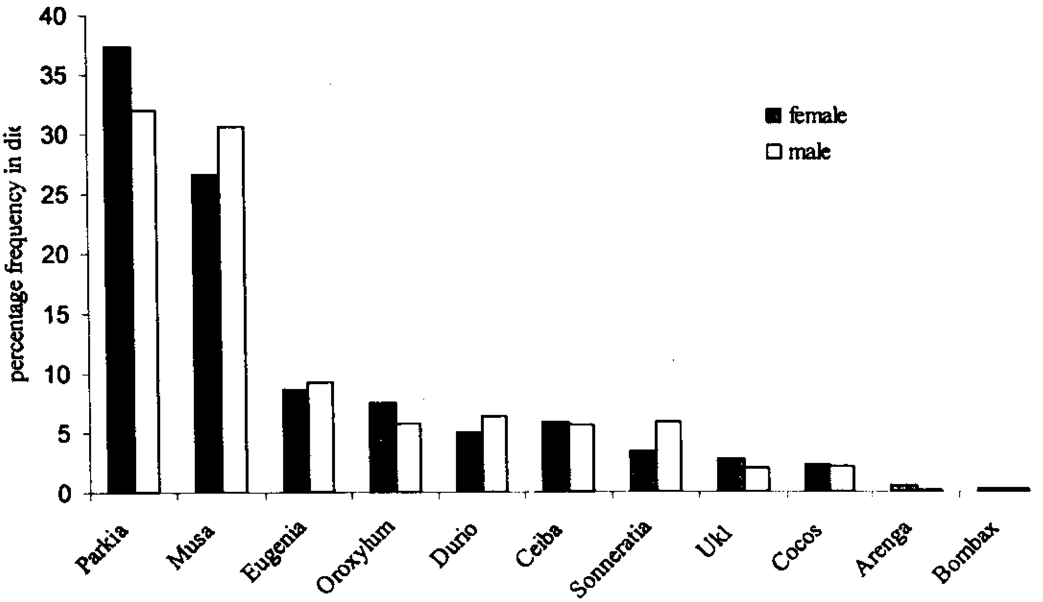

Fig. 3 Frequency percentage of each plant in the diet of adult male (n = 302) and adult female (n = 189) *E. spelaea* revealed by faecal analysis during June 2002- May 2003.

Reproductive biology of *E. spelaea*

Lactating and late pregnant female *E. spelaea* was found in nearly every month. There were nine months that more than 40% of adult female were lactating, but peak of lactation was not quite clear. It appears that there are two periods where higher proportion of female lactate; July –November, and February – May (Fig. 4). Most female (>60%) was found pregnant in three months (December, January, and June). More than half (53.70%) of all pregnant female (n = 54) are given birth for the first time. About three-fourth (72.41%) of lactating female (n = 87) were attached by their offspring when were captured. No female attached by more than one offspring. Juvenile bats were also found in every month. Sex ratio of adult bats is male: female = 1: 0.56 (n = 524) while sex ratio of juvenile ones is 1:2.36 (n = 74).

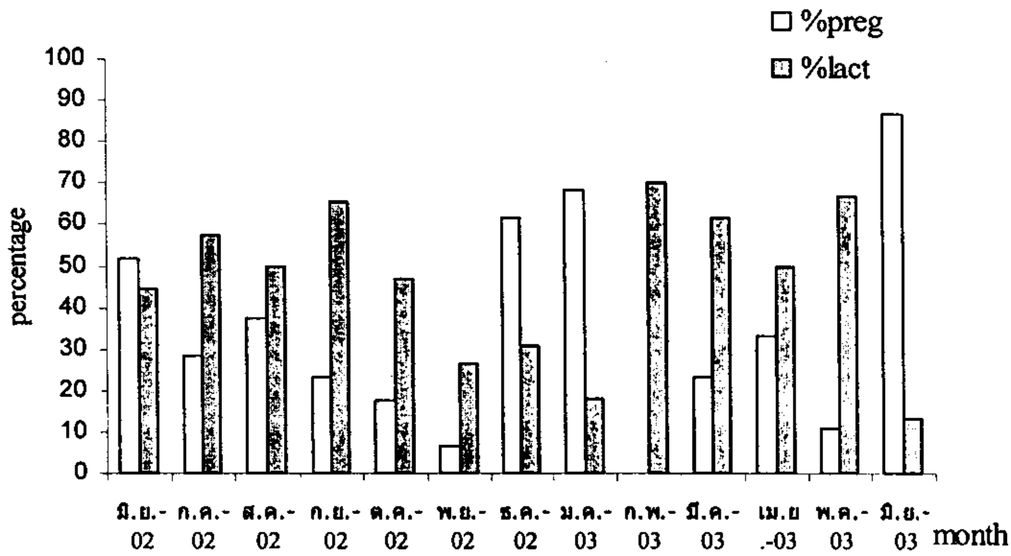

Fig. 4 Percentage of lactating and late pregnant female *E. spelaea* during June 2002-June 2003. This based on 219 captured bats. The number of captured adult female in each month was between 8-27 bats (mean ± SD = 16.84 ± 5.87).

Sexual variation in morning return time of *E. spelaea*

The return pattern of bats was determined for eight months (except September 2002, October 2002, February 2003, and May 2003). The return pattern differ between sexes in relation to time ($F = 3.536$, $df = 10$, $p < 0.001$) and this pattern is consistent between sampling months ($F = 0.817$, $df = 1$, $p = 0.368$). Most mature male return early the night, with some of them regularly return till morning compared with most female which return in the early morning (Fig. 5)

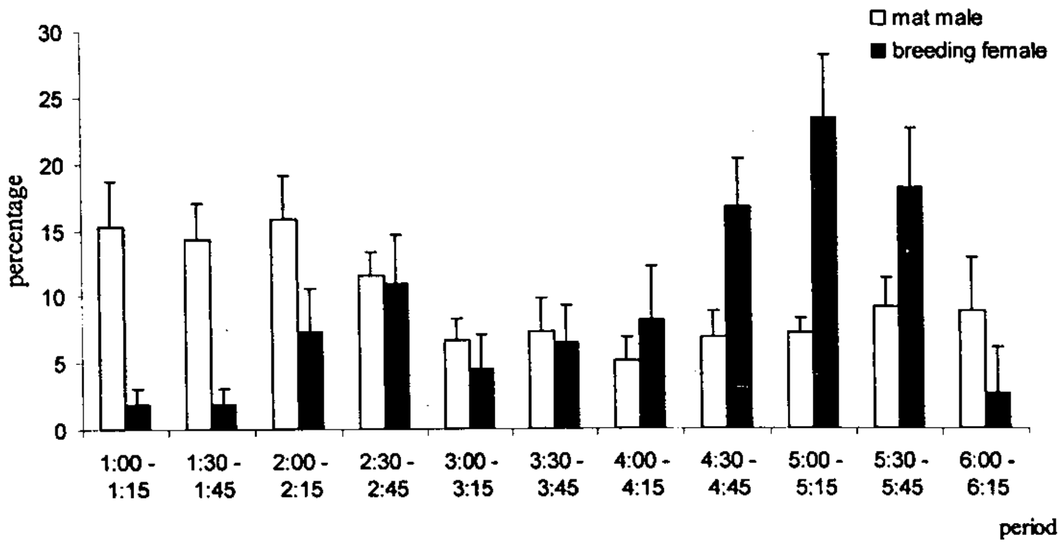

Fig. 5 Average percentage of adult male and breeding female(either pregnant or lactating) captured within 15 minutes period of half an hour interval from 0100h till 0630h during June 2002- April 2003 (except September, October 2002 and February 2003). This information based on 39-68 captured bat per month.

Discussion

Diet

Obviously, the present study indicates the significantly difference in the proportion of major diet item of *E. spelaea* when different techniques were applied. Much higher percentage of Parkia in faeces-collected technique while greater proportion of Musa in fur-collected technique. Additionally, some rare species can only revealed from faecal analysis only, and thus number of plant species from fur-collected technique is smaller. The proportion of *Oroxylum indicum* by fur-collected is half of that faecal analysis one. The incompatible between results from these techniques can be partly explained in terms of timing of flower visitation. A recent study indicated that the highest activity of *E. spelaea* at flowers of *P. speciosa* at 2000h-2300h and *P. timoriana* is 2000-2100h, while peak of visit in *Musa* is later, around 2200-2300h (Ekapong 2005). In addition to post-feeding grooming which is common in nectarivorous and fruit-eating bats, pollen from earlier visit is probably lost or transferred when bats visit to next flower thus less probability of pollen from early visit remain on bat's fur compared to later visit plants. Consequently, diet from fur-collected sampling is more bias toward those plants that bat visit later the night. This is probably more pronounced in this case, since groves of wild *Musa* is widespread and common in newly open areas and along dirt tracks around the study cave (S. Bumrungsri, pers. observ.). This also explains the smaller proportion of O. indicum in fur-collected sampling. In this species, anthesis is at 1900h and flower drop by 0200h (Sritongchuay 2006). On the other hand, pollen from earlier visit and later visit is probably more equivocal in faeces-collected samples from the evidence that rare species only found by faeces-collected sampling. Although the transit time of nectar bat is rapid, and the data on the diet based on fur-collected sample can be detected for longer period especially when grooming is not 100% effective (Thomas 1988), recent evidence indicated that retention time of seeds in alimentary tract of fruit bat can sometimes as long as 24 hours (Shilton 1999). This could be also true for pollen, however, further experiments on how long pollen can be detected in both sampling techniques is needed for firm conclusion.

In addition to some bias of each sampling technique, diet information from the present study suffers from some inherent bias including the under-representation of fruit and leaves in faecal and fur-collected techniques. Amorphous and chewed leaves were found over trays set below day roost of this bat in some particular month (S. Bumrungsri, unpublished data). It is quite likely that one of fruit eaten by *E. spelaea* is rambutan since bats were found to feed on the fruit when available (S. Bumrungsri, pers. observ.)

From the present study, result from both sampling techniques share some common features including *Parkia* and *Musa* are the most important diet items, flowering plants that available for long period of the year (e.g. *Parkia*, *Musa*, *Oroxylum*, *Cocos*, *Eugenia*, and *Sonneratia*) are the majority of bat's diet (ca. 85%). However, at the finer scale, some flowering trees, when available, which bear a number of flowers within short period (e.g durian and uk 1) are the major diet in a particular month as seen in Table 1.

In previous study, Start (1974) examined the diet of *E. spelaea* by faecal analysis of pollen below day roosts in peninsular Malaysia, and listed 31 plant species consumed by this bat. *Duabanga*, *Artocarpus* and *Soneratia* are the major diet (12-30%) while *Parkia* (11.1%), *Musa* (trace) and *Eugenia* (4.3%) contribute relatively small percentage. However, it is not comparable to the present study since Start (1974) used the proportion of each pollen type to all counted pollen, which inherently bias toward those plants produced numerous pollen grains. In addition, some pollen type (e.g. *Musa*) is broken down rapidly in guano (Start and Marshall 1976). Fundamentally, using individual bat as a sampling unit is more independence than using number of pollen grains, and thus more accurate in determination of relative importance of each diet items. However, individual-base technique could be less accurate in terms of diversity of diet items since it can sample only a small proportion of a study colony. Since diet of a certain bat species can vary geographically (Start 1974), similar study on the diet of *E. spelaea* in other area is vital to understand on which food source that maintains bat population.

Although it is too premature to assume that *E. spelaea* is the pollinator of plant species found in its diet, strong evidence from pollination experiments confirm that this bat is the principal pollinator of al least some species including *Parkia speciosa* and *P. timoriana* (Bumrungsri *et al.* submitted), durian (Soepadmo and Eow, 1976; Bumrungsri *et al.*, unpublished manuscript), *Oroxylum indicum* Vent.(Sritongchuay 2006). These plants are economically important food resources in SE Asia, and in turn, economic importance of this bat to this region can be estimated. The contribution of this bat to pollination success of other food plants in its diet is also warrant further study.

Intraspecific diet variation

Overall, diet of male and female are relatively comparable. The slightly difference in their diet probably reflect foraging strategy influence by its return pattern. Most male return in early hour of the night, probably reflect territory defense, feeding on clump-distributed food can save searching and commuting time. Thus, male can spend shorter time outside the roost. While female which devote themselves for breeding most of year can fulfill its reproductive requirement by getting longer time for both searching and commuting for high quality and quantity throughout the night, especially most lactated female that usually carry suckling young. Start (1974) using capture information and pollen from captured bats, revealed sexual variation in feeding habitat of *E. spelaea* in peninsula Malaysia. Higher proportion of female captured at the coast, while more male captured on the hills.

Reproductive biology of *E. spelaea*

Similar to other studies, either lactating and pregnant female were found in every month (Beck and Lim, 1962; Bhat *et al.* 1980; Heideman and Utzurrum 2003). It appears that April and August is the mid point of each observed lactation period in the present study. In Philippines, birth period of *E. spelaea* is synchrony, and it was centered in March and August (Heideman and Utzurrum 2003). Although early pregnant in the present study is gone undetected, it appear that many female must experience early pregnancy during lactation(since high proportion of female lactate in following period), and suggested that female often give birth to two young annually. Beck and Lim (1962) and Heideman and Utzurrum (2003) also reach a similar conclusion. This breeding characteristic is termed as extended seasonal bimodal polyestry (Heideman and Utzurrum 2003) with post-partum estrus following at least one of the birth periods. This breeding pattern is similar to other nectarivorous bat, *Macroglossus minimus* (Heideman and Utzurrum 2003), but differ from sympatric fruit eating bat, *Rousettus amplexicaudatus* (Heideman and Utzurrum 2003), *Cynopterus brachyotis* (Bumrungsri *et al.* 2007).

Although quantitative food availability is not yet studied, it appears that there is greater diversity of food plant available in dry season compared to rainy season. While *Parkia* which are the major food source is plentiful in rainy season. Thus, this bat may time its lactating and weaning period when food is diverse or major food plants is common. It has been proposed by a number of studies that food diversity and food availability (reviewed by Racey and Enwistle 2000) are major determinant for timing pregnancy or lactation.

Calcium is proposed to be a limiting resource for reproductive female fruit bats since their diet contains relatively low calcium content while fruit bats raise their young to near full size before weaning. Extend seasonal bimodal polyestry can be possible when calcium requirement is met. Barclay (2002) showed that nectar of bat-visiting plants contain higher calcium that other plants. However, it is tremendously varied between plant species of calcium content even in the same genus. Thus, time the breeding period when diversity of plant flowering can complement calcium content of these plant or when flowering time of calcium-rich plant is available.

Sexual variation in morning return pattern

From the return pattern that most male return earlier than female, it is indicated that most male spend longer time in roost compared to female. This is similar to foraging pattern during breeding period reported in those polygynous fruit bats that maintain the harem. Mature male of a tent-making bat, *Cynopterus brachyotis* spend a higher proportion of time at their roosts than mature females during the breeding periods (Bumrungsri 2002). Likewise, harem males of several fruit bats spend significantly more time and energy at roost than other bats(e.g. spear-nosed bat, *Phyllostomus hastatus*, Kunz *et al.*, 1998; *Artibeus jamaicensis*, Morrison and Morrison, 1981; *Cynopterus brachyotis*, Bumrungsri 2002). Moreover, previous studies indicated that harem male forage mostly in the vicinity of their harem roosts. Harem male allocate more time and energy for roost surveillance and defense a roost independence of the the presence of female. Females, on the other hand, spend more time in foraging during the breeding periods (Bumrungsri 2002, Kunz *et al.* 1998). Radiotracked female *C. brachyotis* visit more feeding areas compared to harem male, and thus spend longer time for foraging during breeding period (Bumrungsri 2002). The nutritional demands of breeding may constrain female bat to visit more feeding areas each night than during the nonbreeding periods. Reproductive females have high demands for calcium(Barclay, 1994, 1995), protein and energy (Herbst, 1986; Speakman and Racey, 1987; Racey and Enwistle, 2000), increasing the diversity of food intake by visiting more feeding areas may complement nutritional deficiencies of each food, thus satisfy females' nutritional requirement. Moreover, the diet-mixing strategy will fulfill bats' requirement more rapidly than any pure diet (Fleming, 1988). Herbst (1986) suggested that lactating *C. perspicillata* need to ingest at least two times more energy and at least four times more nitrogen than nonreproductive females. Since *E. spelaea* breed year round, it is not surprise to see the consistency of return pattern, which appear relate to breeding period, between different sampling months.

Regarding the male that return in same time as female, they are probably a nonharem and/or bachelor male. Similar foraging pattern between female and bachelor male have been demonstrated in *P. hastatus* (Kunz *et al.* 1998). Although our evidence suggests that *E. spelaea* most likely to maintain a harem social organization, it is remain to carry out intensive study to test such hypothesis, and to determine detailed foraging behavior of harem male.

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