The dawn bat, *Eonycteris spelaea* Dobson (Chiroptera: Pteropodidae) feeds mainly on pollen of economically important food plants in Thailand

Sara Bumrungsri[1, 4], Duncan Lang[2], Colin Harrower[2], Ekapong Sripaoraya[1], Kitika Kitpipit[1] and Paul A. Racey[2, 3]

[1]*Department of Biology, Prince of Songkla University, Hat Yai, Songkhla, Thailand*
[2]*School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, Great Britain*
[3]*Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, TR10 9EZ, Great Britain*
[4]*Corresponding author: sarabumrungsri@gmail.com*

The diet of *E. spelaea* was determined for bats captured monthly between June 2002–June 2003 at a cave entrance in Songkhla Province, Southern Thailand. Faecal analysis and pollen collected from the bats' fur were used to identify the plant species ingested. From 1,155 diet records from 506 samples, at least eleven plant taxa were identified. Individual bats feed on flowers of up to six plant species each night. *Parkia* spp. (34%) and *Musa* spp. (28%) have the highest percentage frequency followed by *Eugenia* spp. (9.4%), *Oroxylum indicum* (6.4%), *Durio zibethinus* (6.2%), *Ceiba pentandra* (5.5%), *Sonneratia* spp. (5.2%), while *Cocos nucifera* and an unknown plant species, made up a minor proportion (<2.5%). *Parkia* and *Musa* were the main dietary items of *E. spelaea* in nearly every month, while the remaining components of the diet varied seasonally. *Durio* spp. is an important contributor to the diet during March–April (39–42%). The results from pollen collected from fur generally corresponded with those from faecal analysis, but *Musa* spp. had a higher percentage frequency on the fur (34%) than *Parkia* spp. (23%). The dawn return patterns of the bats to their roosts differ significantly between sexes. Most mature males return early in the night while most females return at dawn. Earlier returning males were significantly heavier than those returning later. This return pattern is similar to that reported during the breeding period for those polygynous fruit bats that maintain a harem. Thus, these results suggest that *E. spelaea* may exhibit a resource-defence polygynous mating system.

Key words: *Eonycteris*, diet, faecal analysis, nectarivorous bat, *Parkia*, pollen, polygyny, return pattern

INTRODUCTION

Diet is fundamental to understanding the interactions between animals and their habitats. In particular, the diet of nectarivores can reveal the plant taxa on which the bats rely to maintain their populations, and also suggests their potential as pollinators of the plants they visit. Such information is of ecological and economical importance. Currently, there are increasing global concerns about pollination failure of food plants (Allen *et al.*, 1998; Kevan and Phillip, 2001). Information about the resource needs of native pollinators, such as their diet, can be used to develop effective strategies for the restoration of pol-linator populations (Kremen and Ricketts, 2000, Menz *et al.*, 2010). In tropical forests, nectarivores play a particularly important role in the maintenance of forest structure and/ or restoration of disturbed forest, since almost all flowering plants (98–99%) in this ecosystem rely on animals as pollinators (Bawa,

1990). *Eonycteris spelaea* is the largest of three exclusively nectarivorous bat species in mainland South East Asia, with a forearm length of between 66–78 mm and weighing 40–70 g. Its specialisation for nectar feeding include a long muzzle, and sharply pointed tongue, with well-developed filiform papillae at the tip (Bates and Harrison, 1997). *Eonycteris spelaea* is a cave-dwelling colonial species which is common throughout its range 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). Previous studies indicated that it feeds on plants of 31 species in Malaysia and travels up to 38 km to do so (Start and Marshall, 1976). In Thailand, stomach content analysis indicated that it consumed at least 19 plant species (Pakarnseree, 1986). Although they provide useful information, diet species lists are of little conservation value since they do not reveal the relative importance of

each food plant (Stier and Mildenstein, 2005). Only Start and Marshall (1976) attempted to provide a quantitative estimate of the contribution of each plant in the diet of this bat.

However, since they compared the number of grains of each pollen type to all counted pollen grains collected from traps for faeces set under day roosts their results may be biased toward those plants producing numerous pollen grains (Thomas, 1988). In addition, some pollen types (e.g., *Musa*) are broken down rapidly in guano (Start and Marshall, 1976), and could be under-represented by such a method. Thus, the actual importance of each food plant to *E. spelaea* is still not clear.

Two methods have been commonly used for the non-destructive dietary analysis of nectarivorous bats: faecal analysis and pollen collected from fur. Although the results from both methods could differ, even if applied to the same bat, no study has yet compared them. The main aims of the present study were to determine the importance of each item in the diet of *E. spelaea* and to compare the results obtained by faecal analysis and pollen collected from fur.

The study also provided an opportunity to examine sexual variation in foraging behaviour which can occur when nutritional or social requirements differ between sexes, especially during the breeding period. Such variation has been reported in several fruit bat species, most of which employ a harem social organisation (Balasingh *et al.*, 1995; Kunz *et al.*, 1998; Bumrungsri, 2002). The calcium content of nectar and pollen of chiropterophilous plants is generally low, and may limit reproduction of nectar bats (Barclay, 1994, 1995). Consequently, females may need to spend longer searching for food to fulfill their requirements especially in colonial species that breed throughout the year. So an additional aim of the present study was to test the hypothesis that, with such a constraint, female nectar bats forage for longer than males. The dusk emergence patterns of *E. spelaea* have already been well established (Start, 1974).

MATERIAL AND METHODS

Study Site

Bat sampling was carried out at the Khao Kao Cave, Songkhla Province, southern Thailand (6°42.45'N, 100°16.64'E, 50 m a.s.l.) which is situated at the base of a limestone hill on the Thailand-Malaysia border. This cave habours ca. 20,000 individuals of *E. spelaea*. A few individuals of insectivorous bat species, including *Hipposideros lylei* and *H. cineraceus*, also share the cave. Rubber plantations (ca. 40%) and tropical lowland forest (30%) cover most of the area within a 20 km radius of the cave. Large patches of mangrove forest occur ca. 19 km

from the cave. Patches of wild banana (*Musa* spp.) are commonly found along the edge of rubber plantations and recently cleared land surrounding the cave. With the exception of protected forest, the area is sparsely inhabited with human settlements. In villages, plants commonly found in backyard gardens include *Parkia speciosa* Hassk. and cultivated banana (*Musa* spp.). Generally, there are two seasons, dry (January to mid April) and rainy (mid April to December). The annual rainfall is 2,118 mm, most of which occurs in October–December. Mean temperature and relative humidity are 28.3°C and 72%, respectively (information from the Kor Hong Meteorological Station, 2004).

Bat Trapping and Pollen Collecting

A mistnet (2.6 × 2.6 m) was set across the cave entrance to capture bats returning in the morning. Since the width of the cave entrance is about the same as the length of the mistnet, each net pole was held by an assistant to ensure the entrance was covered, and at a slight angle (ca. 10 degrees) from the vertical plane toward the cave interior since this was found to increase capture rate. A preliminary study in May 2002 suggested that the number of captured male bats was relatively low when the mistnet was set between 03:00–06:00h, and more bats were captured when netting ceased for a while between capture sessions. Consequently, bats were netted for 15 minute periods separated by 15 minute intervals, during which no netting took place, from 01:00h to 06:30h, or until the bats stopped returning. This sampling regimen was successful in catching more males, and the temporal pattern of morning returns was also revealed. This cave has two entrances, and bats were captured at the lower smaller entrance (2 × 3 m) during the first three months. The capture site was then changed to the larger upper cave entrance (3 × 3 m) after most bats were seen to use it. Video observations revealed that many bats still used the upper entrance even after the netting had ceased, suggesting that disturbance from capture was not excessive.

Bats were captured once a month for 13 months (June 2002–June 2003). Thirty-nine to 72 bats were caught in every month. Two techniques were used to obtain information on diet: collection of faeces, and collection of pollen adhering to the bats face and body. The latter was implemented one month later than the former, but each method was adopted for 12 months. After bats were captured, a piece of adhesive tape about four cm long was dabbed on their head including face and muzzle as well as the anterior thorax, to collect pollen grains. The adhesive tape was placed on a sterile slide with a number corresponding to the captured bat. Each captured bat was then kept separately in a clean numbered cotton bag. Each individual bat was weighed with a 100 g Pesola spring balance. Sex, age (juvenile or adult) and, for female bats, reproductive status (non-reproductive, late pregnant, lactating) was noted following Racey (2009). Adult bats are those with completely ossified phalangeal epiphyses and adult pelage. Pregnancy was detected by palpation. Juvenile bats were excluded from further analysis. Bats were kept for about two hours or until the sampling period was finished. All bats were released in the cave by 09:00h. Sugared water was given to most bats before release. After a bat was released, each bag was examined for faeces, which when present, was scraped into a labeled Eppendorf tube. In cases where a bat produced very liquid faeces which could not be scraped into a tube, adhesive tape was applied to the faeces and then placed on a sterile labeled slide.

Slide Preparation and Pollen Identification

Faecal material

A premixed solution of 95% ethanol and ethylene blue was added to the tube containing faeces until the volume reached 1ml. The solution was then thoroughly shaken and the faeces broken up using a stirrer until they were fully dispersed. Using a dropper, three drops of faecal suspension were placed on a sterile slide and the dropper was then washed. Once the alcohol had evaporated and the faecal sample had dried, a drop of polyvinyl alcohol (PVA) was added followed by a cover slip taking care to avoid trapping air bubbles. Finally, the slide was left in a warm place until it was completely dry and it was then labeled. Three slides were made from every faecal sample. All slides were examined under a compound light microscope at 4, 10 and 40 times magnification. Pollen was identified to species if possible by comparison with a reference collection and illustrations in Start (1974). Pollen of any species that was not immediately identifiable was listed as an unknown, with a brief description and sketch, and its position on the slide noted. Later the unknown was then photographed using an Olympus Digital Camera attached to the light microscope. Identified pollen was scored as present/absent after Thomas (1988). Pollen of any species was categorized as present in two cases: 1). at least two pollen grains were found on any slide prepared from each tube, and 2). one pollen grain was found on at least two of the three slides prepared. Thus, using these criteria, the under-representation of plants with a small number of pollen grains is probably small. Intraspecific diet variation was examined with a Chi-square contingency test.

Pollen collected from the fur

Slides with adhesive tape attached were examined using a light microscope. Pollen was identified, and scored as present/absent following the same criteria used for faecal material. Taxa with only one pollen grain in a slide were excluded from further analysis. For both faecal materials and pollen from bat fur, the contribution of each item in the diet was expressed as the percentage frequency: the number of occurrences for a particular category divided by the total number of occurrences for all categories, multiplied by 100 (McAney *et al.*, 1991).

Temporal Pattern of Return to the Roost

The number of mature males and breeding females (late pregnant and lactating) returning to the roost in each 15 minute period was counted. A generalised linear model was applied to determine sexual variation in return time over eight months during which trapping started as early as 01:00h. Sex and time were treated as factors, and number of return bats as the dependent variable. A Poisson loglinear model was selected. Models with and without interaction between sex and time were compared for their AIC. The model with interaction had lower AIC, and it was therefore selected. The mean body mass of adult males returning before and after 04:00h was calculated and Student's *t*-test was used to examine the difference in body mass of adult males returning at dawn. Data were transformed to meet the assumption of homogeneity of variance and normality. This test was not carried out in breeding females since their body mass increased during pregnancy. All statistical analyses were performed with SPSS 16 and Minitab 14. In the present study, the temporal pattern of dusk emergence was not investigated since a single attempt to capture bats during this time caused them to abandon emergence and return to roost in the cave.

Results

Diet

Faecal analysis

Six hundred and seven bats were captured. Based on 1,155 diet records from the faeces of 506 bats, at least eleven taxa of pollen were found. Pollen of *Parkia* spp. and *Musa* spp. showed the highest percentage frequency with 33.9% and 28.1% respectively, followed by *Eugenia* spp. (9.4%), *Oroxylum indicum* Vent. (6.4%), *Durio zibethinus* Merr. (6.2%), *Ceiba pentandra* Gaertn. (5.5%), *Sonneratia* spp. (5.3%) whilst several other items (unknown, *Cocos* spp., *Arenga* spp., and *Bombax* spp.) made up a minor proportion, between 0.3–2.4% (Fig. 1).

Temporal variation in the diet of E. speleaea

Since the overall percentage frequency may obscure the importance of each dietary item in a particular period, the diet in each month was examined. It was found that different species of plants contributed to the diet of *E. spelaea* at different times of the year. Generally, *Parkia* and *Musa* were the most important in nearly every month. *Parkia* spp. contributed more than half of the diet in June–July 2002 and May 2003, and it was generally the main food during the rainy season. *Musa* spp. consistently contributed to the diet in every month (17–36%). Although *Durio* spp. was available for a short period (March–April), it was the most important food resource (39.2–42.4%) during that time. The contribution of *Eugenia* spp. to the diet was greatest from November 2002 to February 2003, and *C. pentandra* from December 2002 to January 2003. In each night, an individual bat fed on flowers of up to six plant taxa ($\bar{x} \pm SD = 2.06 \pm 1.21$). Faecal analyses revealed that 3–9 taxa of chiropterophilous plants were visited each month. Generally, there was higher species diversity of available food plants in the late rainy to early dry seasons compared to the rest of the year (Fig. 2).

Pollen collected from fur

At least nine taxa of pollen were identified from 1,598 diet records of 607 captured bats. *Musa* spp. contributed the greatest percentage frequency (34.3%), followed by *Parkia* spp. (23.2% — Fig. 1), thus reversing the order obtained from faecal
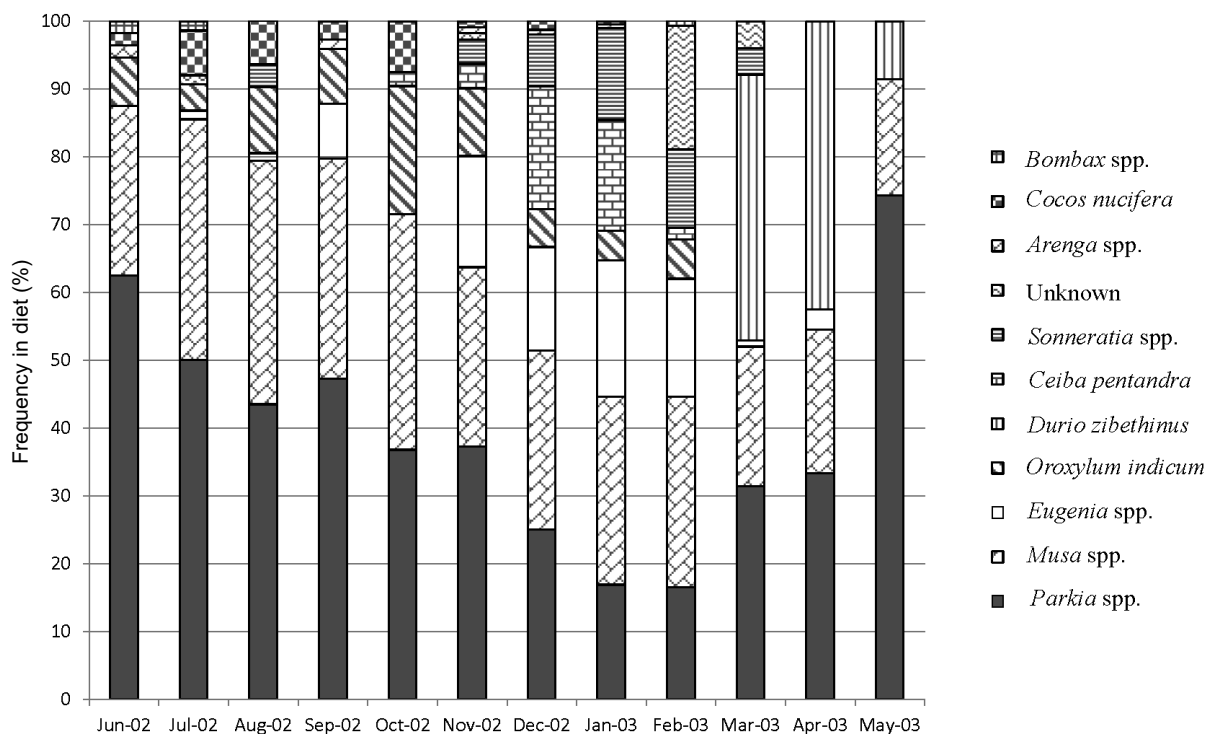
Fig. 1. The percentage frequency of plants ordered according to their abundance in the diet of *E. spelaea* for each month from 506 bats captured during June 2002–May 2003

analysis. The contribution of *Eugenia* spp., *C. pentandra*, *Sonneratia* spp. and *Durio* spp. generally corresponded to the results from faecal analyses, although the percentage frequency of *O. indicum* was half that recorded from faecal pollen. One to six pollen taxa were found on each individual bat ($\bar{x} \pm SD = 2.61 \pm 1.28$, $n = 607$).

Intraspecific diet variation

Sexual variation in the diet of adult bats (302 male, 189 female) was investigated. Adult males and females were captured in every month. Faecal analyses revealed a higher percentage frequency of *Musa* in adult males than in adult females (30 versus 26.2%), while the other dietary items were similar (Fig. 3). It appears that females are more inclined to feed on plants that are more isolated (*Eugenia*, *Oroxylum*, *Ceiba*) while males show a higher pre-ference for plants normally growing in clumps (*Musa*, *Sonneratia*). Statistically, the diet of mature males and females was not significantly different ($\chi^2 = 11.05$, *d.f.* = 9, *P* = 0.27). Consistently, a greater percentage frequency of *Musa* (36.1 versus 33.9%) was evident in pollen collected from fur of males although sexual variation was not significant ($\chi^2 = 14.64$, *d.f.* = 8, *P* = 0.07).

Temporal Variation in Pattern of Return to the Roost

The return pattern of bats was determined for eight months (June–August, November, December 2002, January, March, April 2003). A generalised linear model with interaction was selected as it had a lower AIC (584.6) than one without interaction (609.1). Sex (likelihood ratio $\chi^2 = 74.13$, *d.f.* = 1, *P* < 0.001) and time (likelihood ratio $\chi^2 = 18.81$, *d.f.* = 9, *P* < 0.05) significantly influenced returning time, as did the interaction between sex and time (likelihood ratio $\chi^2 = 42.46$, *d.f.* = 9, *P* < 0.001) indicating variation in return time between males and females. Most adult males returned early in the night compared to breeding females, most of which returned in the early morning, although some returned earlier and were represented by a minor peak between 02:00–03:00h (Fig. 4). In particular, more than 70% of captured adult males returned by 03:00h in April, June and July. When adult males were separated into two groups, those returning earlier than 04:00h, and those returning after 04:00h, the body mass of the former ($\bar{x} \pm SD = 67.30 \pm 5.91$, range 51.5–84.5, $n = 144$) was significantly greater than the latter (64.01 ± 5.81, range 45–79, $n = 67$) ($t = 3.76$, *d.f.* = 208, *P* < 0.001). No bats were observed to leave the roost again after their dawn return.
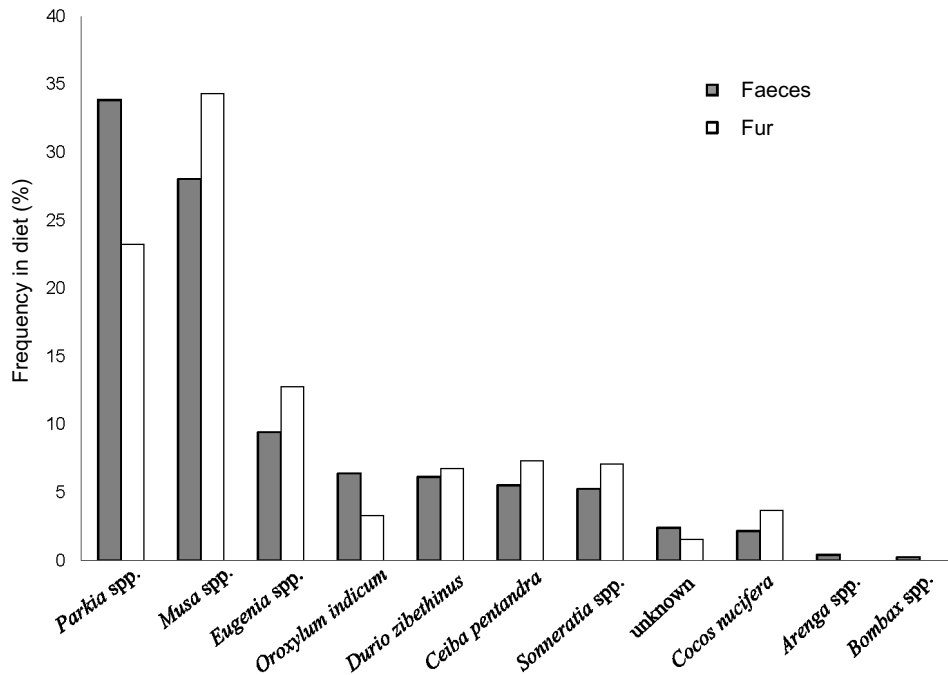
FIG. 2. The percentage frequency of each plant in the diet revealed from faecal analysis (filled) (1,115 diet records from 506 bats) and fur-collected pollen (open) (1,598 diet records from 607 bats)

DISCUSSION

Diet

Results from both sampling methods adopted during the present study share some common features including the finding that *Parkia* and *Musa* are the most important dietary items. Flowers of *Musa* are widespread and available throughout the

year. Pollen of *Parkia* spp could be mostly assigned to two species: *P. speciosa* Hassk. and *P. timoriana* Merr. These congeners are commonly planted in backyard gardens in the study area, and flower at different times of the year. *Parkia speciosa* flowers mostly from April to October while *P. timoriana* flowers during December and January. However, the pollen of these *Parkia* is indistinguishable (Start, 1974). Apart from these two core taxa, different
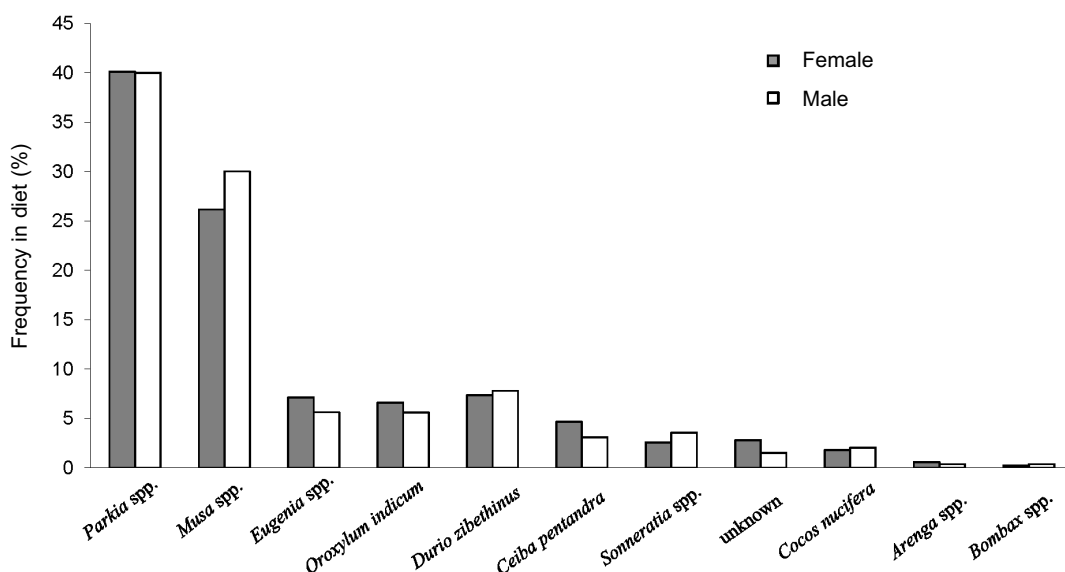

FIG. 3. The percentage frequency of each plant in the diet of adult male (*n* = 302) and adult female (*n* = 189) *E. spelaea* revealed by faecal analysis during June 2002–May 2003
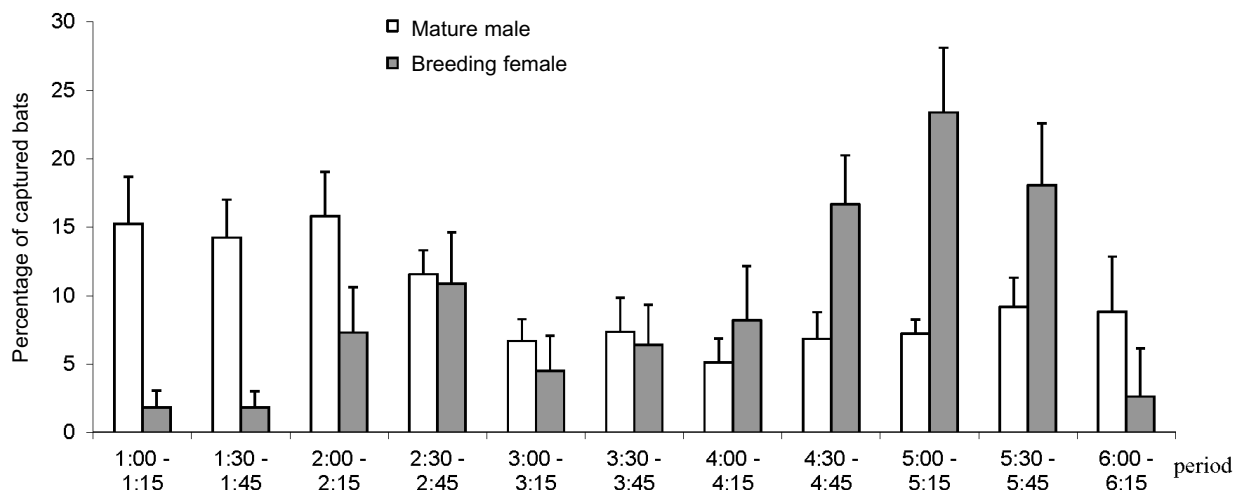
FIG. 4. Average percentage of adult males and breeding females (pregnant or lactating) captured during 15 minute netting sessions at half hour intervals from 01:00h–06:30h during June 2002–April 2003 (except September and October 2002 and February and May 2003). This information is based on 50 ± 10 (range: 39–68) bats captured per month

plant taxa were sequentially important in the diet of *E. spelaea* in different times of the year. For instance, *Durio*, which could be mostly assigned to *D. zibethinus*, and *Ceiba pentandra* which bear a large number of flowers within a short period, were the major food items when they were flowering. In a previous study, Start and Marshall (1976) examined the diet of *E. spelaea* by analysis of faeces collected below day roosts in peninsular Malaysia, and indicated that *Duabanga*, *Artocarpus* and *Sonneratia* were the major dietary items (12–30%) while *Parkia* (11.1%), *Musa* (trace) and *Eugenia* (4.3%) contributed a relatively smaller percentage. However, their results may not be comparable to those of the present study since their method was inherently biased toward those plants producing numerous pollen grains (Thomas, 1988). Using the individual bat as a sampling unit is more statistically independent than using the number of pollen grains, and thus more accurate in determining the relative importance of each dietary item. However, individual-based sampling could be less accurate in revealing the diversity of dietary items since it may sample only a small proportion of this colonial species. Given that the diet of some bat species can vary geographically (Start, 1974), similar studies on the diet of *E. spelaea* in other areas, especially in habitats with stronger seasonality, should be undertaken since it is vital for understanding the food resources required for maintaining populations of this bat in a particular locality. In addition, temporal variation in diet should also be considered since mast flowering is characteristic of plant phenology in SE Asia.

Some plant species may flower in some years or differ in their flower abundance between years. Thus, diet study should ideally span several years to account for such variation.

However, the different methods used also produced some slightly different results. A higher percentage frequency of *Parkia* spp. in the diet was revealed by faecal analysis while a greater proportion of *Musa* spp. was revealed from fur-collected pollen. Additionally, the proportion of *O. indicum* revealed by faecal analysis is twice that determined by fur-collection, while some rare plant species were revealed only by faecal analysis. The difference between these two methods can be partly explained by the interaction between the timing of flower visits and variation in the pollen-retaining ability of the gastro-intestinal tract and the fur. A recent study indicated that the highest activity of *E. spelaea* at flowers of *P. speciosa* was between 20:00–21:00h and for *P. timoriana* between 20:00–21:00h, while peak visits to *Musa* occurs later, around 22:00–23:00h (Sripaoraya, 2005). Post-feeding grooming, which is common in nectarivorous and fruit-eating bats (Howell, 1979; Bonaccorso and Gush, 1987; Law, 1992), probably accounts for pollen lost from their fur. Moreover, some pollen from earlier visits is likely to be transferred to stigmas when bats subsequently visit flowers, so the probability of pollen from early visits remaining on the fur is smaller than pollen from later visits. Consequently, diet determined by analysis of pollen collected from the fur of bats captured at dawn is more biased toward those plants that the bats visited

later during the night. This is probably more pronounced in the present study, where groves of wild *Musa* are common in recently cleared areas and along tracks around the cave (S. Bumrungsri, personal observation), which bats may visit during their last feeding bout before returning to the cave. Many captured bats, mostly males, were observed over many months with muzzles completely covered with white *Musa* pollen (S. Bumrungsri, personal observation). The timing of flower visitation also explains the smaller proportion of *O. indicum* in fur sampling. In this species, anthesis occurs at 19:00h and flowers drop by 02:00h, and the peak of bat visits is 22:00–23:00h (Srithongchuay *et al.*, 2008). On the other hand, the timing of flower visitation probably has less effect on diet revealed by faecal analysis, since pollen needs to pass through intestinal tracts before being defaecated. Law (1992) reported that the mean retention time of *Banksia* pollen ingested by the nectarivorous bat, *Synconycteris australis* is 163 minutes. In addition, seeds can be retained in the alimentary tract of fruit bats for many hours (Shilton *et al.*, 1999). This could be also true for pollen, however, and further experiments on how long pollen can be detected by both sampling techniques are needed.

Fruits and leaves also contribute in the diet of *E. spelaea*. Unidentified amorphous fruits and chewed leaves were found several times on trays set below its day roosts (S. Bumrungsri, unpublished data). The occurrence of fruit and leaves in the diet is apparently under-represented by analysis of faeces of captured bats. At least two fruit species, rambutan (*Nephelium lappaceum* L.) and *Palaquium obovatum* (Griffith) Engler. were visited by *E. spelaea* when they were available (Hodgkison *et al.*, 2004; S. Bumrungsri, unpublished data). Similarly, some commercially grown *Musa* varieties produce no pollen which could be under-recording. Previous studies suggested that folivory, which has been reported in fruit-eating bats, may be a way of obtaining calcium, or secondary plant compounds important for reproduction (Kunz and Ingalls, 1994; Kunz and Diaz, 1995; Nelson *et al.*, 2005). Calcium is probably a limiting resource in nectarivorous bats, since the nectar and pollen of bat-visiting plants are not rich in calcium (Barclay, 2002). An equally important consideration is how this nectarivorous bat obtains enough essential amino acids to meet its requirements, particularly during reproduction. Pollen may be an important contributor in this respect, since Long and Racey (2007) showed that the pollen of *Agave sisalana*, which was the single most

important food source for *Pteropus rufus* in their study site in south-east Madagascar, consisted of 36% protein of which the bats could digest 73% (Long, 2002). Further investigation on the nutritional content and digestibility of the pollen diet of the truly nectarivorous *E. spelaea* is recommended.

Sexual Variation in Pattern of Return to the Roost

From the present study, a majority of male *E. spelaea* spend more time in the roost than females, especially in some months. Our three emergence counts indicated that all bats normally leave the cave within an hour after the first bat emerges (S. Bumrungsri, unpublished data). The longer time spent in the roost by male *E. spelaea* is similar to that of several resource-defence polygynous fruit bat species in which harem males spend significantly more time and expend more energy at their roosts during the breeding period than other species (e.g., *Artibeus jamaicensis* — Morrison and Morrison, 1981; *Carollia perspicillata* — Fleming, 1988; *C. sphinx* — Balasingh *et al.*, 1995; Bhat and Kunz, 1995; Karuppudurai *et al.*, 2008; *Phyllostomus hastatus* — Kunz *et al.*, 1998; *Cynopterus brachyotis* — Bumrungsri, 2002; *Balionycteris maculata* — Hodgkison *et al.*, 2003). In these bats, harem males allocate time and energy for roost surveillance and roost defence. Moreover, harem males of *B. maculata* (Hodgkison *et al.*, 2003) and *A. jamaicensis* (Morrison and Morrison, 1981) forage mostly in the vicinity of their roosts. Female *C. brachyotis*, on the other hand, spend longer foraging during the breeding period by visiting more feeding areas each night than males (Bumrungsri, 2002). Reproductive females have high demands for calcium (Barclay, 1994, 1995), protein and energy (Herbst, 1986; Racey and Speakman, 1987; Speakman and Racey, 1987; Racey and Entwistle, 2000). Although the nectar of chiropterophilous plants has a higher calcium content than plants not visited by bats (Barclay, 2002), nectar and pollen contain relatively little calcium, and low calcium levels limit reproduction in bats (Barclay, 1994, 2002). Female bats have either to forage on plants with a higher calcium content (Barclay, 2002) or spend more time foraging than males. Further investigation to verify these predictions should be carried out. Since female *E. spelaea* breeds year round, it is not surprising to see the consistency of the return pattern between different sampling months. The smaller earlier return peak of breeding females was examined, and it was clear that it consisted of late pregnant individuals as well

as lactating females with and without young, all of which showed a similar return pattern. These earlier returning breeding females may have foraged close to the roosting cave and were able to return earlier than those foraging further away. Data on individual movements and foraging distance is nevertheless needed to confirm this hypothesis.

Heavier male *E. spelaea* return to the roost earlier than the lighter males. Since previous studies found that harem males are heavier than other males (Kunz *et al*., 1998; Ortega and Arita, 1999; Voigt *et al*., 2001; Karuppudurai *et al*., 2008), our results raise the question of whether *E. spelaea* has a harem social organisation. In addition, these earlier returning males may also be older than the late returning ones since body mass of fruit bats tends to increase with age (Fleming, 1988). Since adult male *E. spelaea* outnumber females during most of the year (sex ratio male: female = 1: 0.56 — S. Bumrungsri, unpublished data), the degree of competition for females between males is relatively high. Therefore, older bats which are more experienced and more efficient foragers, are able to shorten their feeding time and re-allocate it to reproductive activity in the roost more than the younger males. Fleming (1988) found that the harem males of *C. perspicillata* tend to be the oldest and heaviest bats. Those male *E. spelaea* that return at the same time as females, are probably bachelor and/or recently adult bats which have similar foraging patterns, as in *P. hastatus* (Kunz *et al*., 1998). Although our evidence suggests that *E. spelaea* is most likely to be a resource defence polygynous bat, this hypothesis remains to be tested.

CONSERVATION

From this diet study, it is suggested that *E. spelaea* is a potential pollinator of several chiropterophilous plants found in the study area. Recent experimental pollination studies demonstrates that this bat is the principal or even the sole pollinator of several self-incompatible plant taxa including *Parkia speciosa* (petai) and *P. timoriana* (Bumrungsri *et al*., 2008), *D. zibethinus* (durian) (Soepadmo and Eow, 1976; Bumrungsri *et al*., 2009), and *O. indicum* (Srithongchuay *et al*., 2008). These plants are economically important as food and medicinal resources in SE Asia. A recent investigation estimated that the annual economic contribution of this bat in pollinating petai and durian in southern Thailand was over 137 million US $ in 2008 (Petchmunee, 2008). The ecological and economical contribution

of this bat to the pollination success of other plants in its diet thus warrants further study.

Since these chiropterophilus plants usually occur naturally in isolation from conspecifics and in relatively low density (Fleming *et al*., 2009), the long distance flying capabilities of *E. spelaea* (ca. 38 km — Start and Marshall, 1976) is thus significant for the pollination success of these mostly self-incompatible plants. However, increasing forest fragmentation may result in a higher degree of pollination failure and lead to smaller plant populations (Menz *et al*., 2010), especially when bat populations are also smaller. Therefore, protection of remnant chiropterophilous trees, even single individuals which can serve as stepping stones for pollinators and thus increase the connectivity between plant populations, is vital for the long-term survival of these bat-dependent plants. Mixed planting of chiropterophilous plants which flower at different times of year is highly recommended for fruit farmers. Such a practice will potentially secure pollination success of food plants as it could result in regular visits of nectarivorous bats. Recent research indicates that *E. spelaea* shows strong fidelity to its feeding areas (P. Acharya, personal communication).

As with other bats in the Old World tropics, the most serious threat to *E. spelaea* is hunting and roost disturbance. This bat normally forms large colonies of tens of thousands of individuals in large high-ceiling caves (Start, 1974), which are easily exploited for food by hunters. In addition, this bat is caught and killed by farmers in the mistaken belief that it destroys the flowers of chiropterophilous plants (Bumrungsri *et al*., 2008). Cave disturbance from a variety of human activities such as guano collection, religious activities and tourism are also common in SE Asia (Kingston, 2010). In many cases, both hunting and cave disturbance occur simultaneously and result in the population decline of local populations of *E. spelaea*. In the study cave, the population decreased from more than twenty thousand individuals during the year of study (2003) to around 500 individuals in 2008 (S. Bumrungsri, unpublished data). The cause of this reduction was investigated, and the excavation of deposits of guano was found to be a serious but transient threat. A few hundred individuals were counted when guano extraction was in progress but tens of thousands of individuals were found after it ceased in 2010. We recommend improved protection for those caves which shelter important populations of pollinators.

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