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Reproductive Biology of *Eonycteris spelaea*, Dobson (Megachiroptera) in West Malaysia

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Abstract

Reproductive information is summarized for 1,060 adult female and 973 adult male *Eonycteris spelaea* collected at Batu Caves in West Malaysia between March 1966 and February 1968. Reproductively active males were present throughout the entire study period, but no definite seasonal activity patterns could be determined. More than 50 % of the adult females were pregnant or lactating at any one time. Peaks in pregnancy rates followed approximately 6–7 months after peaks in rainfall. Females of *E. spelaea* are polyoestrous; successive pregnancies can begin in the late stages of lactation. Young remain attached to their mothers' nipples for approximately 2 months post partum. Reproductive maturity for both sexes is reached sometime after 1 year.

Introduction

Detailed information on the reproductive biology of tropical bats is limited (ASDELL, 1964). Much of the published data has been accumulated in conjunction with studies on ecology, taxonomy, and distribution. Early studies reported a discrete, monoestrous sexual cycle in the megachiropteran *Pteropus giganteus* (MARSHALL, 1947; BAKER & BAKER, 1936) and a polyoestrous cycle in the microchiropteran *Nycteris luteola* (BRAESTRUP, 1933; MATTHEWS, 1939, 1941). RAMAKRISHNA (1947) reported a polyoestrous cycle in *Cynopterus sphinx*. More recent studies have indicated a great variation in the reproductive behavior of tropical bats from both suborders. MARSHALL & CORBET (1959) found that *Chaerephon hindei,* a molossid bat, bred throughout the year in Uganda. They considered this species, at least the males, to be monoestrous. HARRISON (1958) examined two adult female *Tadarida (Chaerephon) pumila websteri,* one from Nigeria and another from Somalia, and found them to be actively lactating and pregnant at the same time. WIMSATT & TRAPIDO (1952) reported similar behavior for *Desmodus rotundus murinus,* an American tropical microchiropteran.

Recent investigations by MUTERE in Uganda (1967, 1968) provide more detailed information on two pteropodid bats, *Eidolon helvum,* which exhibits a single seasonal, synchronized breeding period, and *Rousettus aegyptiacus,* which displays a bimodal, polyoestrous cycle. Work in press by MUTERE on the molossid bat *Tadarida condylura* describes a bimodal breeding pattern for this bat.

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In West Malaysia, *Cynopterus brachyotis* appeared to have 3 pregnancy peaks in 1 year (LIM, 1970). LIM observed most pregnancies between March and April of 1967, which was also the main fruiting season. He postulated that the abundance of food during this period contributed to post-partum mating and resulted in 2 or more pregnancies per adult female during a single year.

MEDWAY (1971, 1972) reported single annually recurrent reproductive cycles for *Miniopterus australis* in East Malaysia and for *Tylonycteris pachypus* and *T. robustula* in West Malaysia. *M. australis* in Borneo appears to have evolved a long gestation period in response to variation in insect abundance.

Methods and Materials

Eonycteris spelaea, Dobson, the subject of this study, is a medium-sized pteropodid bat. Adult males weigh 55–60 grams with a head and body length of about 120 mm. Adult females are smaller, with non-parous weights of 35–40 grams. *E. spelaea* is colonial and cavernicolous. Colonies in Malaysia range from a few dozen in shallow limestone shelters to tens of thousands in caves in the larger massifs. *E. spelaea* flies out of its cave roosts at dusk to feed on pollen, nectar, and juice from very ripe fruits.

Collection trips were made at approximately 2-week intervals to the Dark Cave, one of the Batu Caves. This particular cave, well described in a recent survey by MCCLURE, LIM & WINN (1967), is located about 7 miles from the Institute for Medical Research, Kuala Lumpur, West Malaysia.

The Batu Caves area is sheltered from the full effects of monsoon rains by the Main Range of the Malay Peninsula and the mountains of Sumatra. There is, however, a fourfold difference between the months of heavy regular rainfall and those with light or irregular rains. The greatest monthly amount usually falls in April, with a second, somewhat lesser amount in November-December (OOI, 1964). We observed a similar pattern during our study period. Rainfall 'seasons' were more distinct in 1965–66 (Fig. 1). Dry periods with less than 6 inches of rain per month occurred between May and October 1966 and again at the end of the study period. The onset of heavy rains varies from year to year, as does the interval between peak months.

The daily temperature range at the Batu Caves Station is about 15 °C. Annual variation is approximately 1 °C at either end of the range. Relative humidity ranges between 55 and 95 %, rising to 100 % during heavy rains. Day length is also relatively constant, varying 20 minutes during the year.

1 or 2 mist nets measuring 12 × 2.4 m were placed in the entrance passage of Cavern A, the outermost portion of the Dark Cave. One net was always set at the entrance, covering 25–30 % of the flightway used by the bats. Whenever possible, a second net was placed about 10 m further back in Cavern A at a low spot in the ceiling. The nets were set up on hand-held poles before the bats began flying and remained in place until the main flight was over. After 10–20 bats became entangled, the net was lowered and the bats were removed. When 2 nets were set, they were lowered and emptied alternately. A 61-mm mesh proved ideal for *E. spelaea.* The bats, except for females with young, could be removed in a few seconds by peeling the net strands from the head, over the shoulders and down the back. Bat species captured other than *E. spelaea* included: *Taphozous melanopogon, Hipposideros diadema, H. galeritus, Megaderma spasma, Rousettus amplexicaudatus,* and *Myotis mystacinus.*

All bats were separated by species and sex into wire cages or cloth bags. Collecting continued until the interval between capture of individuals increased to several minutes. A sample of 5–20 *E. spelaea* was set aside for examination

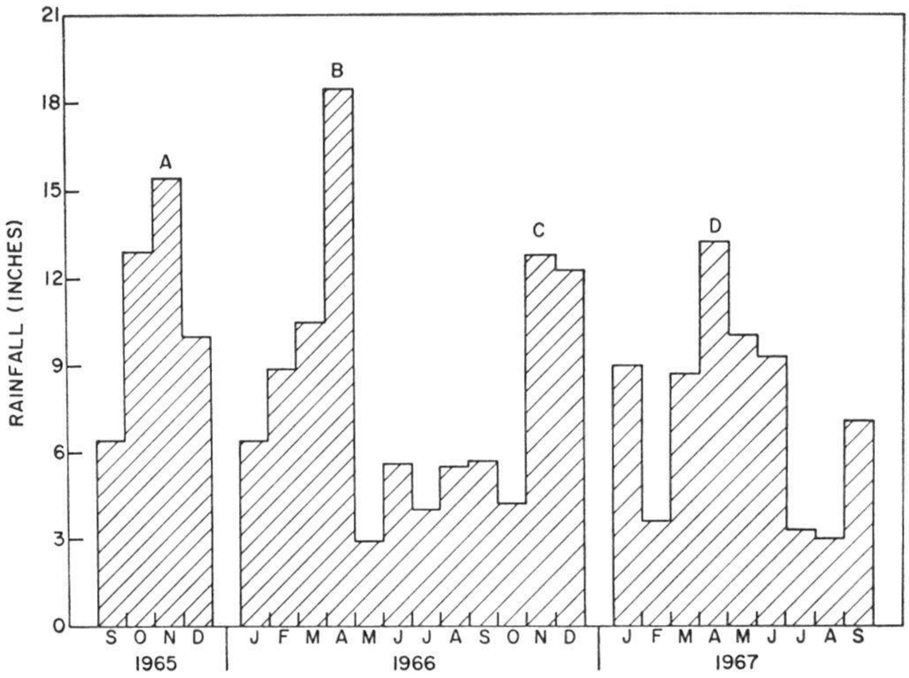

Fig. 1. Rainfall monthly totals – Batu Caves Station September 1965 – September 1967.

in the laboratory. The rest of the catch were examined at the cave. Age and reproductive state were recorded for each individual. The bats were then banded with numbered aluminum-alloy bird bands and released.

Age class was based on tooth wear and general appearance of the animal. Immature bats were obvious because of their smaller size and the shape of the phalanges. Evidence of reproductive activity, pregnancy, lactation, post-lactational states, or enlarged scrotal testes was considered the definitive criterion for adulthood. Age classes used were: *suckling young* (still attached to the mother); *young* of the current year or less than 1 year old; *subadults* – more than 1 year old, of adult size but without signs of reproductive activity; and *adults*.

The reproductive state of adult males could not always be determined accurately. Most adult males had scrotal testes, which rapidly increased in size when the bats were exposed to temperatures above 80 °F or when the animals were excited. Recording of reproductive conditions of individual males was discontinued in the early part of this study. Reproductive states for females were more easily established. Immature and subadult females were recorded as non-parous, as parity was used as an indicator of maturity. Pregnancy was determined by palpation, and we were able in the latter half of the study to estimate the trimester of pregnancy and predict approximate dates of parturition. Early stages of lactation were obvious, as *E. spelaea* females carry their young firmly attached to their nipples for several weeks. We use the term *late lactation* to indicate females with young that were able to detach and fly on their own or females with active mammary glands but not captured in the net with young ones. Concurrent states of late lactation and early pregnancy were determined by palpation and confirmed by dissection.

Bats brought back to the laboratory were included in total sample numbers. Many were dissected to verify reproductive states, and some of these were saved for histological examination. Ectoparasites were collected from each bat brought to the laboratory, and tissues were removed from 142 bats for virus isolation procedures.

Table 1. Age, sex, and reproductive data on *Eonycteris spelaea* collected at Batu Caves

Date	Total No.	Immature bats, both sexes	Adult males	Adult females: No. examined	Pregnant *	Lactating with young attached *	Lactating without young attached *
1966							
March	100	43	36	21	4 (19)	9 (43)	5 (25)
April	22	17	0	5	0 (0)	3 (60)	2 (40)
May	39	13	19	7	3 (43)	1 (15)	
June	91	17	30	44	41 (92)	1 (2)	
July	95	37	32	26	6 (24)	15 (58)	
August	226	70	83	73	11 (15)	40 (56)	1
Sept.	197	71	58	68	7 (10)	18 (26)	10 (15)
Oct.	157	55	61	41	14 (39)	6 (15)	
Nov.	241	68	91	82	37 (45)	13 (16)	3 (4)
Dec.	177	39	77	61	14 (24)	19 (31)	
1967							
January	130	43	35	52	19 (36)	23 (44)	1 (2)
February	127	51	38	38	6 (16)	13 (34)	5 (13)
March	217	89	57	71	8 (11)	35 (45)	
April	168	30	61	77	34 (44)	9 (11)	6 (6)
May	143	33	57	53	26 (49)	21 (40)	2 (4)
June	69	20	14	35	17 (45)	14 (40)	1 (3)
July	18	6	6	6	1 (17)	3 (50)	2 (33)
August	260	88	80	92	32 (35)	50 (55)	5 (6)
Sept.	89	18	32	39	26 (67)	10 (26)	
Oct.	169	72	47	50	18 (36)	25 (50)	1 (2)
Nov.	149	62	37	50	24 (48)	14 (28)	2 (4)
Dec.							
1968							
January	157	66	22	69	18 (26)	38 (55)	3 (4)
Total	3,041	1,008	973	1,060	366	371	48

* Figures in parentheses are percentages.

Results

Reproductive data were obtained on 3,041 *E. spelaea* from the Batu Caves between March 1966 and February 1968. Reproductively mature adults included 1,060 females and 973 males. The remaining 1,008 were immature bats of both sexes, including 371 suckling young attached to the nipples of lactating females. 35 banded bats were recaptured once or more. Supplementary data were recorded on 100 additional *E. spelaea* collected in other areas of West Malaysia.

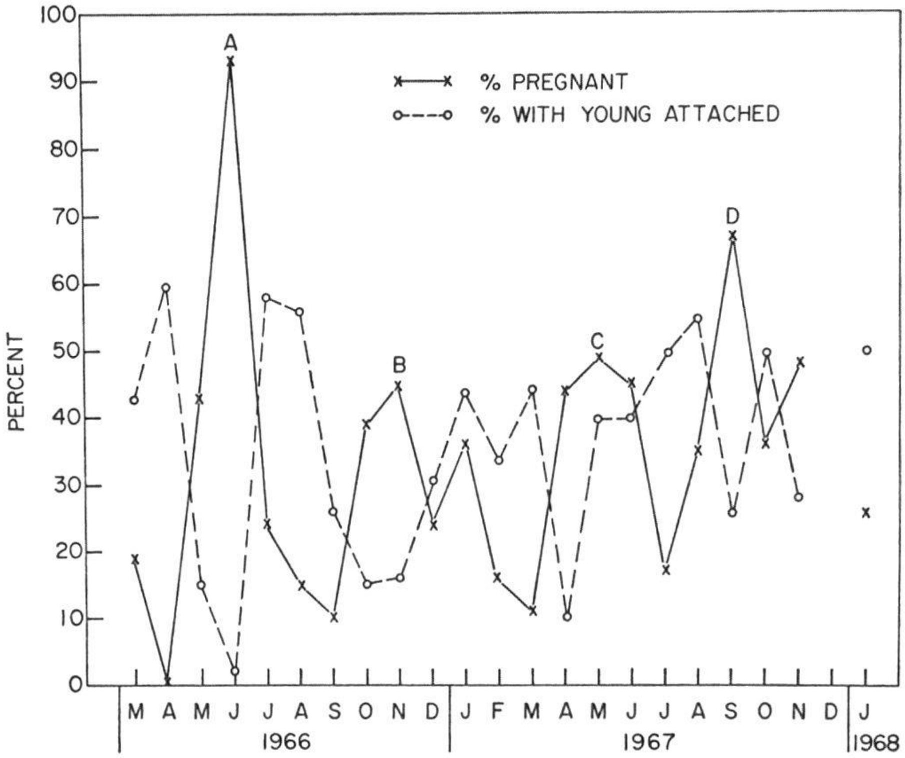

Fig. 2. Monthly rates of detectable pregnancies and lactation in *Eonycteris spelaea* – Batu Caves.

The distribution of the catch by age and sex was relatively stable throughout the study period (Table 1). Immature bats were about one-third of most catches, and the numbers of males and females were approximately equal. A definite reproductive state could be determined for 802 (75 %) of the females examined including 17 which were neither pregnant nor lactating. Only a few of the remaining 258 adult females were dissected; most were released and recorded as of unknown reproductive status.

Table 1 and Fig. 2 summarize female reproductive data. We attempted to collect at least 100 *E. spelaea* each month at the Batu Caves, but primary research responsibilities in other areas of Malaysia commanded precedence. Heavy evening rains prevented or restricted collections on several nights. We concentrated our main efforts on adult females because observations on males were equivocal.

Based on our limited number of recaptures, the gestation period seems to be slightly more than 6 months, possibly as long as 200 days. A single foetus or attached young or both were usual, but 2 foetuses were found in rare instances. No females were captured with more than 1 young attached.

Definite proof of concurrent states of early pregnancy and late lactation was obtained in November 1967 from a series of *E. spelaea* collected in the state of Kelantan. A number of lactating females were dissected and found to be in the first trimester of pregnancy. Closer examination of later collections of *E. spelaea* from the Batu Caves and of preserved specimens indicated that this phenomenon is common but not invariable. Recaptures of at least 2 individual females added further evidence. An adult female with 1 young attached to the nipple was banded (060-25505) on 18 October 1967 and recaptured on 4 January 1968 and found to be in the second trimester of pregnancy. A lactating female *E. spelaea* without young attached was first captured and banded (060-11455) on 15 February 1967 and then recaptured on 17 August the same year with young attached to a nipple.

Shortly after birth each young attaches to a nipple and remains firmly attached for 4–6 weeks. If forcibly detached, suckling young less than 4 weeks old do not seem able to reattach readily. Females with young attached were captured flying in and out of caves and in feeding areas. After about 6 weeks, young can detach at will and begin short weak flights in the cave or foraging areas. By the eighth week, the young begin leaving the cave by themselves, roosting and flying with the adult females for a few more weeks. Large young estimated to be 3 months old, with milk in their stomachs and stools, were captured in nets next to adult lactating females.

Our recapture data indicate that sexual maturity is reached between 1 and 2 years, although males may require more than 2 years to mature sexually.

At least 50% of the females examined in every month were pregnant, lactating or both (Table 1, Fig. 2). The rate of pregnancy ranged from zero in the small sample of April 1966 to more than 92% in June the same year. The pregnancy rate exceeded 50% in only one other month, September 1967. The overall rate of pregnancies was 30%, but many very early pregnancies probably went undetected.

Peaks of pregnancy in the Batu Caves colony occurred in May–June and October–November 1966 and in April–May and September 1967. A large percentage of females with small young attached and a notable decrease in numbers of pregnant females in January 1968 suggested that parturition had taken place in the previous month and that the rate of pregnancy in December may have equaled or exceeded that of the preceding September. Unfortunately, no collections were possible in December 1967. Known periods of parturition for large numbers of females were recorded in June and November 1966 and June and September 1967.

Increases in the numbers and percentages of lactating females followed decreases in pregnancy rate (Fig. 2), an indicator of population stability at Batu Caves. There were, however, 2 instances, in January 1967 and 1968, of a small rise in percentage of pregnant females 2 months after a major peak in the preceding November. The overall rate of adult females with young attached to nipples was 44%.

Only 48 actively lactating females were caught without young attached, and most of these were adjacent to a young bat in the mist nets. Only limited information was obtained on females that were still lactating while in the early stages of a subsequent pregnancy.

Adult males with enlarged scrotal testes were collected in every month of the year. Testicular size also changed rapidly due to temperature and other stresses imposed by handling and confinement. All epididymal smears for sperm from adult males were positive. On several occasions throughout the study period males were captured with fresh seminal fluid on the penis and midventral areas. Variation in the size of testes of old adult males indicated periodic regression and development, but conclusive evidence based on long-term observation of individuals was not obtained.

Discussion

No single reproductive pattern was evident for all individuals in the Batu Caves population of *Eonycteris spelaea.* More than 50 % of the adult females were pregnant or lactating in each month of observation. A few lactating females were also in the early stages of pregnancy. A large percentage of females exhibited apparent synchrony in pregnancy and lactation, but the rates for either seldom exceeded 60 % in any month. Adult males with enlarged testes and epididymal sperm were also collected throughout the year.

Rainfall was the most variable physical factor, although a true dry season with no rainfall did not occur during our study. Parturition and lactation periods fell within periods of heavy, extended rains and of low rainfall, showing no correlation with the amount of precipitation or any other physical factor. There were, however, peaks in the pregnancy rate 6–7 months after the periods of heavy rains, and these peaks followed a similar pattern to that of rainfall in the previous years. The relationship is probably not direct, but is mediated through the effects of extensive rainfall on the flowering of local trees and shrubs. This sort of relationship also seems true for *C. brachyotis* but is related to actual fruiting times rather than flower production, following the food habits of the 2 species of bats. Preliminary comparisons indicated that *E. spelaea* and *C. brachyotis* have complementary reproductive patterns. This could be coincidental or might be due to the long interval between peak periods of flowering and the appearance of mature fruits. It is not likely to be due to intraspecific competition.

The two species of *Tylonycteris* in West Malaysia have overlapping periods of parturition (MEDWAY, 1972). Ovulation may be induced by higher temperatures during the onset of the dry season in January with parturition and lactation occurring during a period of abundant insect food, 2–3 months later.

Approximately one-fourth of the adult female *E. spelaea* are out of synchrony with the reproductive patterns of the rest of the population. This may reflect a general tendency towards asynchrony or may be caused by individual physiological variations due to age, reproductive experience and dependence upon environmental stimuli. BECK (unpublished data) found variation due to age and reproductive experience in 2 species of vespertilionid bats in northern California. Long term banding studies on *Antrozous pallidus* indicate that first-year females tend to have one young each, while older females have a high proportion of twins. More limited observations on *Plecotus townsendi* suggest that second-year and older females have a higher pregnancy rate than do first-year females. Individual differences in growth rate and onset of sexual maturity also add to variations in reproductive behavior, especially during the first years. Sensitivity to, and dependence upon, environmental cues and the relative strength of these cues would also produce time differences in the reproductive patterns of colonies and populations. In the case of *E. spelaea* the presumptive stimulus, flower production, is dependent upon a second variable – rainfall. This double set of variables would compound variation in the reproductive cycles of *E. spelaea*.

With the present data and general state of knowledge, we cannot predict whether *E. spelaea* are evolving towards or away from synchronized reproductive patterns. It will be necessary to study this species in an area where rainfall patterns are regular and the difference between wet and dry seasons is more pronounced.

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Zusammenfassung

Das Fortpflanzungsverhalten von 1060 erwachsenen Weibchen und 973 erwachsenen Männchen von *Eonycteris spelaea* wurde von März 1966 bis Februar 1968 in der Batu-Höhle in West-Malaysia beobachtet. Da während dieser ganzen Zeit sexuell aktive Männchen beobachtet werden konnten, scheint keine jahreszeitlich bedingte Brunst vorhanden zu sein. Zu jeder Zeit waren durchschnittlich mehr als 50% der adulten Weibchen trächtig oder säugten. Der Höhepunkt der Trächtigkeit erfolgte 6 bis 7 Monate nach dem Höhepunkt der Niederschläge. Die Weibchen sind polyöstrisch, und eine neue Trächtigkeit kann schon im End-

stadium der Laktation beginnen. Die Jungtiere verbleiben ungefähr 2 Monate lang nach der Geburt an den Zitzen des Muttertieres. Beide Geschlechter erreichen die Geschlechtsreife nach einem Jahr.

Résumé

Des recherches ont été effectuées entre mars 1966 et février 1968 au sujet de la reproduction d'*Eonycteris spelaea* provenant des Cavernes Batu de l'Ouest de la Malaisie. Les données portent sur 1060 femelles adultes et 973 mâles adultes de cette espèce de chauves-souris. Les mâles étaient sexuellement actifs pendant toute la période étudiée; aucune activité saisonnière typique n'a pu être déterminée. Plus de 50 % des femelles adultes étaient gravides ou allaitantes. Une poussée du taux de gestation a lieu 6–7 mois après le maximum de pluviométrie. Les femelles de *E. spelaea* sont polyœstrus et une nouvelle gestation peut commencer durant les derniers stades de la lactation. Les jeunes restent attachés aux mamelons après la naissance pendant environ 2 mois. La maturité sexuelle des deux sexes est atteinte approximativement à l'âge d'un an.