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Reproduction in the Indian Sheath-tailed Bat

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The Indian sheath-tailed bat, Taphozous longimanus Hardwicke 1823 (Family Emballonuridae) exhibits a clearly defined breeding season at Varanasi (25°N), India. The female breeds twice during the year in quick succession. The first pregnancy commences in mid-January and terminates in late April to mid-May. Within a short period after parturition the female copulates and experiences the second pregnancy which terminates in August. Females remain sexually quiescent from September to December. The peaks of spermatogenic activity of male synchronise with the breeding periods of females. The secretory activity of the male accessory sex glands and the concentration of fructose in the accessory sex complex follow the pattern of testicular activity confirming that the species breeds twice in the year. Spermatozoa are, however, found in the epididymis throughout the year. A post partum oestrus appears likely in this species. The first pregnancy of the year has a longer duration than the second. Both ovaries are functional and both uterine cornua are equally developed; only one young is produced in each litter. The incidence of functional alternation of the two sides of the genitalia in successive pregnancies seems likely. The breeding cycle of *T. longimanus* at Varanasi differs markedly from that of the species at Nagpur (21°N), India, where females show evidence of pregnancies throughout the year. *T. longimanus* appears to be geographically variable with regard to the reproductive cycle.

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I. INTRODUCTION

Our knowledge of reproduction in the members of the family *Emballonuridae* comprising about 50 species is restricted to records of breeding in a few species (Harrison, 1958; Brosset, 1962; Basra, 1967; Fleming *et al.*, 1972; Anciaux de Faveaux, 1973; Topal, 1974; Khaparde, 1976; Sinha & Advani, 1976) and Gopalakrishna's (1955) study on *Taphozous longimanus* and Kitchener's (1973) on *T. georgianus* (=*T. hilli*). Gopalakrishna (1955) noted that in Nagpur, Central India (21°N) *T. longimanus* breeds throughout the year and each female becomes pregnant more than once in a year. By contrast, *T. georgianus* of Western Australia is monoestrous, even though in males spermatogenesis proceeds throughout the year and spermatozoa are found in the epididymis in all months of the year (Kitchener, 1973). During an investigation

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into the reproduction in certain Indian bats (Krishna, 1978) it was noted that in contrast to Gopalakrishna's finding at Nagpur, *T. longimanus* exhibits a restricted breeding season in Varanasi, Northern India $(25^{\circ}N)$. The problem was therefore investigated in detail and the results are reported here.

II. MATERIAL AND METHODS

Specimens of Taphozous longimanus were trapped alive in the Banaras Hindu University campus and adjacent places from September 1974 to August 1976. Even though over 500 adult specimens were collected, only 88 adults (42 males and 46 females) were used for histological and biochemical investigations. In the remaining specimens only gross anatomy of the reproductive organs, the secretory activity of the gular glands and that of the mammary glands in the females were recorded. Males weighing 20 gm or above and with a wing-span exceeding 35 cm were found to be sexually mature. In sexually mature females body weight exceeded 20 gm and wing-span 40 cm; the mammary teats were also visible. At least three males and three females were sacrificed each month for histological study. Since the same conditions existed in the bats in a given calendar month in both years, they have not been separately identifed in reporting the results. At autopsy the testes, epididymides and accessory glands from males and the entire reproductive tract from females were fixed in Bouin's fluid for 24 hr. The materials were weighed from 70% alcohol; subsequently they were embedded in paraffin, sectioned at 5-6 μ and stained with Mayer's haemalum and counterstained with eosin. Fructose in the accessory sex complex was estimated by the method of Lindner & Mann (1960).

III. RESULTS

1. Reproduction in the Male

The monthly variations in testicular weight are shown in Fig. 1A. Testicular recrudescence began in September (Fig. 2) reaching a short peak in October when spermatozoa were seen in the seminiferous tubules. Following an arrest of spermatogenic activity in December (Fig. 3) testicular recrudescence continued at a gradually accelerating pace and full spermatogenic activity was achieved in January which persisted up to the end of the month (Fig. 4). Marked testicular regression was evident in February and March and the seminiferous tubules generally showed primary spermatocytes as the terminal stage (Fig. 5); disorganized spermatids and spermatocytes were also seen in the tubules. Testicular recrudescence was again initiated in March resulting in the third peak in testicular weight and spermatogenic activity in April which persisted up to the end of May. In June testicular regression was more complete than in February. Testicular quiescence was clearly evident in July (Fig. 6) and August. Variations in epididymal weight (Fig. 1B) and histology paralleled the testicular activity. However, spermatozoa were seen in the epididymides throughout the year, even during periods of marked reduction in spermatogenic activity. The accessory sex glands (Fig. 1C, E), especially the ampullary glands, seminal vesicles and prostate, were distinctly cyclic, varying in gross weight, microscopic characteristics and secretory

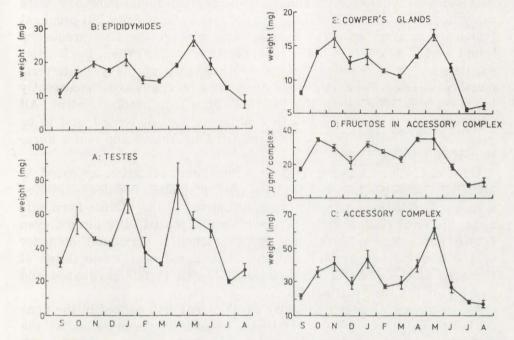


Fig. 1. Monthly variations in the (A) weight of testes; (B) weight of epididymides;
(C) weight of male accessory complex (prostate, seminar vesicles and ampullary glands);
(G) fructose content in accessory complex and (E) weight of Cowper's glands to Taphozous longimanus. Vertical bars represent the S.E.M.

activity and showed three peaks corresponding to the peaks of testicular activity in November, January and May. Fructose content of accessory complex (prostate, ampullary gland and seminar vesicle) exhibited a parallel seasonal fluctuation (Fig 1D) corresponding with changes in spermatogenic activity.

2. Reproduction in the Female

In September the ovary contained several secondary and a few tertiary (antral) follicles (Fig. 7). The number of secondary follicles increased in November and the tertiary ones continued to grow (Fig. 8). In December and January, prior to mating the ovary contained three or four large vesicular follicles (Fig. 9). Ovulation began sometime in the second week of January since corpora lutea were first found in the ovaries of bats collected in the third week of January. Some females obtained in the third week of January were carrying cleaving eggs while others had not yet ovulated. All females collected after mid-February were carrying fetuses. Parturition began in the last week of April but pregnant females near term were collected up to mid-May. The first pregnancy lasted for 105 ± 5 days. Within a short period after parturition the females copulated and experienced the second pregnancy of the year. Several females collected in late May and June were pregnant and concurrently lactating, thus confirming the incidence of a post partum oestrus. All adult females trapped from early June up to August were found to be pregnant. The second pregnancy terminated in August and had a duration of 86 ± 5 days.

Only one ovum was released at a time and ovulation appeared to alternate between the two ovaries. All pregnant females exhibited a single *corpus luteum* in the ovary ipsilateral to the uterine horn carrying the fetus (Fig. 10). The *corpus luteum* appeared fully formed even before implantation of the blastocyst, reached a maximum diameter of 220 μ shortly after implantation and occupied nearly two thirds of the area of the ovary. Luteal involution began in late pregnancy and was completed after parturition.

As pregnancy advanced follicular development was noticed in the nonovulated ovary; however, the follicles underwent degeneration at the vesicular stage. In advanced stages of pregnancy, the nonovulated ovary showed some developing Graafian follicles (Fig. 11).

Lactating females were found from late April to early June and from August to early September. Pregnant females near term were captured up to 23 August and lactating females with nursing young were collected until the first week of September. Hence the period of lactation appears to last 2 to 3 weeks.

Adult females remained sexually quiescent from September to November. During this period not even a single pregnant female was collected. In these females follicular development was arrested at the stage of medium sized follicles. The uterus was markedly reduced in size and showed involuted glands and dense stroma.

IV. DISCUSSION

The data presented above suggest that at Varanasi T. longimanus breeds twice in the year in quick succession bringing forth one young

each time. The first pregnancy of the year commences in mid-January and terminates in late April to mid-May. A *post partum* oestrus and mating results in the second pregnancy which terminates in August. The two peaks in the incidence of lactating females again suggest that the species breeds twice in one year. The occurrence of ovarian quiescence from September to December provides evidence in favour of a restricted breeding season in this species.

Changes in the testis provide clear confirmation that peak spermatogenic activity occurs in October, January and from April to May. Since pregnant females are not seen from October to December and since ovary remains quiescent at this time, the testicular recrudescence seen in males in October cannot be regarded as constituting another breeding season. The occurrence of females in early stages of pregnancy in January and again in late May to early June suggests that peaks of spermatogenic activity in the male synchronise with the breeding periods of females. The secretory activity of the accessory sex glands and the concentration of fructose in the accessory complex also follow the pattern of testicular activity confirming the incidence of two breeding seasons in *T. longimanus*.

It is obvious that the breeding cycle of *T. longimanus* at Varanasi differs markedly from that of the species at Nagpur where adult females show evidence of pregnancies throughout the year (Gopalakrishna, 1955). *T. longimanus* thus appears to be geographically variable with regard to its reproductive cycle. Topal (1974) reported sexual rest in females of *T. longimanus* collected in August from Elephanta Island near Bombay and in December from Calcutta, India. The related species, *T. melanopogon* (Khaparde, 1976) of India and *T. nudiventris* (Basra, 1967) of Iraq are monoestrous. According to Brosset (1962), *T. kutchensis* breeds in March in Delhi and Madhya Pradesh, India. Geographical variability in the breeding biology is reported in several monoestrous chiropterans of Central Africa (Anciaux de Faveaux, 1978).

Since breeding (copulation and implantation) in *T. longimanus* occurs in January, when environmental temperature is low and day length is short, and again in May when environmental temperature is high and day length is extended, it is doubtful whether variations in temperature and day length play a decisive role in the regulation of reproduction in this species. It is not known whether availability of food (*e.g.* insects) is a critical factor in the timing of reproductive activities in this species. The bimodal polyoestry as shown by *T. longimanus* at Varanasi is reported in several phyllostomid bats (Carter, 1970; Fleming *et al.*, 1972; Wilson, 1973) and in small tropical pteropids such as *Rousettus aegyptia*-

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cus (Mutere, 1968), R. leschenaulti (Gopalakrishna, 1964) and Epomophorus anurus and Epomops franqueti (Okia, 1974a, b).

The incidence of post partum oestrus in T. longimanus is suggested by the fact that the first pregnancy follows the second in quick succession and by the occurrence of pregnant females with nursing young in May and June. Post partum oestrus is reported in certain species of bats (Wimsatt & Trapido, 1952; Okia, 1974a, b). In some chiropteran species there is the physiological dominance of the genitalia of the right side over the left (Matthews, 1937, 1941; Wimsatt, 1945, 1979; Pearson et al., 1952; Kitchener, 1973; Khaparde, 1976). In T. longimanus both ovaries are functional and both uterine cornua are equally developed. However, as in Desmodus rotundus murinus (Wimsatt & Trapido, 1952) and Carollia sp. (de Bonilla & Basweiler, 1974), ovulation in T. longimanus appears to alternate between the two ovaries. The presence of developing Graafian follicles in the nonovulated ovary in

Table 1

Species	Place	Mode of Breeding	Source
Taphozous longimanus	Nagpur (India)	Aseasonal Polyoestry	Gopalakrishna, 1955
Taphozous longimanus	Varanasi (India)	Bimodal Polyoestry	Present author
Taphozous melanopogon	Bhubaneswar (India)	Seasonal Monoestry	Khaparde, 1976
Taphozous nudiventris	Iraq	Seasonal Monoestry	Basra, 1967
Taphozous georgianus	Western Australia	Seasonal Monoestry	Kitchener, 1973
Taphozous mauritianus	Africa (Ethiopian)	Aseasonal Polyoestry	Anciaux de Faveaux 1973
Coleura afra	Africa (Ethiopian)		Anciaux de Faveaux 1973
Rhynchonycteris naso	America (Neotropical)	Polyoestry	Dalquest, 1957
Saccopteryx bilineata	America (Neotropical)	Seasonal Monoestry	Fleming et al., 1972
Saccopteryx bilineata	America (Neotropical)	Polyoestry	Carter, 1970
Balantiopteryx plicata	America (Neotropical)	Polyoestry	Carter, 1970

Breeding cycles of some Emballonurid species.

pregnant females near term also suggests the incidence of functional alternation of the two sides of the genitalia in successive pregnancies. This is in agreement with the findings of Gopalakrishna (1955) in this species. The differences in the length of the two pregnancies in T. longimanus may be due to the differential rate of embryonic development. Racey (1969, 1973) has shown that pregnancy is bats is extended in

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response to adverse conditions in the environment and questions the concept of a standard gestation period for heterothermic animals like the bats.

So far only a limited number of species of the family *Emballonuridae* have been studied and the variety they show in their mode of breeding at the family, or even generic level, is surprising (Table 1). In spite of the fact that all these species live in the tropics, they exhibit all the three principal breeding patterns, viz. monoestry, seasonal polyoestry and aseasonal polyoestry. *T. longimanus* is furthermore geographically variable with regard to the reproductive cycle as demonstrated by our study in Varanasi and by Gopalakrishna's (1955) in Nagpur. Even though it is difficult to identify the specific factor(s) that regulate breeding activity in emballonurids, it seems likely that whatever proximate or ultimate factors that may be postulated to regulate breeding in one species may not apply uniformly to all the species.

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ROZMNAŻANIE TAPHOZOUS LONGIMANUS

Streszczenie

Nietoperz Taphozous longimanus, Hardwicke 1823 (rodzina: Emballonuridae) zamieszkujący okolice Varanasi (25°N) w Indiach, posiada wyraźnie określony sezon rozrodu. Samice rodzą dwukrotnie w ciągu roku. Pierwsza ciąża zaczyna się w połowie stycznia a kończy pod koniec kwietnia lub w połowie maja. W czasie krótkiego okresu po porodzie samic zostają pokryte, a druga ciąża trwa do sierpnia. Następnie samice pozostają nieaktywne od września do grudnia. Szczyt spermatogenicznej aktywności samców jest zsynchronizowany z sezonem rozrodczym samic. Inne przejawy aktywności testicularnej wskazują, że gatunek ten rozradza się dwukrotnie w ciągu roku. Plemniki są jednakże znajdowane w najądrzu w czasie całego roku. Post partum oestrus jest możliwy u T. longimanus. Pierwsza ciąża w roku trwa nieco dłużej niż druga. Oba jajniki funkcjonują sprawnie i oba rogi macicy są jednakowo rozwinięte, mimo iż w każdym miocie jest tylko jedno młode. Sugeruje się, że kolejne zarodki implantowane są przemiennie w obu rogach macicy.

Cykl rozrodu T. longimanus z Varanasi, różni się znacznie od cyklu rozrodu tego gatunku z okolic Nagpur (21°N) w Indiach, gdzie samice mają oznaki ciąży w ciągu całego roku. T. longimanus cechuje się wyraźną geograficzną zmiennością cyklu rozrodczego.

EXPLANATIONS OF PLATES III-IV

Plate III.

Fig. 2. Testis in September to show signs of recrudescence. Primary and secondary spermatocytes and spermatids are visible in the seminiferous tubules. \times 108. Fig. 3. Testis in December. Note the arrest of spermatogenesis in the seminiferous tubules. \times 108.

Fig. 4. Testis in January. Note the bundles of spermatozoa in the seminiferous tubules. \times 108.

Fig. 5. Testis in March. Note the arrest of spermatogenesis. imes 148.5.

Fig. 6. Testis in July. Note the seminiferous tubules almost devoid of any content except a few layers of spermatogonia and spermatocytes. \times 148.5.

Plate IV.

Fig. 7. Ovary during sexual quiescence (September). Note the presence of mediumsized follicles; Graafian follicles are absent. \times 67.5.

Fig. 8. Ovary in November to show signs of recrudescence. In addition to the medium-sized follicles, some Graafian follicles are also seen. \times 67.5.

Fig. 9. Ovary of a female in oestrus phase (January). Note the rapid growth of the follicles; a number of Graafian follicles are seen. \times 67.5.

Fig. 10. Ovary soon after implantation. Note the single corpus luteum occupying the major portion of the ovary. \times 67.5.

Fig. 11. Non-ovulated ovary in late pregnancy to show the presence of a number of maturing follicles. \times 67.5.

