STUDIES ON THE EMBRYOLOGY OF MICROCHIROPTERA

Part I. Reproduction and Breeding Seasons in the South Indian Vespertilionid Bat—Scotophilus wroughtoni (Thomas)

By A. GOPALAKRISHNA

(Lecturer in Zoology, College of Science, Nagpur)

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(With Two Plates)

Introduction

This is the first of a series of papers on the embryology of Microchiroptera. It attempts to record the breeding seasons of one of the species of Insectivorous bats—Scotophilus wroughtoni (Thomas), collected at a place about 18 miles from Bangalore (South India). The climatic conditions of this place do not vary much during the year, the place being in the tropical zone. The present paper does not attempt to describe in detail the histological changes which occur in the reproductive tract of the bat during breeding This will be dealt with in a subsequent paper. and non-breeding seasons. It attempts only to record the salient features of the cyclical changes as observed in different months of the year and other phenomena of special interest in relation to the breeding habits of the bat. The work was based entirely upon the collections of wild specimens since the taming of these bats in the laboratory was found to be impossible. Captivation and consequent domestication of these bats might have considerably impaired the normal sexual rhythm, and might thus have given misleading results.

HISTORICAL

The subject of the reproductive process of bats has engaged the attention of many workers for over a century. A review of the literature dealing with the reproduction of the Insectivorous bats has been made by several authors. One such attempt was made by Duval (1895 a) who reviewed all the earlier work. Later a good summary of the literature was given by Hartman (1933). Baker and Bird (1936) in a paper on the "Seasons in a Tropical Rain-forest (New-Hebrides). Part 4.—Insectivorous bats" gave a short resumé of the work done on the reproductive cycle of the Insectivorous bats. At the time when Baker and Bird published their paper they were

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almost the pioneer workers on the tropical species of microchiroptera. Since then quite a large number of workers have described the reproductive process in bats, not only of the temperate and cold climates but of the tropics also. Particular mention must be made of the valuable work done by Harrison Matthews (1937) and Mary J. Guthrie (1933) on the European, South African, and American bats. Harrison Matthew's record of the breeding seasons of the South African bats, though based on a very imperfect collection, gives a fairly clear idea of the sexual rhythm of the tropical bats.

Pagenstecher (1859) was almost the first to notice that there was something peculiar about the breeding habits of the bats. Working on *Pipistrellus pipistrellus* in Germany, he noticed that in winter the uterus of the female was swollen, and this swelling was due to the presence of live spermatozoa, though there was no sign of a ripe Graafian follicle in the ovary. He naturally concluded that copulation occurred in the bat earlier than ovulation and the sperms were capable of being stored in the genital tract of the female for a fairly long time, throughout the winter.

Van Beneden (1875) also observed sperms in the uteri of bats, but concluded that fertilisation occurred immediately after copulation and the fertilised ovum remained dormant till the end of winter. Emier (1879 a and b), however, confirmed the view of Pagenstecher and showed that in *Pipistrellus pipistrellus* and *Nyctalus noctula* copulation occurs late in autumn and the sperms hibernate during winter inside the uterine tract of the female.

Benecke (1879) and Fries (1879), working on a number of species— Pipistrellus pipistrellus, Plecotus auritus, Vespertilio murinus, Vespertilio nathusii, Rhinolophus hipposiderus, came to the conclusion that copulation occurred before hibernation and the sperms lived in the uterus of the female throughout the winter and ovulation and fertilisation took place during early spring. The young born in the summer do not copulate in the same season. They thus believed that spermatozoa hibernated in the uterus of the female for a period of at least 4½ months.

Later, Rollinat and Trouessart (1895–97) published their classical work dealing with the reproduction of two different species of microchiroptera, Vespertilio murinus and Rhinolophus ferrum-equinum. They clearly stated that sperms existed in a dormant state throughout the winter for about $4\frac{1}{2}$ months, from October to the beginning of April, and ovulation and fertilisation occurred at the beginning of spring 8–10 days after the bats 'awoke' from their winter hibernation. Further their experiments with hibernating bats indicated that if the 'sleeping' females were brought to a warm room, ovulation, and consequent fertilisation and pregnancy resulted.

Grosser (1903) described a very remarkable phenomenon occurring in Nyctalus noctula, wherein copulation occurred very early—in July or August—and at the end of autumn the cervical canal was blocked by an increase in the amount of connective tissue and the sperms were thus stored up in the vagina. Ovulation and fertilisation occurred at the end of March or in early April when the genital canal was found to be free. This phenomenon which was not described in any other species proved beyond any doubt that copulation must have occurred early in winter or late autumn and fertilisation and pregnancy during spring and summer. Such a blocking of the vaginal passage was not noticed in Vespertilio murinus, or Placotus auritus.

A parallel instance has been recorded by Courrier (1927) in the males of Pipistrellus pipistrellus where he noticed that the testes had degenerated at the beginning of winter leaving only the spermatogonia and sertoli cells, and the testes resumed activity only in the next autumn. He had previously observed (1924) that in Pipistrellus pipistrellus, the uterine glands were active during winter and believed that the secretion of the glands acted as nourishment for the hibernating spermatozoa. Rendez (1929) working with Vespertilio murinus and Placotus auritus showed that in the males the testes did neither exhibit spermatogenetic activity during spring nor the epididymis contain any active sperms. He also concluded that fertilisation occurréd in spring by stored sperms received during autumn copulation.

Harrison Matthews (1937) working on the British horse-shoe bats— Rhinolophus ferrum-equinum and Rhinolophus hipposideros minutus, conclusively proved that copulation occurred in autumn and the spermatozoa stored through winter in the vagina fertilised the ovum which was liberated in spring. He writes, "The occurrence of the vaginal plug in the horse-shoe bats gives some evidence on this question in Rhinolophidæ. In specimen taken during the third week of April the vaginal plug was still in position and exactly similar in all respects to that found in the bats up to that date. In addition, there were present, as usual, spermatozoa in the uterine glands and Fallopian tubes. The presence of the plug entirely filling the vagina showed that copulation had been impossible since that plug hardened in the previous autumn. But the particular point of interest was a large and well-developed corpus luteum in the right ovary and the blastocyst was just passing through the uterus. The ovum must, therefore, have been fertilised by one of the spermatozoa stored in the upper part of the genital tract and the spermatozoa must have been deposited in the previous autumn...". "These specimens show conclusively that in the Rhinolophid bats the spermatozoa stored in winter can and do fertilise the ovum in spring, some five

months later." This account of Harrison Matthews is conclusive enough. But it is a matter of regret that the crucial experiment of keeping inseminated bats segregated until spring, and then examining them for pregnancy was not done by him. Further, he did not give any details regarding the condition of the gonads and accessory structures in the males.

From the foregoing account it is evident that the view held by these authors is that copulation takes place during autumn and that the spermatozoa are stored in the genital tract of the female till ovulation and fertilisation which occur in spring. This observation would apply to Pipistrellus pipistrellus, Nictolus noctula, Plecotus auritus, Vespertilio murinus, Rhinolophus ferrum-equinum, and Rhinolophus hipposideros minutus.

The other view that effective copulation, ovulation, and fertilisation take place in spring is equally strongly advocated by various workers with respect to the bats of the cold climates. Some authors regard this as an exceptional phenomenon occurring either in those bats which have failed to copulate the previous autumn or in the young ones in the first year of sexual life. But these researches have so far been confined to the temperate bats only.

Vogt (1881) was the first to notice the occurrence of non-pregnant females of *Vespertilio murinus* and *Rhinolophus ferrum-equinum* in spring. He believed them to have missed copulation in the previous autumn. He does not mention if he observed spring copulation normally occurring in these bats.

Rollinat and Trouessart, though they categorically deny spring copulation, still record the instance one male specimen of *Eptesecus serotinus* which, when brought to a warm room in early February, woke up from hibernation and tried to copulate. Duval (1895) actually observed spring copulation though not under normal conditions. Similar artificial induction of spring copulation was conducted by Zondek (1933) and Caffier (1934).

Hartman and Cuyler (1927) who worked out completely the life-cycle of *Nyctinomus mexicanus* stated that spring copulation was the rule in these American bats. They recorded the occurrence of sperms in the uterine tract of the female only in March and in no other season. Soon after copulation, fertilisation and gestation followed as in any other mammal. However, in a species of *Myotis* (sp.) from the same locality sperms were seen in the uterus of the female during winter.

Apart from the observations of Hartman and Cuyler quite a large amount of circumstantial evidence has been adduced by the supporters of spring

copulation theory in various species. The conclusions were mainly based on a study of the male reproductive organs. Fries (1879) described that throughout winter and spring the male genital apparatus was full of sperms and the accessory reproductive organs were in full swing of activity. Courrier (1927) made a more detailed study on *Pipistrellus pipistrellus* and recorded that the interstitial cells of the testes and the accessory sexual organs were in full activity during winter, though the seminiferous tubules contained no sperms, but only spermatogonia and sertoli cells. Rollinat and Trouessart had also observed the storage of spermatozoa in the epididymis and the bladder of the male during winter. Nakano (1928) also recorded the storage of spermatozoa in the epididymis throughout winter. There has, however, not been any conclusive proof that fertilisation occurred by the spermatozoa stored in the genital organs of the males during winter.

Caffier and Kolbow (1931), though they accepted the possibility of fertilisation being effected by the spermatozoa received in autumn copulation, they made the startling discovery that the testes showed spermatogenesis not only in November but also in March in many species such as Pipistrellus pipistrellus, Plecotus auritus, Barbastella, Eptesecus, Myotis, Rhinolophus hipposideros, etc.

The only conclusive evidence in support of effective spring copulation was given by Mary J. Guthrie (1933) who observed the normal occurrence of only spring copulation in many species of North-American insectivorous bats.

There is thus a vast amount of literature available regarding the breeding habits of the insectivorous bats inhabiting temperate and cold climates. Unfortunately there is no complete account of the breeding cycle of the tropical species of microchiroptera, and the little knowledge we have is derived only from records of pregnancy. With regard to the copulating season there is practically no information except for the casual observation of the occurrence of visible secondary sexual characters in different seasons in the males of a few species of microchiroptera. Braestrup (1933) recognised in two males of Chærophon pumilus in tropical Africa a large crest of hair on the neck and back and that the scrotum was swollen. This season varied at different places. Thus no generalisation could possibly be made regarding the exact season of copulation and sex cycle on such meagre and casual observations.

A fairly clear account of the breeding seasons of *Miniopterus australis* was given by Baker and Bird (1936). They noticed that, "Conception in this species occurred in the beginning of September...". "And the young

were probably born in the second half of December, and the duration of gestation is about 110 days". Further in the middle of August (11th) the examination of the uteri for sperms gave negative results there being no sperms in the uteri or uterine glands. There was a large Graafian follicle with much liquor folliculi in the ovary and there were signs of early metacestrus condition of the uterine glands. The authors recorded that, "Presumably insemination and ovulation would have taken place two or three weeks later".

Their examination of the male specimens substantiated the results of the examination of the female. An abundance of spermatozoa in the epididymis was seen in July, August, and September. From October onwards there was a decrease in the spermatozoa and till May next the epididymis was practically empty. They therefore observed, "One sees clearly that copulation takes place about the end of August and the development of the embryo starts at once. Copulation occurs at a time of the year, when the days are beginning to get longer and the temperature is rising, *i.e.*, in spring"....." Thus Miniopterus australis falls into the same category as Nyctinomus at Texas, which Hartmann and Cuyler (1927) showed to copulate only in the northern spring".

After the classical work of Baker and Bird there has been very little work on the tropical bats. Harrison Matthews (1941) in his paper 'On the genitalia and reproduction of some South African bats' summarised that in the tropical species there was nothing comparable to the winter hibernation of the temperate bats. Only in the case of *Miniopterus dasythrix* he mentions "Possibly that impregnation had taken place weeks, or even months, previously and that spermatozoa had been stored in both sexes as in some European bats". However, in the "summary", he observed, "for early in July the females were pregnant with only blastocysts, indicating mating at a season corresponding with the earliest beginnings of the southern spring. It is of course possible that insemination took place in the preceding autumn and that fertilisation or development had been delayed, as in some bats of the temperate regions, but it does not appear to be likely because there is no evidence that this species hibernates".

We thus see that though a great controversy exists regarding the exact seasons of copulation and fertilisation in the insectivorous bats of the temperate and cold climates, there seems to be entire agreement among the workers on the tropical bats, that copulation occurs in early spring and is immediately followed by fertilisation and gestation.

My study of the reproduction of the South Indian Vespertilionid bat Scotophilus wroughtoni (Thomas) confirms the above view. There is no storage and hibernation of spermatozoa.

MATERIAL AND METHODS

Bats of this species were collected round about Bangalore from the forests of Hoskote (about 17 miles east of Bangalore). Some were also collected at Seringapatam about 75 miles west of Bangalore. This does not alter the results of the work as both the localities conform to the same plan of breeding. Scotophilus wroughtoni is essentially an arboreal species living inside hollows of large trees. A few excursions were made to the caves and dungeons near Bangalore and Seringapatam, but at no time could we collect a single specimen of this species though many other species were collected in large numbers. Further, it appears that this particular bat is always found to live in association with two other species of insectivorous bats—Scotophilus temminki and Taphozoas longimanus, for all our collection of bats included all the three species.

Scotophilus wroughtoni is a fairly large bat with a brown coloured belly and the back of darker hue. The tail projects slightly beyond the interfemoral membrane. The bats hang down from projections inside the hollows of trees. They were caught by using a net. They are ferocious and are to be handled with care, as they bite otherwise.

The specimens were killed by chloroform and immediately dissected and the genital structures removed. The carcases are all preserved in formalin for further study. The reproductive organs were fixed in various fluids. But Bouin's picro-formal gave the best results. After fixation the material was transferred to 70% alcohol. In the females the mammary glands and in the males the adrenal bodies were similarly fixed. Serial sections of the ovaries, Fallopian tubes, the uterus and vagina were taken in all cases where there was no visible signs of pregnancy.

An account of the changes in the male reproductive and detailed histological œstrous changes in the female will be dealt with in the next part.

Collections of bats began in the month of May 1945 and is still being continued to the present day. Attempts were made to collect as many times as possible in all months of the year to complete the data regarding the breeding habits.

Table I gives the record of the collection of the bats so far made.

| TABLE I | | | | | |
|------------------------|-----------|---------|--------|----------------|--|
| Scotophilus wroughtoni | (Thomas): | Monthly | record | of collections | |

| Month | Males | Females | Pregnancy in Female | |
|------------------------------------|-------------------|---|--|--|
| February March April May June July | 3 5 2 4 2 1 1 1 2 | 5 3 4 40 30 2 1 1 2 17 | Non-pregnant ,, Early morulæ Early blastocysts Advanced pregnancy Full term Non-pregnant ,, ,, | |

The above numbers do not probably indicate the sex-ratio because in practically all our collections the females outnumbered the males. One thing worth recording is that during the months of January and February there were a greater number of males than during the other months. This fact taken with the other things might probably indicate that during this period only do the males and the females live together, while at other periods males live segregated from the females. No definite generalisation is, however, possible at this stage.

OBSERVATIONS

(a) Number of embryos in a litter.—At each pregnancy there are two embryos, and each ovary shows a corpus luteum—a fact which is of very rare occurrence among the microchiroptera, single embryos being the rule. Two embryos were also observed in Scotophilus temminki. Occurrence of double embryos was noticed by Ramaswamy (1933) in another Vespertilionid Harrison Matthews (1942) states, "One bat, Vesperugo leisleri (Kuhl). of the most interesting characters of the female genitalia in the microchiroptera is the bilateral assymetry which occurs in varying degrees of intensity"...." Most bats, except those of the family Phyllostomatidæ, have a bicornuate uterus, but nearly always bring forth only one young at a birth; consequently as a rule, only one uterine cornu is occupied by pregnancy. It has been found in very many species of different families that there is a constant tendency for the right side of the genitalia to be the functional one. In many European Vespertilionids, although pregnancy can occur on either side, the majority of pregnancy has been found in the right cornu". In Rhinilophus hipposideros he has shown that "the left ovary appears to be degenerate and never to produce mature ova, the pregnancy being always on the right side" (Matthews, 1937 a). I have also observed that in many of the species of microchiroptera that I collected there was always a single embryo in the uterus. Thus, Scotophilus wroughtoni differs from a majority of the microchiroptera in having two embryos in the litter. However, there is one specimen in my collection in which the left ovary shows two masses of corpora lutea and two unimplanted blastocysts in the left horn of the uterus but at different levels. Probably double implantation never occurs in this species in the same uterine cornu, the ovum, before or after fertilisation moving into the other cornu for implantation even in those exceptional cases where double corpora lutea occurred in the same ovary. This surmise seems to be correct, because after the establishment of the placenta, there was no case where a double embryo occurred in the same uterine cornu. A similar migration of the ovum from the ovary to the opposite uterine horn for implantation has been described as a normal occurrence in the case of Miniopterus dasythrix (Temm.) (Harrison Matthews, 1942).

- (b) The breeding seasons.—Pregnancy records show that the female has a very sharply defined annual breeding season. Pregnancy was observed only from the 22nd March upto about the end of June, and at no other period was a pregnant specimen collected. This seems to confirm the observations of Baker and Bird (1937) on Miniopterus australis which "presents a very sharply defined annual breeding season", where pregnancies occurred only during the months of September, October, November and December, and no pregnancy during the other months of the year. This is also the case in all the species of temperate and cold climates so far examined by various authors. Marshall (1922) states, "it does not appear to be known whether the poly-æstrous condition ever occurs in bats." However, Ramaswamy (1933) observing pregnant uteri in early January in Vesperugo leisleri (Kuhl) suggests, "It is also possible that there is another season when these begin to breed "....." It looks as though after a very short anæstrum following the summer gestation the pro-æstrous cycle again commences ending in the copulation of the females in cold weather." Harrison Matthews is the only other author to record a poly-æstrus condition in Nycteris luteola (Thos.) and Nycteris hispida (Schreb.), wherein he observed pregnancies in lactating bats and concluded, "The quick succession of pregnancies also points to the possibility that this species, unlike all other bats as far as they are known, may be poly-æstrus." But Scotophilus wroughtoni without any doubt has only one annual breeding season.
- (c) The æstrus and copulation.—The uterus which shows inactive glands as late as November suddenly springs to activity in February, and the glands

hypertrophy with a definite increase in the vascularisation of the uterine submucosa (Fig. 1). A very careful microscopic examination was made to detect the presence of spermatozoa but in specimens collected in November, December, January and February no sperms were seen in the uterus, vagina, or the Fallopian tubes. The ovaries of the February specimens showed great. activity and exhibited a large number of developing Graafian follicles (Fig. 2). Ovulation does not certainly occur upto the 10th of February. Examination of specimens collected on the 24th of March clearly shows that ovulation not only has occurred but in all females early morulæ were present. These were lying loose in the uterine lumen. Further the vagina showed large numbers of degenerating spermatozoa. Another curious fact noticed was that out of the twelve females collected on 1st of April all were pregnantpregnancy being recognised only after careful microscopic examination of the uterus, and in all the cases the blastocysts were in the same stage of development, lying loose in the uterine cavity (Fig. 3). This fact clearly shows that fertilisation occurred in all the specimens at about the same period, if not on the same day. This, taken along with the fact that the females collected on the 10th of February showed no spermatozoa, indicates that the period of copulation is also very sharply marked, and it must have occurred between the 10th of February and the 24th of March. Judging by the age of the morula on the 24th of March one can easily place the time of fertilisation somewhere about the third week of March. It is, however, not possible to clearly decide whether copulation occurs before or after ovulation because I have unfortunately no collection made during the 1st, 2nd, or the 3rd week of March. But probably copulation might have occurred a day or two after ovulation because no sperms were seen in the Fallopian tubes while sperms were quite abundant in the uterine lumen in the specimens collected on 24th March. There is no instance of a tubal ovum in my collection.

Pregnancy was noticed in all specimens collected between the months of April and June at progressively advanced stages. The June embryos were far advanced in development, though not of full term. Parturition can safely be placed at the last week of June or the first week of July. The period of gestation thus extends from 105 to 120 days.

In the whole of my collection there was no instance of pregnancy in a lactating female.

(d) Age and growth.—All females captured during April, May and June were pregnant without a single exception. This seems to be a very interesting feature, and Baker and Bird omit to make a mention of this.

Rollinat and Trouessart working on some of the Rhinolophid bats observe "frequently the young females in their second year do not experience æstrus, and consequently their first æstrus does not occur until their third autumn". These authors divided their material into four groups: virgin animals in their first autumn; virgins in their second autumn; animals experiencing their first æstrus, some in their second and some in their third autumn; and parous animals, some in their third and some at least in their fourth autumn" (Harrison Matthews, 1937).

Harrison Matthews (1937) also records, "Young bats do not reach their first cestrus until their second autumn, when they are at least 15 months old. Parous bats will at least reach their second cestrus when they are 12 months older, and at least 27 months of age. By the time when they have weaned their second young one they will be 34 months old". He thus endorses the view-point of Rollinat and Trouessart.

He also tried to determine the age of his specimens by their pregnancy records. He says, "the present series of specimens show clearly that both species of British horse-shoe bats normally do rear a second young one, and consequently must reach an age of at least three years "...." Further on purely theoretical grounds these bats must live to an age of at least four years, because each pair must produce more than two young in its life-time, to allow for wastage, if the species is not to become extinct. Females must therefore produce at least three young each, and accordingly reach an age of four years."

Theorising on similar lines regarding Scotophilus wroughtoni, as there is no non-pregnant female during the gestation season, i.e., April to June, and also as there is no record to show that the bats might become pregnant during any other month of the year, as it is monæstrous, the species must get into sexual activity in its first year and become pregnant. Thus, before it has completed its one year of age, it will have given birth to young ones. Furthermore, the growth of the young one is very rapid as is indicated by the ovaries of the specimens collected in February. That the non-occurrence of non-pregnant females during the months of April, May and June, during 1945 and 1946, cannot be an accident. It must be presumed that all females had become pregnant. All these facts clearly indicate that the young born in the month of July the previous year get into sexual activity during next February and March.

Purely on theoretical grounds, and fitting with the conclusions of Harrison Matthews, these bats must produce at least three young ones each, to perpetuate the race, and hence must at least live for two years. As this particular species under study bears two young ones in each litter it is quite possible the bat becomes pregnant at least twice in its life-time. Further, there is no indication to show that the bat had become pregnant more than twice as revealed by the residual placental discs. This taken along with the fact that the bat experiences an annual breeding season indicates that it must live for atleast two years and that it may not become pregnant a third time. Furthermore, Anderson (1917) states that the length of the period of immaturity will, as a general rule, in some vague sort of way, enable us to form an opinion of the normal age the individual is destined to obtain, a mammal which quickly becomes full grown will probably have a rather short series of years to live as adult, and vice versa." Anderson places the age of the bat Rhinolophus rouxi "at five or six years as the extreme possible age of the bats", as calculated from their tooth-wear. Taking all these things into consideration Scotophilus wroughtoni does not probably live as long as Rhinolophus rouxi, or the British horse-shoe bat, which are supposed to have a longevity of about four and a half to five years but might live, without doubt, up to about three years and probably not more. A more clear and definite figure will be arrived at by examining the tooth-wear on the same lines as Anderson did, which will be shortly undertaken.

CONCLUSIONS

Two very important facts are recognised by the study of the reproductive phenomena in Scotophilus wroughtoni. In the first place, there is a very sharply defined breeding season confined to about the middle of March. and secondly all the females collected during the months of April, May and June are pregnant. In an unvarying tropical climate the occurrence of an annual monœstrous condition is by itself remarkable, and much more so in the case of a bat which is confined to the hollows of trees—considering the non-conductivity of the wood to temperature, and thereby living under an almost constant environmental condition throughout the year. Baker and Bird (1936) also make a similar discovery in the bats of New-Hebrides and come to an identical conclusion. The seasonal change in the temperature alone does not probably determine the onset of the breeding activity. as was supposed by a few of the early workers on the bats of temperate and Furthermore, too much stress cannot be laid on the factor cold climates. of light and of the lengthening of the day, considering the fact that the bats are essentially nocturnal creatures. Unless experimental data is available regarding the influence of light on the breeding habits of bats, this conclusion cannot be accepted at present.

As copulation is immediately followed by fertilisation and gestation the problem of winter hibernation of the spermatozoa, as occurs in the bats of cold climates, becomes unnecessary.

SUMMARY

- 1. A study of the literature in the reproduction of bats reveals that there are two types of sexual phenomena exhibited by bats, some bats experiencing a definite hibernation during winter after copulation in autumn, and others where copulation is immediately followed by fertilisation and gestation in spring. The bat *Scotophilus wroughtoni* does not show any evidence of a winter "sleep" and thereby falls into the second category.
- 2. Scotophilus wroughtoni has a sharply defined breeding season, copulation occurring at about the middle of March and followed immediately by fertilisation and gestation.
 - 3. The period of gestation is about 105 to 115 days.
- 4. The age which this bat attains, as determined by its pregnancy records, may safely be placed at about three years.

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The abbreviations are according to the "World List of Periodicals". References marked in asterisks were not available in original.

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