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Autor: Mutere, Festo A.

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Department of Zoology, Makerere University College, Kampala,
and the East African Virus Research Institute, Entebbe, Uganda

The Breeding Biology of the Fruit Bat *Rousettus aegyptiacus* E. Geoffroy Living at 0° 22′ S.

By FESTO A. MUTERE

Introduction

The only references to the breeding of *Rousettus aegyptiacus* E. Geoffroy encountered in the literature are those by BAKER & BAKER (1936), ANDERSON (1902) and KULZER (1958) all of which are mentioned by ASDELL (1964). According to ANDERSON (1902), captive bats of this species have bred all the year round in Egypt. BAKER & BAKER (1936) record that freeliving, these bats mate in September and October and the single young is born in February or March. KULZER (1958) on the other hand, reports that mating takes place at the end of April and the young are born from February to November.

Two observations in the above literature are worthwhile mentioning. First, the information so far available on the breeding of *R. aegyptiacus* is so fragmentary that it is not possible to gain an overall picture of its annual breeding cycle. Secondly, there is an obvious difference between the observations reported by BAKER & BAKER (1936) and KULZER (1958) on the times of mating and birth in this bat in the wild.

The purpose of this paper is to report the findings of a two-year study of the breeding ecology of *R. aegyptiacus* living at latitude 0° 22′ S. with the view of filling the gaps just mentioned as well as discussing matters connected with the whole question of seasonal breeding in the tropics and the environmental factors that may be involved.

All the 733 bats that were examined in the course of this study came from caves situated between Lakes Victoria and Nabugabo in Masaka District, Uganda. The actual locality, Kasokero, latitude 0° 22′ S. and longitude 32° E. lies on the edge of Jubiya Forest Reserve which is almost certainly an important source of food for this frugivorous bat. Here the bats appear to be resident as there was no single month when they were found to be absent. They were always present in thousands, covering the roof and walls of the caves, mostly at the high levels. The caves are very accessible and, for most of the day, are well lit. One of them is about 20 feet high at the centre of the entrance, about 200 feet from this point to the back and about 50 feet across the entrance. It gets narrower towards the back wall. The floors are covered with about one foot thick of guano which suggests that these bats have been in these caves for a long time.

Thus *R. aegyptiacus* is a cave dwelling bat. Elsewhere in Uganda it was found in a cave with an understream in the Maramagambo Forest and in the caves of Mt. Elgon. According to ANDERSON (1912), this bat has a very wide distribution. In Africa, it is found between Angola and Egypt. Outside Africa, it occurs in Syria and Palestine. Information on its breeding may thus vary according to the provenience of the material but this is not known.

Material and Methods

By raising a mist net held between two poles across the entrance of the cave, it was easy to trap and recover many bats in a short time. These bats are very restless in their caves and on being approached, many attempt to leave the caves and alight in the trees in the immediate neighbourhood where they continue to make incessant noise. They are thus easily caught in the net both on their way out and on attempting to return into the cave. Once they were disturbed, there was so much flight to and from that even with a hand net, it was always possible to catch many bats. The material thus obtained was taken to the laboratory for examination.

In the laboratory the bats were killed with chloroform. Then they were weighed, measured and dissected. Information on their weight, the length of the forearm was, as shown below, useful in ascertaining growth rates and attainment of sexual maturity. The adult female bats were examined for pregnancies and where these occurred, the foetuses were dissected and weighed. Information thus obtained over each year elucidated the female sexual cycle (Fig. 4). To elucidate the male sexual cycle, both testes of each adult bat were dissected out and weighed fresh. The length of the epididymis equal to that of the corresponding testis was always included. The mean monthly weights of the testes of the adult bats were plotted to show how they varied at different times of the year (Fig. 4).

Results

Growth and sexual maturity

Figures 1 and 2 are growth curves of the male and female bats respectively, based on the length of the forearm and the body weights. The similarity between the two curves suggests the same rate of growth in the two sexes. On the criteria of body weight and length of forearm, both sexes appear to attain the adult size at the body weight of 90 gm. and the forearm length of 90 mm. ANDERSEN (1912) gives a minimum of 88 mm. and a maximum of 99 mm. for length of forearm. There was no single pregnant female bat in this sample which weighed under 90 gm. excluding the foetus. It would therefore seem reasonable to conclude that an adult bat capable of reproduction must have at least, a forearm length of 90 mm. and a body weight of 90 gm. However, I found a few male bats fulfilling these conditions but with extremely tiny testes compared to those that obviously had larger testes undergoing active spermatogenesis. The males may therefore have to be somewhat larger at sexual maturity. On the whole, by taking the criteria just outlined into account, it was possible to separate juvenile bats from the adult ones as it was necessary for the construction of Table 1.

Births occurred in March and September within this colony. Fig. 3 is a growth curve of the bats based on the length of the

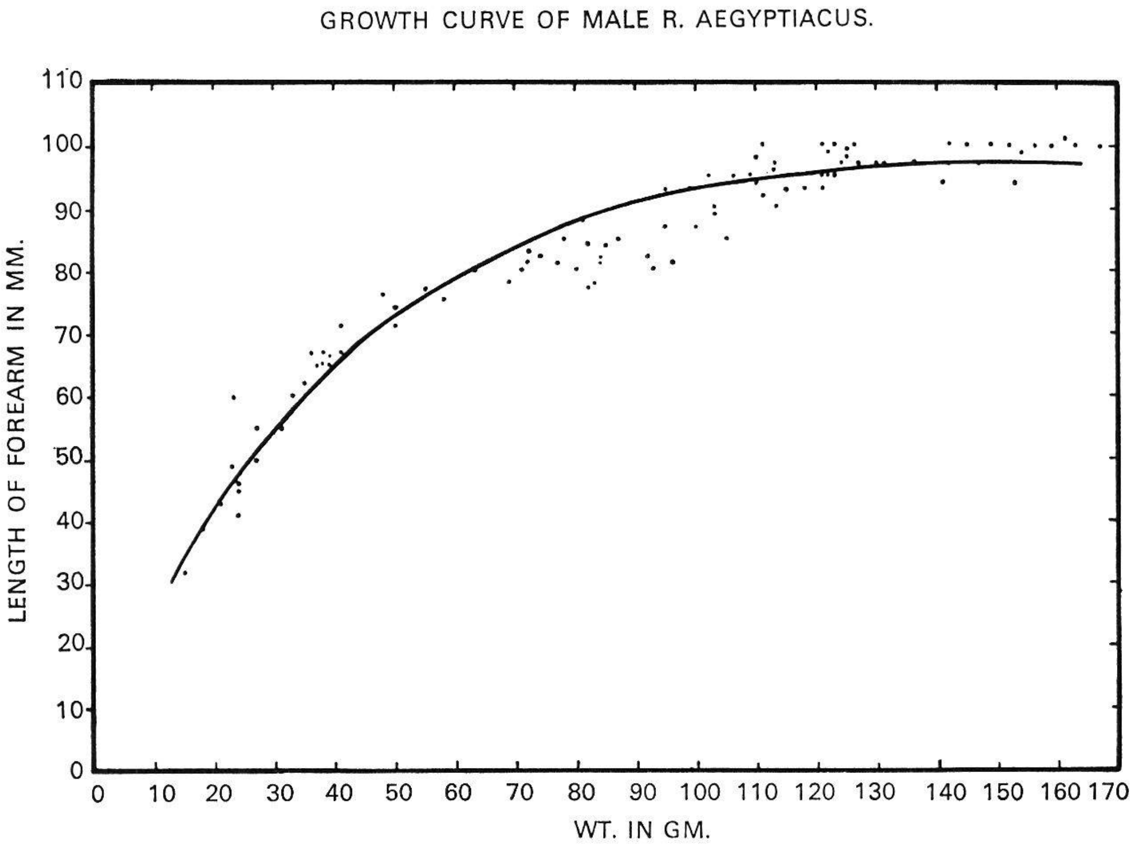

GROWTH CURVE OF MALE R. AEGYPTIACUS.
LENGTH OF FOREARM IN MM.
WT. IN GM.
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170

Fig. 1

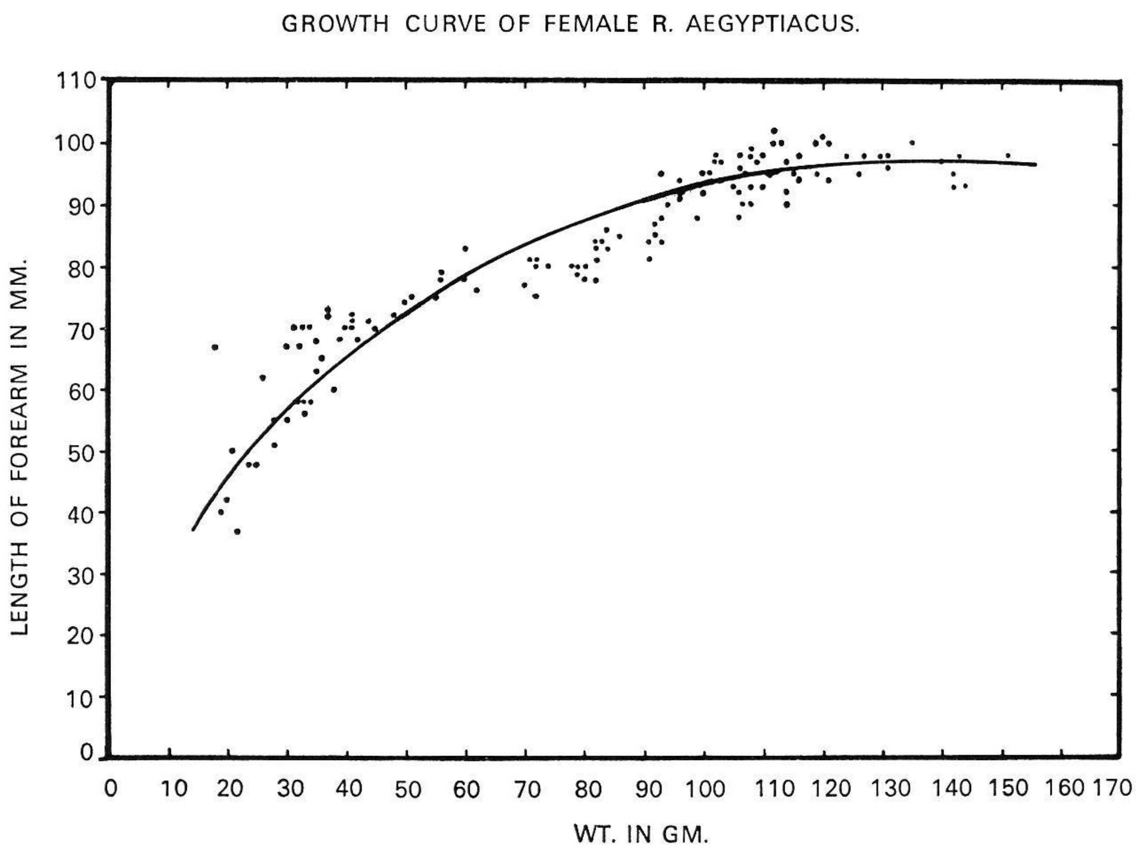

GROWTH CURVE OF FEMALE R. AEGYPTIACUS.
LENGTH OF FOREARM IN MM.
WT. IN GM.
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170

Fig. 2

forearm commencing with the newly born bats in March. It can be seen that it takes about 9 months for a newly born bat to attain the adult length of forearm of 90 mm. The development during the first four months is very rapid but the pace slows down considerably after that. Can the 9-month-old bats be said to be sexually mature and therefore ready to breed? This would be unlikely since it would not fit into the breeding rhythm of the bat as shown in Fig. 4. It would therefore appear that a whole year at least, would have to elapse between birth and attainment of sexual maturity.

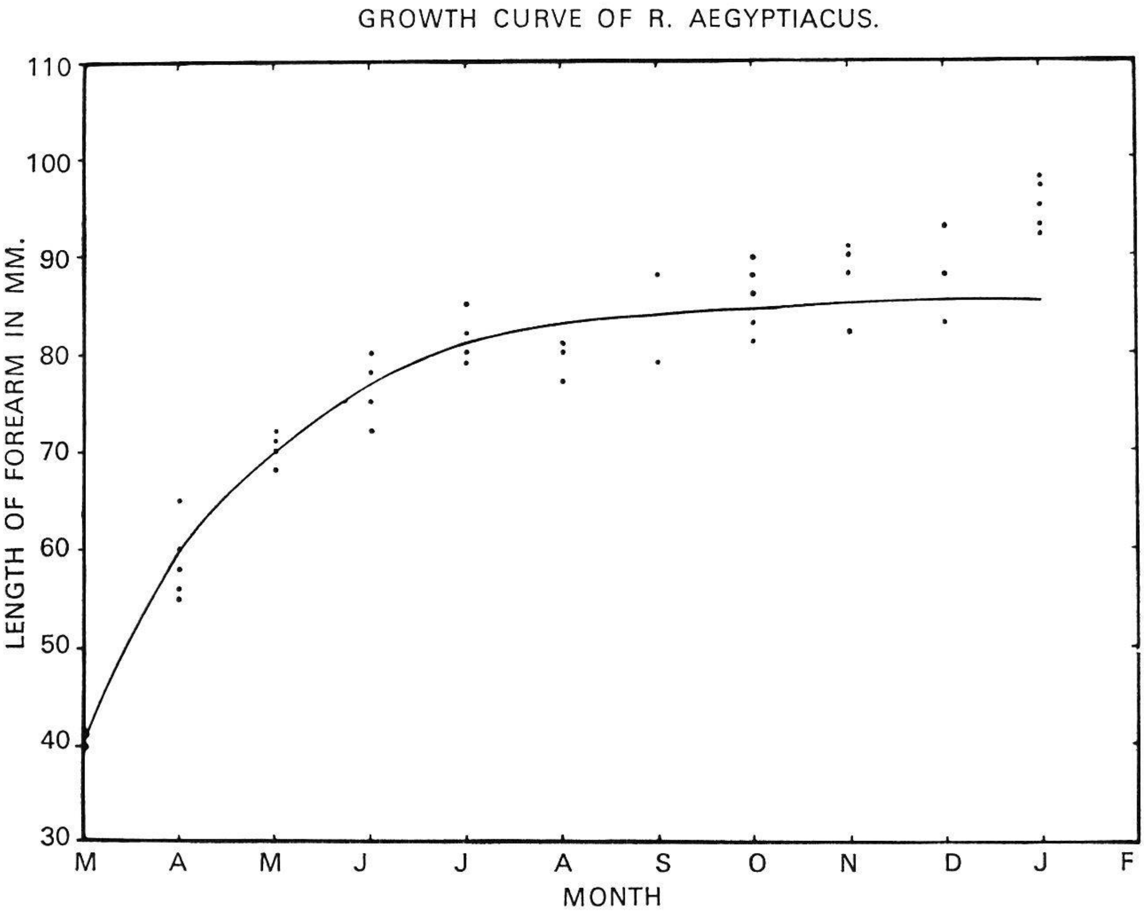


Fig. 3

The male sexual cycle

In Fig. 4 are plotted the mean fresh weights for two consecutive years of the testes of the adult bats for each month. Histological investigation of the relative abundance of spermatozoa in representative testes of the adult bats by OGWANG (1967, unpublished) showed two peaks. He found that there was no time in the year when spermatozoa were wanting and that they were most abundant when the testes were heaviest and least abundant at the minimal testicular weight. In other words, the pattern of variation in sperm abundance conforms to the pattern of the weight of the testes. When the testes weighed least, the seminiferous tubules appeared shrunk and almost spent with only a few rows of spermatocytes remaining. The testicular interstitial tissues also appeared small. At the maximum weight of the testes, on the other hand, the seminiferous tubules as well as the epididymides appeared fully extended and their lumens filled with spermatozoa. This state of affairs is not peculiar to *R. aegyptiacus* but has been observed in other fruit bats such as *Pteropus geddiei* MacG. (BAKER, 1936) and *Eidolon helvum* Kerr (MUTERE, 1967). In the latter case, histological evidence was produced to show that such peaks in the testicular weight and the corresponding sperm abundance occurred at the time of copulation. Thus copulation in *R. aegyptiacus* may be expected to take place at the same time.

It is clear then that the testes of the adult bats undergo a cycle with two peaks; one in April and the other in September. The number of bats involved per month, with respect to the mean weight of the testes of the adult bats only, varied from 7 to 24. The lowest mean weight of the testes was 0.9 ± 0.1 gm. while the highest was 3.5 ± 0.5 gm. The gaps in Fig. 4 mean that no collections were made in the months when they occur.

The female sexual cycle

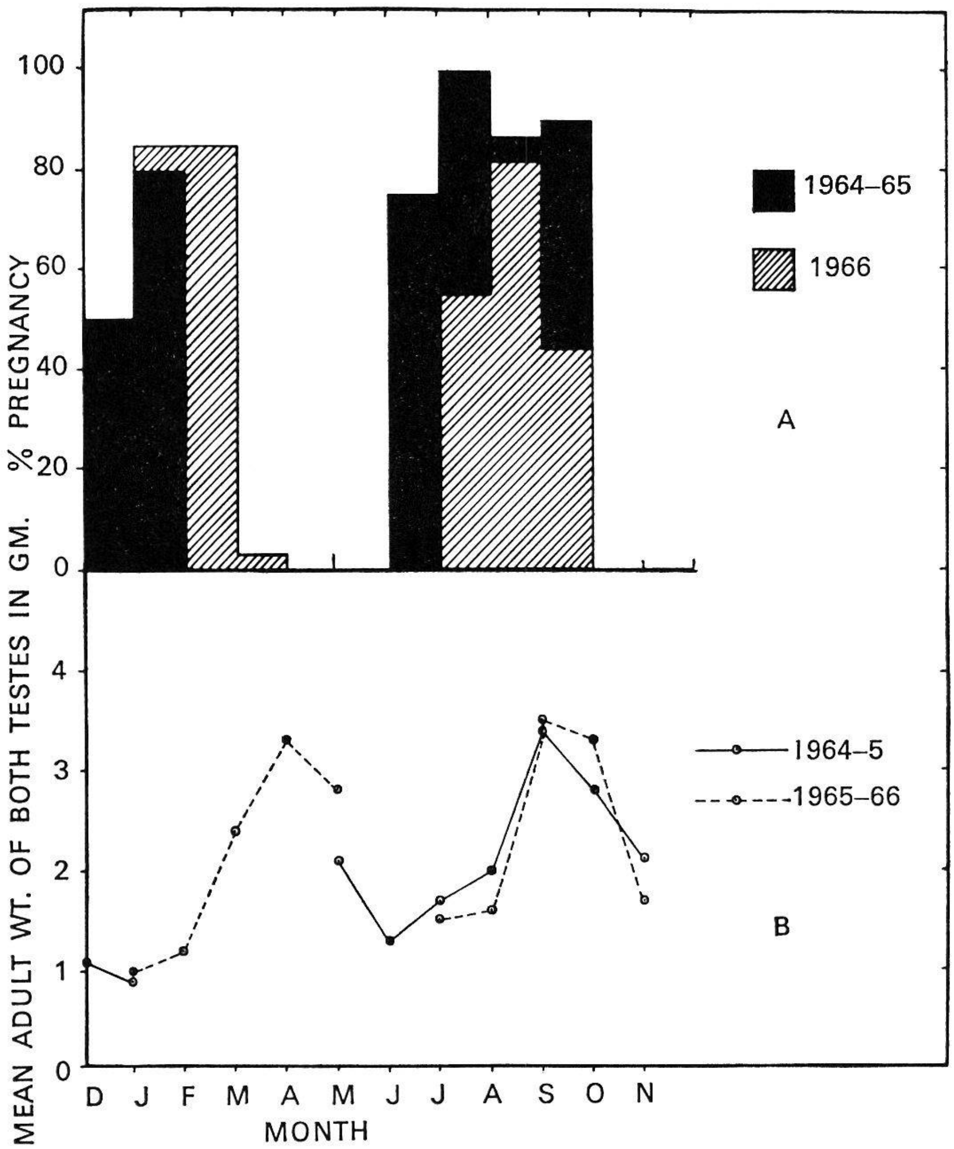
It is obvious from Fig. 4 that *R. aegyptiacus* has a bimodal breeding pattern. The only other fruit bats studied and all of which are tropical have a single breeding season in the year.

As in most bats, *R. aegyptiacus* has a bicornuate uterus and new embryos which occur in either horn with about the same frequency are in evidence in December last until March during which month births take place. There is then a break of two months which is followed by the June pregnancies which last until September when the second batch of births takes place. Only a single young is born to each bat.

Thus *R. aegyptiacus* has a bimodal annual breeding pattern. This is something new among the frugivorous bats for no single worker has reported it previously. It contrasts with *Pteropus geddiei* (BAKER, 1936), *Eidolon helvum* (MUTERE, 1967) and *Pteropus giganteus* (MARSHALL, 1947) all of which are tropical and have a single breeding season per year. Bimodal breeding has also been demonstrated in a tropical free-tailed insectivorous bat, *Tadarida (Mops) condylura* A. Smith (MUTERE, 1967).

The gestation period at either breeding season lasts for four months. The lowest weight of a newly born bat observed was 18.7 gm. which weight is about one fifth of that of a lactating mother. This observation and others concerning the closure of eyes at birth, the presence of some fur and the milk teeth in the form of spikes is in agreement with what is reported by KULZER (1958).

Since the pregnancy rate at each peak is of the order of 80% (see Fig. 4), each female bat must breed twice a year. This is not incompatible with the observations made here on the maternal behaviour in the cage (see also KULZER, 1958) which have revealed that lactation only lasts six weeks. This period which may even be shorter in the wild, falls well within the two month break between the two breeding seasons.



The sexual cycle of R. aegyptiacus A = Female and B = Male

Fig. 4

Environmental factors affecting the breeding season

Among the environmental factors which are known to affect sexual cycles in vertebrates are light, daylength, temperature, food and rainfall. While these factors may be important in the case of breeding among the arctic and subarctic species (BISSONETE 1930, ROWAN 1929, BAKER & RANSOM 1932 and others), they may not all necessarily apply to the tropical and subtropical regions where climatic conditons are believed to vary but little.

It has already been mentioned that the location of the bats studied here is a forested habitat between two adjacent lakes. The humidity here may therefore be expected to be constantly high and varying but little. However, the rainfall pattern in this locality, as exemplified by the data for Bukakata for 24 years, Fig. 5, a small pier on Lake Victoria and situated very close to the caves, shows two distinct peaks which can be correlated with the bimodal breeding pattern of *R. aegyptiacus.*

Births in *R. aegyptiacus* occur just before the peaks in rainfall. Whether it is the rainfall itself or the saturation deficit that is important, it is not possible to tell from the available information. But one thing that may happen is that the onset of rain may stimulate

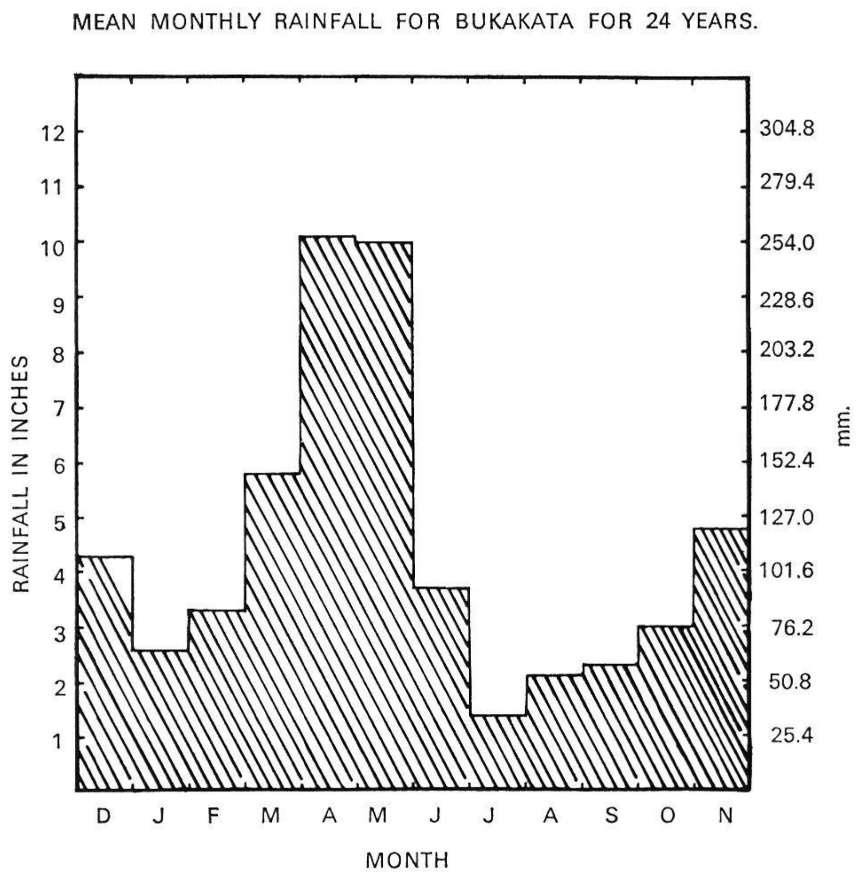


Fig. 5

reproductive activity in the neighbouring forest such that an ample supply of food for the young is certain. Food would therefore be as an ultimate factor in this particular breeding cycle. A definite decision on this matter would require sufficient data on the food of the bat in question but such information is lacking at the moment.

If copulation in *R. aegyptiacus* takes place at the time of the peak mean weight of the adult testes as indicated elsewhere in this paper, then it would appear to coincide with the time of births. A more likely thing to happen is that copulation may actually take place a little later than the time of births, that is, after the attain-

TABLE 1

Age distribution of R. aegyptiacus

				Adult		Juveniles		
Date	Total	Males	Females	Males	Females	Males	Females	% Young
Dec. 1964	19	11	8	7	5	4	3	
Jan. 1965	17	7	10	7	6	0	1	
Feb.	–	–	–	–	–	–	–	
March	–	–	–	–	–	–	–	
April	–	–	–	–	–	–	–	14
May	23	8	15	8	14	0	1	
June	37	23	14	21	10	2	4	
July	16	11	5	10	5	1	0	
August	50	26	24	26	24	0	0	
Sept.	45	24	21	24	21	0	0	
Oct.	28	22	6	15	4	7	2	15.5
Nov.	44	12	32	8	19	4	13	
Dec.	–	–	–	–	–	–	–	
Total	279	144	135	127	104	18	24	
Jan. 1966	40	20	20	18	20	2	0	
Feb.	55	21	34	20	32	1	2	
March	60	26	34	19	21	7	13	28.4
April	52	20	32	11	19	9	13	
May	37	17	20	13	13	4	7	
June	–	–	–	–	–	–	–	
July	48	17	31	16	25	1	6	
August	32	21	11	18	11	3	0	
Sept.	32	14	18	11	17	3	1	26.2
Oct.	48	25	23	16	13	9	10	
Nov.	50	26	24	13	15	13	9	
Total	454	207	247	155	186	52	61	
Grand total	733							

ment of the peak mean weight of the testes of the adult bats. This is a point which could be settled by histological examination of the female reproductive tracts of the adult bats which are expected to have mated. This work has not been undertaken. However, the bimodal pattern in the male sexual cycle also correlated with the rainfall pattern is clearly indicated.

Discussion

The main objective of the Oxford University Expedition to the New Hebrides in 1933–34 was to study the seasonal phenomena under climatic conditions which showed little change throughout the year. The main finding which was based on the study of a fruit bat *(Pteropus geddiei)*, an insectivorous bat *(Miniopterus australis)*, and other animals was that all these species, contrary to expectation, exhibited seasonal breeding.

Since the publication of this work (BAKER 1947), several other examples of seasonal breeding in tropical vertebrates have been reported. Examples of these are the work by MARSHALL (1947) on the fruit bat *Pteropus giganteus*, MARSHALL & HOOK (1960) on the reproduction in the lizard *Agama agama lionatus* Boulenger, and MUTERE (1967) on the breeding of the fruit bat, *Eidolon helvum* Kerr. However, continuous and acyclic breeding in tropical species is also on record. Among the species that exhibit this phenomenon are the frugivorous bat, *Epomophorus anurus* (HERLANT, 1953), the insectivorous bats, *Tadarida (Chaerophon) pumila* (MUTERE, 1967), *Taphozous longimanus* of India (BROSSET, 1962; GOPALAKRISHNA, 1955) and the sanguivorous bat *Desmodus rotundus* of Panama (WIMSATT & TRAPIDO 1952). To this variety of breeding patterns in the tropics comes a third one, the bimodal pattern of which the present report is perhaps the first one among the frugivorous bats. There is an insectivorous bat, *Tadarida (Mops) condylura* A. Smith which also exhibits a bimodal breeding pattern (MUTERE, 1967). Among the tropical birds too, the sparrow *Zonotricha capensis* has been known to exhibit this phenomenon (MILLER, 1962).

Thus the belief that the tropical climatic conditions, as distinct from those in temperate countries, are virtually constant and therefore conducive to continuous breeding can no longer be upheld. Indeed what is found is a variety of situations, a restriction to either one or at most two sharply defined seasons or continuous breeding. It may well be asked whether the climatic conditions in the tropics are as constant as is generally believed. While this constancy may apply generally to such factors as temperature and daylength, it could not apply to rainfall. It is common and proper to talk about dry and wet seasons in the tropics and these, as can be seen in Fig. 5, are quite distinct. The synchrony of the rainfall and the breeding patterns of the animal species so far studied in the tropics and which have already been mentioned above, is such that it is difficult to resist deducing a close relationship between the two phenomena. It would therefore appear pertinent to enquire whether the conclusion by BAKER (1947) that the breeding seasons of the tropical vertebrates in the New Hebrides are controlled by environmental factors not affecting the sense organs or meteorological instruments of man is of universal application in the tropics.

On the other hand, examples of continuous acyclic breeding in the tropics have already been referred to. These conform to the expected continuous breeding under what are generally believed to be unvarying climatic conditions. The fact that, even under such conditions, a variety of breeding patterns emerges, calls for investigation of the individual cases from the point of view of the environmental factors that may be involved. There is as yet no room for generalisations.

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Zusammenfassung

1. Flughunde der Gattung *R. aegyptiacus* wurden zwei Jahre lang in ihrem natürlichen Lebensraum in einer Gegend von 0° 22′ südlicher Breite beobachtet, wobei zwei Fortpflanzungsperioden festgestellt werden konnten.

2. Die erste Fortpflanzungsperiode dauert von Dezember bis März, die zweite von Juli bis Oktober. Die Trächtigkeitsdauer beträgt vier Monate.

3. Es scheint, daß immer nur ein Junges geboren wird. Nach einem Unterbruch von zwei Monaten kann das gleiche Muttertier wieder tragen. Es gibt also pro Jahr zwei Würfe.

4. Die Testikel der adulten Männchen erreichen zum erstenmal im April und zum zweitenmal im September ein Maximalgewicht. Es wird vermutet, daß die Kopulation unmittelbar danach stattfindet.

5. Nach der Geburt wächst das Junge sehr rasch, und nach neun Monaten erreicht es die Größe und das Gewicht eines adulten Tieres, d. h. 90 g Körpergewicht und eine Unterarmlänge von 90 mm. Wahrscheinlich können sich Flughunde von dieser Größe bereits fortpflanzen.

6. Die Geburt findet im März und im September statt gerade kurz vor Beginn der Regenzeiten. Die Regenfälle regen das Wachstum der Vegetation an, und damit ist die Ernährung der Jungen gesichert.

7. Bei den Adult- wie auch bei den Jungtieren war das Verhältnis der Geschlechter 1 : 1.

8. Im zweiten Jahr der Beobachtung schienen die Flughunde doppelt so fruchtbar gewesen zu sein wie im ersten Jahr.

Résumé

1° Deux ans d'étude sur le Chiroptère frugivore *R. aegyptiacus,* vivant sous 0° 22′ de latitude sud, ont révelé un double mode de reproduction.

2° La première période de reproduction a lieu de décembre à mars, la seconde de juillet à octobre. La gestation dure quatre mois.

3° Il semble qu'un seul petit vienne au monde par portée. Après une interruption de deux mois, la même femelle peut vraisemblablement porter une seconde fois. Il y aurait donc deux portées par année.

4° Le poids des testicules des mâles adultes présente deux maxima : le premier en avril et le second en septembre. L'auteur suggère que la copulation de *R. aegyptiacus* a lieu juste après chacun des deux maxima.

5° Après la naissance, le jeune grandit rapidement et en 9 mois il atteint les dimensions et le poids de l'adulte, c'est-à-dire 90 g et 90 mm pour la longueur de l'avant-bras. On pense que les chauves-souris de cette dimension sont capables de se reproduire.

6° La naissance a lieu en mars et en septembre juste avant le début des pluies. Celles-ci stimulent le développement de la végétation qui assure une ample réserve de nourriture pour les jeunes.

7° A l'époque de cette étude, le rapport des deux sexes dans les populations juvénile et adulte semblait être de 1 : 1.

8° Au cours de la seconde année de cette étude, les chauves-souris semblent avoir été deux fois plus prolifiques qu'au cours de la première année.