Seasonally monoestrous reproduction in the molossid bat, *Tadarida aegyptiaca* from low temperate latitudes (33°S) in South Africa

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A histological study of reproduction in Egyptian free-tailed bats (*Tadarida aegyptiaca*) from the Eastern Cape Province of South Africa (*c.* 33°S) showed that females were seasonally monoestrous. Copulation, ovulation and fertilization occurred in August, at the end of winter, and births in December, after a four-month pregnancy. These results are compared with those of other molossid bats from lower latitudes in Africa. We conclude that the monoestrous habit of the Egyptian free-tailed bat at 33°S may be due to its relatively long pregnancy, and to the short summer period during which minimum temperatures are high enough to ensure an abundance of nocturnal flying insects.

'n Histologiese ondersoek van Egiptiese losstertvlermuise (*Tadarida aegyptiaca*) van die Oostelike Kaap Provinsie van Suid-Afrika (*c.* 33°S) toon dat dear slegs 'n enkele estrus per jaar is en dat dit seisoensgebonde is. Paring, ovulasie en bevrugting vind plaas gedurende Augustus, aan die einde van die winter, met geboortes gedurende Desember na 'n dragtigheidsperiode van vier maande. Die resultate word vergelyk met die van ander molossiede vlermuise van laer breedtegrade in Afrika. Ons maak die gevolgtrekking dat die enkele estrus van Egiptiese losstertvlermuise teen 33°S verklaar kan word deur 'n lang dragtigheidsperiode en die kort tydperk gedurende die somer wanneer die minimum temperature hoog genoeg is om te verseker dat daar 'n oorvloed vlieënde naginsekte is.

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Free-tailed bats of the Family Molossidae occur from Southern Europe and Asia, throughout the islands of the Pacific Rim to Australia, and throughout Africa, excluding the Sahara. In the New World, their distribution stretches from central USA to Argentina and Chile (Hill & Smith 1984). The family has radiated widely in Africa, with 32 species south of the Sahara (Hayman & Hill 1971; Corbet & Hill 1991) and 14 species south of the Limpopo river (Smithers 1983). The Angolan free-tailed bat (*Tadarida condylura*), the little free-tailed bat (*T. pumila*) and the Egyptian free-tailed bat (*T. aegyptiaca*) have extensive geographic ranges throughout Africa (Smithers 1983) and are thus suitable species with which to study the interactions between latitude, climate and reproduction. Considerable comparative data are available for *T. condylura* and *T. pumila* from a wide range of latitudes (10°N–25°S) which show that *T. pumila* responds to increasing latitude by reducing the number of reproductive cycles in a season, while *T. condylura* always has two pregnancies per season, and responds to increasing latitude by reducing the interval between pregnancies (Harrison 1958; Marshall & Corbet 1959; Kock 1969; Smithers 1971; Mutere 1973a; McWilliam 1976 in Happold & Happold 1989; Smithers & Wilson 1979; O'Shea & Vaughan 1980; Ansell 1986; van der Merwe, Rautenbach & van der Colf 1986; van der Merwe, Giddings & Rautenbach 1987; and see Happold & Happold 1989, 1990 for reviews). There are no data for these species from more temperate latitudes in Africa, and the available information on reproduction of the Egyptian free-tailed bat from Africa is meagre. In an attempt to fill this gap in our knowledge of molossid reproduction, we describe here the reproductive cycle of the Egyptian free-tailed bat from 33°S in the Eastern Cape Province of South Africa, and discuss the relationship between latitude, climate and reproduction.

Materials and Methods

Although the Egyptian free-tailed bat is common in the Eastern Cape Province, its habit of roosting in exposed cliff faces and the roofs of houses and churches made collection difficult. It was not possible to collect sufficient specimens in one year and small numbers of adult specimens were collected monthly from January 1991 to December 1993 (Table 1). In order to establish whether reproductive maturity was reached in the first year, a small number of young bats (adult size but with unworn teeth) were collected in April, June, July, August and October. All specimens were collected as they emerged from roosts in the Grahamstown (33°20'S, 26°30'E) and Alexandria (33°40'S, 26°25'E) regions of the Eastern Cape Province of South Africa.

Table 1 Summary of the monthly samples of adult Egyptian free-tailed bats

Month	Sample size: Female	Male
January	3	3
February	4	3
March	4	7
April	3	3
May	4	4
June	3	3
July	3	4
August	3	4
September	4	5
October	5	4
November	4	4
December	4	3

Specimens were killed with an overdose of sodium pentobarbitone (Euthanase; Centaur Labs, Johannesburg), weighed to 0,1 g and the forearm measured to 1 mm. Reproductive organs were removed, fixed for about one month in Bouin's fluid, and thereafter prepared for light microscopy using standard techniques. Sections (5 μm) were stained with Ehrlich's haematoxylin and counterstained with eosin. Testes and attached epididymides and the male reproductive accessory gland complex were weighed (to 1,0 mg) before fixation. Changes in spermatogenic activity were assessed by examining 100 randomly selected sections through seminiferous tubules of each testis and classifying each section as being either spermatogenically inactive (seminiferous epithelium lined by spermatogonia and Sertoli cells only), or in early spermatogenesis (spermatogonia and spermatocytes present but no spermatids), or in late spermatogenesis (spermiogenesis occurring with spermatozoa in the lumen of the seminiferous tubules and the epididymides). A bat was placed into a specific category if more than 50% of the seminiferous tubules were in a particular condition. The diameter of 20 seminiferous tubules per testis and the height of the seminiferous epithelium in the same 20 tubules was measured with an optical micrometer for each specimen. Changes in female reproductive activity were qualitatively assessed by recording the presence or absence of secondary and Graafian follicles and corpora lutea in each ovary, the structure of the uterine wall, the presence or absence of a conceptus, the developmental stage of the conceptus, and whether lactation was occurring.

Climatic data were obtained from the Rhodes University weather station in Grahamstown.

Throughout this report data are presented as mean ± 1 *S.D.* Means have been compared using one way ANOVA and the Tukey multiple range test.

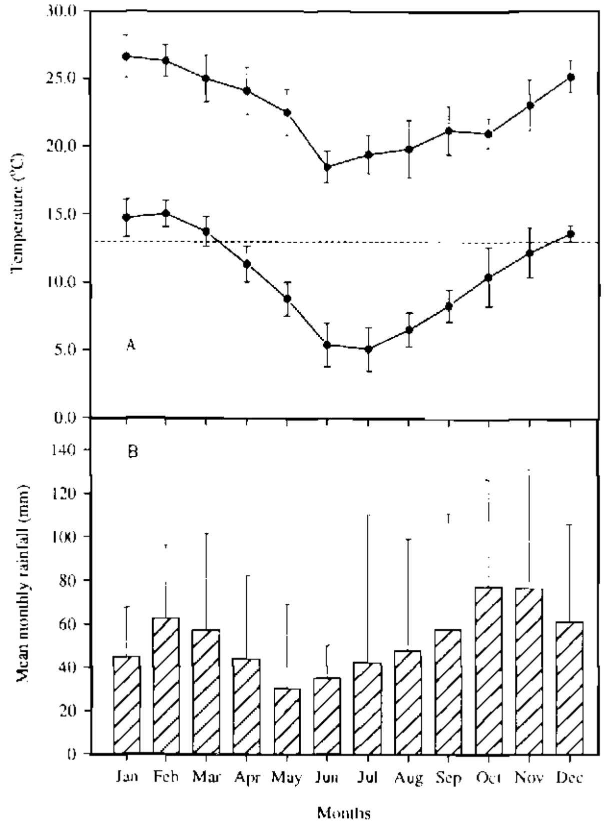

Figure 1 Monthly changes in mean maximum and minimum temperatures (Figure 1A) and rainfall (Figure 1B) for the period 1984 1994 recorded at the Rhodes University weather station, Grahamstown. The horizontal line in 1A is at 13°C.

Results

The male reproductive tract comprised paired abdominal testes and associated epididymides which remained within the abdominal cavity throughout the year. The male reproductive accessory complex consisted of paired ampullary glands and seminal vesicles, a compound prostate gland and bilobed urethral gland.

The climate of the study area is strongly seasonal with a single hot season from October to April and cooler season from May to September (Figure 1). Seasonality in rainfall is masked by the tremendous variability but typically the warm summer months are wetter and the cool winter months drier (Figure 1B).

Spermatogenesis commenced in February (Figure 2) with the appearance of primary spermatocytes in the germinal epithelium, and during February and March more than 90% of all seminiferous tubules were in early spermatogenesis. Between April and June there was an increase in the number of seminiferous tubules in which spermiogenesis was occurring (April 12%; June 87%) and in July more than 90% of all seminiferous tubules were in late spermatogenesis. Spermatozoa were first released to the epididymides in July and remained stored in the cauda epididymis until September. In August and September the seminiferous tubules regressed and from October to January they were spermatogenically inactive. The cycle of spermatogenic activity was mirrored by changes in testis mass, the diameter of seminiferous tubules (not illustrated) and the height of the seminiferous epithelium, all of which were significantly greater during late spermatogenesis (July and August) than during spermatogenic inactivity (October to January; $p < 0,05$; Figure 2). The components of the reproductive accessory complex were secretorily active between July and September, and inactive during the remainder of the year. The mass of the accessory gland complex was significantly greater during the period of activity (July to September) than at any other time of the year ($p < 0,001$; Figure 2).

The uterus of the Egyptian free-tailed bat was bicornuate and in adults ($n = 44$), the right uterine horn (3,1 × 1,0 mm) was significantly larger than the left (1,9 × 0,9 mm; $p < 0,01$), and the right ovary, (1,8 ± 0,2 mm) was significantly larger than the left ovary (1,4 ± 0,2 mm; $p < 0,05$).

Follicular development was typically mammalian and developmental stages up to the secondary follicle occurred in both ovaries. Large secondary and Graafian follicles, and the corpus luteum occurred in the right ovary only. Follicular development began in April with the appearance of developing secondary follicles in both ovaries. Small Graafian follicles occurred in the right ovary in May and by July preovulatory Graafian follicles were present. Coinciding with this period of follicular development, the uterine endometrium underwent a period of development in which it became increasingly glandular and vascularized. Copulation, ovula-

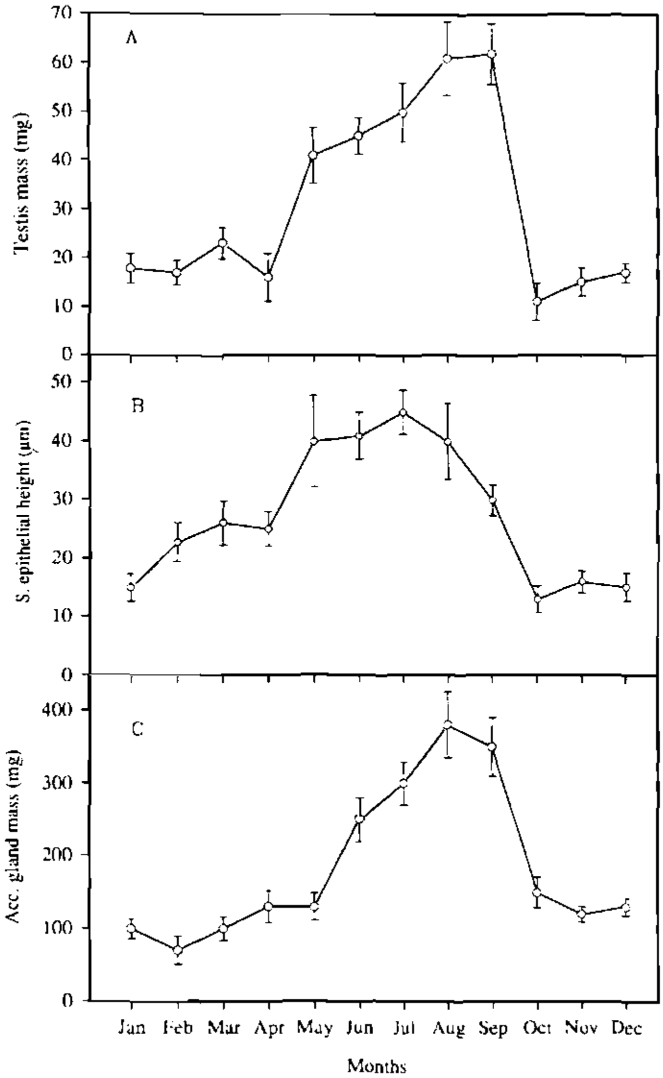

Figure 2 Monthly changes in tests mass (2A), height of the seminiferous epithelium (2B) and mass of the male reproductive accessory complex (2C) of the Egyptian free-tailed bat. Data are presented as means ± 1*S.D.*

tion and fertilization occurred in August when all three specimens had spermatozoa throughout the female reproductive tract and two had a newly formed corpus luteum in the right ovary. From September to December all females were pregnant with a corpus luteum in the right ovary. A second period of follicular development, which did not culminate in ovulation, occurred between October and December when developing Graafian follicles were present in the right ovary. Of the four specimens collected in December three were in late pregnancy and one was lactating. Lactation continued in January and by February females were in anoestrus. There was no evidence of a period of reproductive delay during pregnancy.

Young males (less than one year old) collected in April, June and July (n = 1 per month) were reproductively inactive, and young females collected in August (1) and October (2) were pregnant.

In summary, the Egyptian free-tailed bat is a monoestrous, monotocous seasonal breeder in which spermatogenesis and follicular development occur during winter. Copulation, ovulation and fertilization occur in August (late winter) and births, in December after a gestation of about four months.

Discussion

Reproductive asymmetry is common among the Chiroptera (Jerrett 1977; Wimsatt 1979 for review) and the dextral functional asymmetry described here for the Egyptian free-tailed bat is typical of the Molossidae (Krutzsch & Crichton 1985; Happold & Happold 1989; Cotterill & Fergusson 1993). The results from the present study, which suggest that male Egyptian free-tailed bats reach sexual maturity, in their second year while females are sexually mature during their first year are similar to those reported for other molossids (Short 1961; Krutzsch & Crichton 1985; Crichton & Krutzsch 1987).

Most bats from temperate latitudes are monoestrous, and it is widely accepted that births, at all latitudes, are timed to coincide with increased insect abundance during summer (Rautenbach, Kemp & Scholtz 1988; Happold & Happold 1990). If this is the case, then populations at different latitudes, exposed to different day lengths, climates and patterns of food abundance, might be expected to show different patterns of reproduction. Indeed, in most cases where sufficient comparative data are available, this is so, and such reproductive flexibility is perhaps best developed in the molossids (Happold & Happold 1990). In temperate latitudes, members of the family are monoestrous and monotocous and reproduction is seasonal and synchronized (Krutzsch 1979; Jerrett 1979; Crichton & Krutzsch 1987; Krutzsch & Crichton 1987). By contrast in subtropical and tropical latitudes, the reproductive season is longer, the species are polyoestrous and the synchronicity may be lost (Happold & Happold 1990). The only exception to this appears to be *Otomops martiensseni* which is a monoestrous, seasonal breeder in the tropics (Mutere 1973b). The single characteristic that appears unaffected by changes in latitude is litter size and most molossids, irrespective of latitude are monotocous (Mutere 1973a,b; Happold & Happold 1990). Reproduction in the little free-tailed bat is aseasonal in Ghana (10°N), with up to five pregnancies per year (McWilliam 1976 in Happold & Happold 1989), and is aseasonal in equatorial Uganda, where although pregnant females are present in all months, there is some synchronization of pregnancy and three periods of birth (Mutere 1973b; Marshall & Corbet 1959; and see Happold & Happold 1989 for review). At both these localities rain falls throughout the year and the aseasonal reproduction is presumably a response to a lack of seasonality in the abundance of food. The response of the little free-tailed bat to changing rainfall, and presumably insect abundance, is clearly seen in Kenya (2°S) where there are two quite short rainy seasons and two synchronized breeding seasons (O'Shea & Vaughan 1980). In subtropical South Africa (25°S), where there is an eight-month long hot, wet summer, reproduction is seasonal with three consecutive pregnancies (van der Merwe *et al.* 1986, 1987). The Angolan free-tailed bat shows a quite different type of variability with two pregnancies throughout its range. In Uganda and Kenya the interbirth interval is three to four months and births coincide with peaks in rainfall. By contrast in Malawi, where there is one long rainy season, the interbirth interval is one month, allowing two pregnancies to fit into the breeding season. A similar pattern of reproduction is seen in the large Madagascar free-tailed bat (*Tadarida fulminans*) except that while one pregnancy coincides with the wet season, the other occurs during the dry season (Cotterill

& Fergusson 1993). These three African molossids may experience a post-partum oestrus under certain conditions, allowing them to complete two or three pregnancies in a single breeding season.

The limited available data for the Egyptian free-tailed bat indicate that births occur in summer (Rautenbach 1982; Smithers 1971; Smithers & Wilson 1979; Herselman & Norton 1985) and results from the present study confirm this. Furthermore, our results show that at low temperate latitudes in Africa, there is no post-partum oestrus and only one pregnancy per year. As such, the cycle is similar to that reported for the same species from India (22°N) where mating occurs in May/June and births in September after a 77–90 day pregnancy (Kashyap 1980). The seasonal monoestry seen in the Egyptian free-tailed bat at 33°S in South Africa is very different from the seasonal polyoestry, with as many as three consecutive pregnancies, seen in the little free-tailed bat at 24°S in South Africa. The little free-tailed bat is smaller and has a shorter gestation (11 g; 60 days, van der Merwe *et al.* 1986) than the Egyptian free-tailed bat (15 g; about 120 days, present study), thus predisposing the little free-tailed bat to polyoestry. However, it is just as likely that the climate of the two areas plays an important part in moulding the patterns of reproduction. At 24°S in the Transvaal lowveld, the mean minimum temperature during the eight month breeding season is always above 13°C, and for four months when 78% of births occur (November to February), it is between 18 and 21 °C (van der Merwe *et al.* 1986). At 33°S mean monthly minimum temperatures are above 13°C for four months only (December–March; Figure 1A). It has been suggested that the prolonged period of relatively high mean minimum temperatures at 24°S in South Africa provides a long summer breeding season, and this, in conjunction with the occurrence of a post-partum oestrus, ensures that the little free-tailed bat can fit three pregnancies into the summer (van der Merwe *et al.* 1986, 1987). It seems reasonable, therefore, to suggest that the seasonally monoestrous habit of the Egyptian free-tailed bat in South Africa may be explained in terms of its long gestation and the relatively short period during which minimum temperatures are high enough to ensure an abundance of nocturnal, flying insects.

In conclusion, our results clearly show that with increasing latitude in Africa, reproduction in molossid bats changes from aseasonal to seasonal and from polyoestrous to monoestrous. It has been suggested that the wide distribution of molossid bats may, in part, be due to their reproductive flexibility (Happold & Happold 1989, 1990) and the data from the present study further support this.

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