Short communications

Reproductive strategy of the Egyptian free-tailed bat, *Tadarida aegyptiaca,* from a subtropical latitude (25°S) in South Africa

Anja le Grange*, Mac van der Merwe & Márthan Bester

Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002 South Africa

Received 12 April 2010. Accepted 11 September 2010

Free-tailed bats (Molossidae) are widely distributed in Africa and exhibit considerable reproductive flexibility. The Egyptian free-tailed bat, *Tadarida aegyptiaca,* is one of the most widespread of the molossids and is therefore an excellent model to study the variation in reproduction through latitudinal changes. Bats were collected during 2008 and 2009 from Pretoria (25°S), South Africa. In males, spermatogenesis was already underway in January (summer) and spermatozoa were first noted in the epididymis during May (late autumn), where they are stored until the end of September. From September, the testes showed little spermatogenic activity and possibly remained quiescent until early summer. In females, follicular development started prior to January with large Graafian follicles present in June. Ovulation, copulation and subsequent fertilization occurred in late August (spring). When compared to the same species from a low temperate latitude (33°S) it is apparent that spermatogenesis and follicular development were initiated earlier in the year at 25°S. We propose that the seasonal monoestry displayed by *T. aegyptiaca* at 25°S may be the norm throughout their distributional range and that a latitudinal difference of just eight degrees could influence the timing of events in the reproductive cycle of a free-tailed bat.

Key words: Reproduction, Egyptian free-tailed bat, *Tadarida aegyptiaca.*

Variations in the reproductive patterns of bats are generally linked to major differences inlatitude and the influence latitude has on seasonal resource distribution (Racey & Entwistle 2000). In temperate regions, where periods of resource abundance are usually short, the majority of chiropterans hibernate and therefore display a seasonal monoestrous breeding pattern (Gustafson 1979; Oxberry 1979). In tropical and subtropical regions, where environmental conditions are less variable and periods of resource abundance are longer, there is little need for hibernation (Vivier & Van der Merwe 1997). The reproductive patterns of these non-hibernating bats range from restricted seasonal monoestrous and seasonal polyoestrous through to aseasonal polyoestrous (Jerret 1979; Happold & Happold 1990). Furthermore the reproductive patterns of individual species have been shown to vary across their latitudinal range (Van der Merwe *et al.* 1986; Vivier & Van der Merwe 1997; Racey & Entwistle 2000). This reproductive flexibility is especially well established in African free-tailed bats (Happold & Happold 1990; Bernard & Tsita 1995).

Free-tailed bats of the family Molossidae occur in temperate, subtropical and tropical regions almost worldwide (Bernard & Tsita 1995). They occur extensively in Africa, and in southern Africa the family is represented by six genera and 14 species (Skinner & Chimimba 2005). Their extensive ranges and apparent reproductive flexibility make African molossids excellent species in which to study the effect changes in latitude have on reproduction (Bernard & Cumming 1997). Despite this, available information on reproduction in molossids from Africa is very limited (Vivier & Van der Merwe 1996, 1997, 2001).

The Egyptian free-tailed bat, *Tadarida aegyptiaca,* is a small (~16 g) molossid that has one of the most widespread distributions of all African bats (Srinivasulu & Srinivasulu 2007). Its range extends from the Western Cape in South Africa, throughout Africa, and as far north as the West Bengal province in eastern India (Herselman & Norton

---

*Author for correspondence.
E-mail: alegrange@zoology.up.ac.za

1980; Srinivasulu & Srinivasulu 2007). These bats are gregarious and colonies roost in caves, rock crevices, tree cavities as well as in roofs and any crevice in brickwork (Skinner & Chimimba 2005). Recently Cory Toussaint *et al.* (2010) demonstrated that 'prolonged, multiday heterothermic bouts' occur in the males of this species during winter in Pretoria, South Africa (25°S). It has also been suggested that the females of this species may undertake seasonal movements to maternity colonies where conditions are more favourable for breeding, however very little work has been done to establish the exact location of these colonies (Herselman & Norton 1980; Skinner & Chimimba 2005; Cory Toussaint *et al.* 2010). The aforementioned findings are sure to have an impact on the reproductive strategy of *T. aegyptiaca.* Regardless of these findings there is only one detailed study on the reproduction of the Egyptian free-tailed bat from Africa to date, this being from a low temperate latitude (33°S) (Bernard & Tsita 1995). *Tadarida aegyptiaca's* extensive range, heterothermy and possible breeding migrations make it an ideal model system to evaluate the interactions between latitude, climate and reproduction.

The aim of this study was, therefore, to investigate the reproductive biology of *T. aegyptiaca* in a high latitude (25°S) subtropical environment through a histological examination of spermatogenesis in males and follicle development in females.

This study was conducted at the Groenkloof educational campus (25°46′9″S, 28°12′33″E) of the University of Pretoria in Pretoria, South Africa. The *Tadarida aegyptiaca* colonies at Groenkloof typically roost in the vertical gaps between roof overhangs and outer walls. Bats were captured with a mist net (4 –10 m) during June, September, October 2008 and January, March and May 2009. Following capture the bats were transported to the main campus of the University of Pretoria for processing.

Bats were euthanased with an overdose of halothane and the testes and ovaries were removed. Material was fixed in Bouin's fluid for 24 hours and then rinsed and stored in 70% ethanol. Following standard paraffin-wax embedding, tissues were serially sectioned at 7 μm, mounted on glass slides, and stained with Ehrlich's haematoxylin and counterstained with eosin (Coetzee & Van der Merwe 1992).

Changes in male reproductive condition were determined by measuring the diameter (from the outer boundaries of the basement membrane) of ten randomly selected epididymal and seminiferous tubules for each specimen, using an eyepiece micrometer (×10 Kellner). Spermatogenic activity was qualitatively assessed according to the stage of spermatozoid formation as described in Jungueira & Carneiro (2003).

Changes in female reproductive activity were assessed qualitatively by noting the presence or absence of primary follicles, secondary follicles, Graafian follicles, corpora lutea and the presence or absence of a conceptus. When present, the largest diameter of any primary, secondary and Graafian follicles, together with the oocyte, was measured for each specimen. Since follicles and oocytes are mostly ovoid the diameter was calculated by halving the sum of two measurements taken at right angles to one another to include both the greatest length and width. Follicle diameter was taken from the outside boundaries of the stratum granulosum and oocyte diameter from the inner boundaries of the zona pellucida.

One-way ANOVA and Tukey *post hoc* analysis was used to test for differences between sampling months and multiple regression analyses were performed to test for relationships. Climatic data were obtained from the South African Weather Bureau.

The climate of the study area is clearly seasonal with a single hot season from September through to March (spring/summer) and a cooler season from April to August (autumn/winter). There is also strong seasonality in the rainfall pattern with most rainfall between November and March (Fig. 1).

In males, spermatogenesis was already in progress during January (summer) with primary spermatocytes present in the seminiferous tubules (Fig. 2A). During March (early autumn) there was an increase in the number of primary and secondary spermatocytes. Spermiogenesis started between March and May since many seminiferous tubules contained spermatids and spermatozoa during May (Fig. 2B). Spermatozoa were first noted in the epididymis in May, where they were stored in the cauda epididymis until the end of September (spring) (Fig. 2C). In September the seminiferous tubulus started to become quiescent with few spermatozoa present in some of the seminiferous tubules (Fig. 2D). In October only spermatogonia were present. Testes possibly remained quiescent until later in the summer.

This pattern of spermatogenic activity was

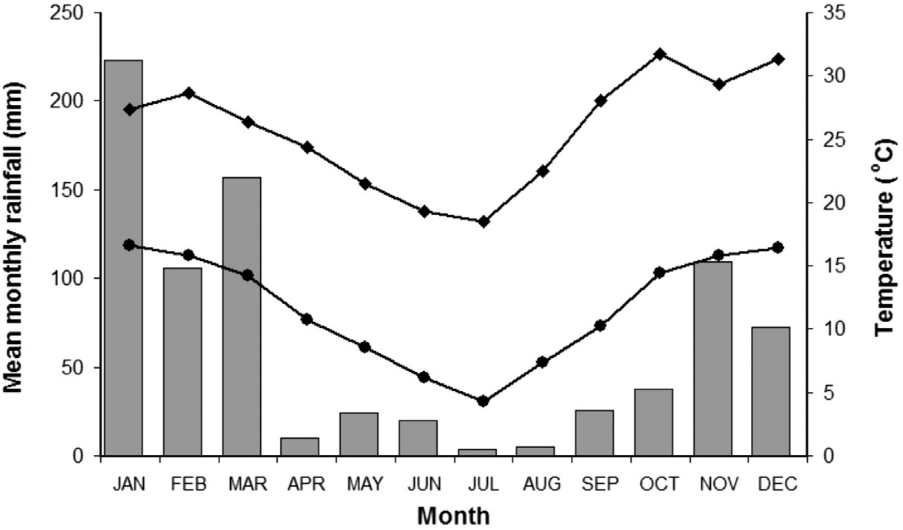

Fig. 1. Mean monthly minimum (●) and maximum (◆) temperatures and mean monthly rainfall (■) for 2008 and 2009 (UNISA weather station, Groenkloof, Pretoria, South Africa).

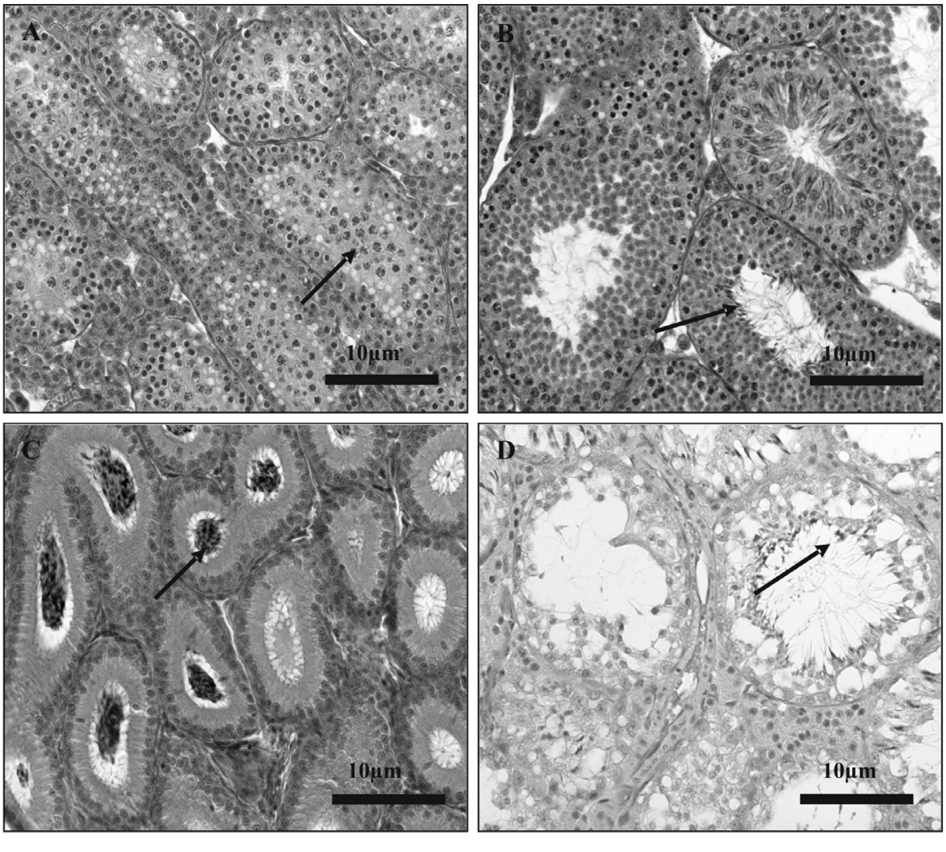

Fig. 2. **A**, Seminiferous tubule of specimen collected in January showing primary spermatocytes (arrow). **B**, Seminiferous tubule of specimen collected in May showing spermatids and spermatozoa (arrow). **C**, Epididymis tubule of specimen collected in May showing spermatozoa (arrow). **D**, Seminiferous tubule of specimen collected in September showing last remaining spermatozoa (arrow) and spermatogonia.

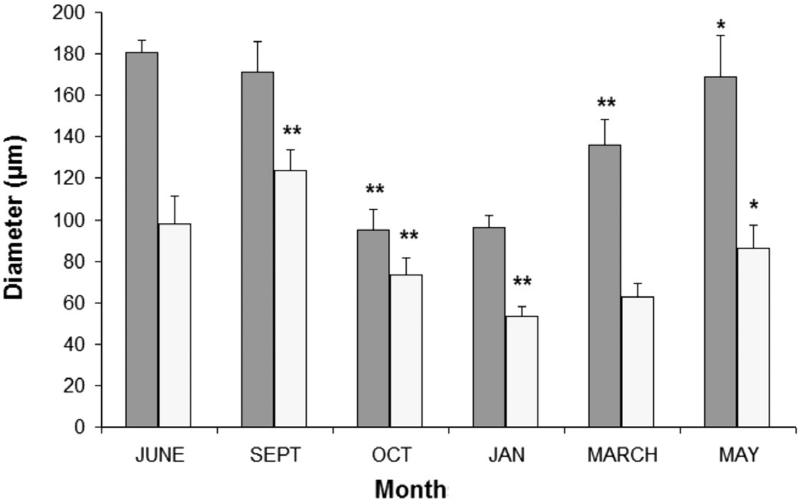

Fig. 3. Mean (±S.D.) seminiferous tubule (■) and epididymis tubule (□) diameter (µm) in male *Tadarida aegyptiaca* (asterisks indicate significant change from preceding month,*$P < 0.05$, **$P < 0.01$).

reflected in the seminiferous and epididymal tubule diameter (Fig. 3). There was a significant decrease in the seminiferous tubule diameter from September to January, followed by a significant increase to March and again to May ($F_{5,27} = 62.33$, $n = 33$, $P < 0.01$). The epididymis tubule diameter significantly increased from June to September, after which there was a significant decrease to January followed by a significant increase to May ($F_{5,27} = 34.91$, $n = 33$, $P < 0.01$).

Female *T. aegyptiaca* have a bicornuate uterus but showed complete dextral dominance. Follicular developmental stages up until the secondary follicle stage was observed in both ovaries but, thereafter follicular development became confined to the right ovary only. Follicular development was already under way by January since young Graafian follicles were already present at this time (Fig. 4A).

Copulation, ovulation and fertilization occurred at the end of August or the beginning of September (spring), since one specimen was observed during September with spermatozoa in the uterine glands and a large preovulatory Graafian follicle in the right ovary (Fig. 4B,C). Three pregnant specimens were also observed, each with a four-cell stage embryo situated in the right oviduct (Fig. 4D).

Growth of the ovarian follicles in relation to growth of their oocytes is presented in Fig. 5. The data indicate that during the primary and secondary follicle stages oocyte diameter and follicle diameter increased in size at a relatively even rate. However, from the small Graafian follicle stage onwards there was a large increase in follicle diameter but not in oocyte diameter. This was mainly due to the formation and expansion of the antrum causing a rapid increase in the follicle size, whereas the oocyte had attained its full size. The data also show a significant positive correlation between oocyte diameter and follicle diameter ($F_{1,\ 42} = 57.31$, $n = 44$, $P < 0.01$, $R^2 = 0.57$).

Atresia is the process whereby ovarian follicles are lost from the ovary other than by ovulation, follicular cells and oocytes die and are disposed of by phagocytic cells (Van der Merwe 1979; Jungueira & Carneiro 2003). Atresia was observed from the primary follicle stage until the young Graafian follicle stage. Primary follicles underwent Type I atresia, where the oocyte degenerates before the stratum granulosa (Vivier 1993). Type II atresia is where the stratum granulosa disappears before the oocyte (Vivier 1993). Secondary and Graafian follicles exhibited both types but Type II was more common. There was a general increase in the observed number of atretic follicles in the ovary from January to September.

Tadarida aegyptiaca is a monoestrous, monotocous seasonal breeder. Spermiogenesis and the final stages of follicular development occur during autumn with copulation, ovulation and subsequent fertilization in late August. These findings agree in part with a previous report on the reproduction of *T. aegyptiaca* collected at 33°S (Bernard & Tsita 1995). The present study revealed that certain reproductive events, such as spermatogenesis and

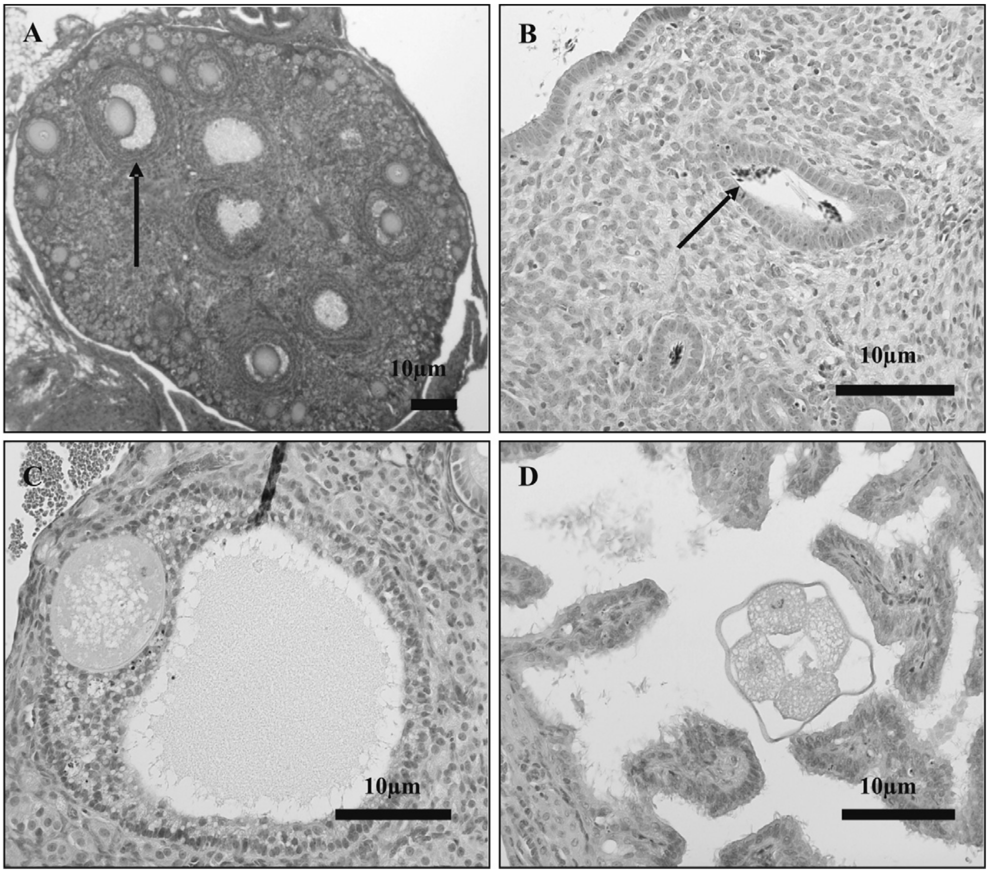

Fig. 4. **A**, Young Graafian follicle in right ovary of specimen collected in January (arrow). **B**, Right uterine horn of specimen collected in September showing spermatozoa in uterine glands (arrow). **C**, Same specimen as in 2B showing a large preovulatory follicle in the right ovary. **D**, Specimen collected in September showing a four-cell stage embryo in right oviduct.

follicular development were initiated earlier in the year at 25°S than at 33°S. In the present study spermatogenesis already started in January, whereas at 33°S it only commenced in February. Follicular development was already under way during January in the present study, while at 33°S follicular development only began in April. Spermatozoa were also noted much earlier in the epididymis, during May, in this study as compared to July at 33°S.

Despite these earlier reproductive developments, ovulation, copulation and subsequent fertilization occurred at the end of August as was reported by Bernard & Tsita (1995). This could be explained by the slightly longer summer period at 25°S; however, at both latitudes the end of August coincides with the end of winter and the rise of minimum temperatures (Bernard & Tsita 1995, Fig. 1). If female *T. aegyptiaca* were to start reproduction at 25°S earlier than August, the energetically most demanding period of pregnancy and lactation would not be synchronized with the period of peak rainfall and insect abundance (Van der Merwe *et al.* 1986; Vivier & Van der Merwe 1997).

It is also possible that ovulation, copulation and fertilization occur earlier at this location but that most of the pregnant females then move to more favourable areas and form maternal colonies. This notion is supported by Cory Toussaint *et al.* (2010), who were unable to capture any females during July. However, without detailed studies on the seasonal movements of the females of this species, this notion remains speculative and should be the focus of further studies.

The monoestry exhibited by *T. aegyptiaca* is interesting compared to the seasonal polyoestry exhibited by the smaller little free-tailed bat (*Chaerephon pumila*) at relatively the same latitude

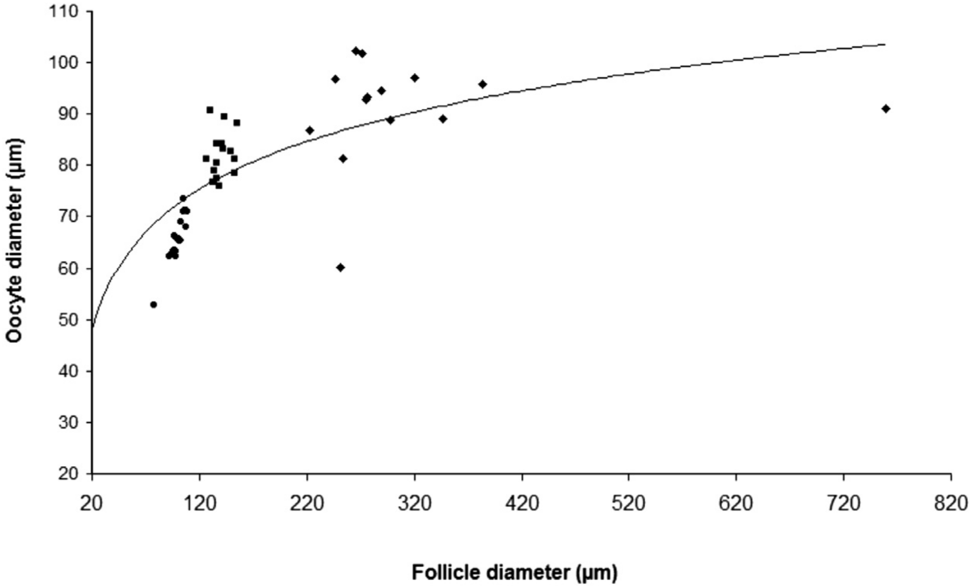

Fig. 5. Diameter (µm) of primary (●), secondary (■) and Graafian (◆) follicles against the diameter of their respective oocytes of female *Tadarida aegyptiaca.*

(Van der Merwe *et al.* 1986). It has been suggested that the monoestry exhibited by *T. aegyptiaca* at 33°S could be the result of a longer gestation period (120 days) and a relatively short summer period (Bernard & Tsita 1995). However, Kashyap (1980) reported a slightly shorter gestation period (77–90 days) in the same species from India (22°N), where they also displayed monoestry. Although no conclusions could be drawn with regard to gestation length in the present study; lactating females have been found during December in Zimbabwe and juveniles during March in KwaZulu-Natal, South Africa (Skinner & Chimimba 2005). These findings suggest that *T. aegyptiaca* could be monoestrous throughout its range.

The molossid family is one of the most diverse amongst the African microchiropterans and some species, such as *C. pumila* and the Angolan free-tailed bat (*Mops condylurus*,) are common and have widespread distributions (Van der Merwe *et al.* 1986). The considerable comparative data available for these species, from a wide range of latitudes (10°N–25°S), demonstrate the plasticity in their reproductive pattern with changing latitude (Happold & Happold 1990). As latitude increases, *C. pumila* reduces the number of reproductive cycles in a season, while *M. condylurus* always has two pregnancies per season but reduces the interval between pregnancies (Van der Merwe *et al.* 1986; Happold & Happold 1990; Vivier & Van der Merwe 1997, 2001). Another southern African molossid that displays an interesting reproductive pattern is the large Madagascar free-tailed bat (*Tadarida fulminans*). This molossid also has two pregnancies per season, but while one pregnancy coincides with the favourable wet season as expected the second occurs during the cool dry season (Cotterill & Fergusson 1993). The unique reproductive patterns shown by these and other molossids could possibly be related to their interesting wingloading characteristics and foraging style (Bernard & Cumming 1997). Molossids are fast, high-flying bats, that are able to cover great distances and are therefore able to exploit insects that are not as accessible to other microchiropteran families (Fenton & Rautenbach 1986). Studies of molossid diets and sampling of insects at their flight level could yield intriguing insights into their reproductive flexibility and should be pursued further.

In conclusion, even though the present study did not show major differences in the reproductive pattern of *T. aegyptiaca* between 25°S and 33°S, it does suggest that a difference in latitude of just eight degrees can influence the timing of events in the reproductive cycle of a free-tailed bat.

We thank Professors A.E. McKechnie and N.C. Bennett for their help and suggestions, and C. Scott for assistance during fieldwork.

REFERENCES

BERNARD, R.T.F. & CUMMING, G.S. 1997. African bats: evolution of reproductive patterns and delays. *Quarterly Review of Biology* **72**: 253–274.

BERNARD, R.T.F. & TSITA, J.N. 1995. Seasonally monoestrous reproduction in the molossid bat, *Tadarida aegyptiaca,* from low temperate latitudes (33°S) in South Africa. *South African Journal of Zoology* **30**: 18–22.

COETZEE, J. & VAN DER MERWE, C.F. 1992. Preparation of biological material for light microscopy. University of Pretoria, Pretoria.

CORY TOUSSAINT, D.C., McKECHNIE, A.E. & VAN DER MERWE, M. 2010. Heterothermy in free-ranging male Egyptian free-tailed bats (*Tadarida aegyptiaca*) in a subtropical climate. *Mammalian Biology* **75**: 466–470.

COTTERILL, F.P.D. & FERGUSSON, R.A. 1993. Seasonally polyestrous reproduction in a free-tailed bat *Tadarida fulminans* (Microchiroptera: Molossidae) in Zimbabwe. *Biotropica* **25**: 487–492.

FENTON, M.B. & RAUTENBACH, I.L. 1986. A comparison of roosting and foraging behaviour of three species of African insectivorous bats (Rhinolopidae, Vespertilionidae, and Molossidae). *Canadian Journal of Zoology* **64**: 2860–2867.

GUSTAFSON, A.W. 1979. Male reproductive patterns in hibernating bats. *Journal of Reproduction and Fertility* **56**: 317–331.

HAPPOLD, D.C.D. & HAPPOLD, M. 1990. Reproductive strategies of bats in Africa. *Journal of Zoology, London* **222**: 557–583.

HERSELMAN, J.C. & NORTON, P.M. 1980. The distribution and status of bats (Mammalia: Chiroptera) in the Cape Province. *Annals of the Cape Provincial Museum (Natural History)* **16**: 73–126.

JERRET, D.P. 1979. Female reproduction patterns in nonhibernating bats. *Journal of Reproduction and Fertility* **56**: 369–378.

JUNGUEIRA, L.C. & CARNEIRO, J. 2003. *Basic histology: Text & Atlas.* 10th Edn. McGraw-Hill, New York.

KASHYAP, S.K. 1980. Reproductive cycle of the Indian molossid bat, *Tadarida aegyptiaca. Current Science* **49**: 251–253.

OXBERRY, B.A. 1979. Female reproductive patterns in hibernating bats. *Journal of Reproduction and Fertility* **56**: 359–367.

RACEY, P.A. & ENTWISTLE, A.C. 2000. Life history and reproductive strategies of bats. In: *Reproductive Biology of Bats,* (eds) E.G. Crichton & P.H. Krutzsch, pp. 363–401. Academic Press, New York.

SKINNER, J.D. & CHIMIMBA, C.T. 2005. *The Mammals of the Southern African Subregion.* Cambridge University Press, Cape Town.

SRINIVASULU, B. & SRINIVASULU, C. 2007. First specimen based record of the Egyptian free-tailed bat *Tadarida aegyptiaca,* E. Geoffroy 1818, (Chiroptera: Molossidae) from Andhra Pradesh, India. *Zoos' Print Journal* **22**: 2943.

VAN DER MERWE, M. 1979. Growth of ovarian follicles in the Natal clinging bat. *South African Journal of Zoology* **14**: 111–117.

VAN DER MERWE, M., RAUTENBACH, I.L. & VAN DER COLF, W.J. 1986. Reproduction in the little free-tailed bat, *Tadarida pumila,* in the eastern Transvaal, South Africa. *Journal of Reproduction and Fertility* **77**: 355–364.

VIVIER, L. 1993. Reproduction in the Angolan free-tailed bat, *Tadarida condylura,* in the eastern Transvaal. M.Sc. thesis, University of Pretoria, Pretoria, South Africa.

VIVIER, L. & VAN DER MERWE, M. 1996. Reproductive pattern in the male Angolan free-tailed bat, *Tadarida (Mops) condylura* (Microchiroptera: Molossidae) in the eastern Transvaal, South Africa. *Journal of Zoology, London* **239**: 465–476.

VIVIER, L. & VAN DER MERWE, M. 1997. Reproduction in the female Angolan free-tailed bat, *Tadarida (Mops) condylura* (Microchiroptera: Molossidae), in the eastern Transvaal, South Africa. *Journal of Zoology, London* **243**: 507–521.

VIVIER, L. & VAN DER MERWE, M. 2001. Aspects of the histology of reproduction in the female Angolan free-tailed bat *Mops condylurus* (Microchiroptera: Molossidae) in Mpumalanga, South Africa. *Journal of Zoology, London* **254**: 495–504.

Responsible Editor: G.N. Bronner