Breeding season of Epomophorus walhbergi in the lowveld of Swaziland

Ara Monadjem^{1*} & April E. Reside²

¹All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland,
Private Bag 4, Kwaluseni, Swaziland, and
Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria,
Private Bag X20, Hatfield, Pretoria, 0028 South Africa

²Centre for Tropical Biodiversity and Climate Change, James Cook University, Townsville, Australia

Received 4 April 2012. Accepted 19 November 2012

The fruit bat *Epomophorus wahlbergi* is abundant in the eastern parts of southern Africa, but its breeding biology remains poorly documented. This study aimed to ascertain the breeding season of this species in northeastern Swaziland where 340 individuals were netted over a 21-month period. Subadults were present throughout the year with two peaks, while lactating females were only present between December and May. These contradictory data are consistent with a bimodal birth peak, and the fact that pregnancy and lactation were both difficult to detect in the field.

Key words: Epomophorus wahlbergi, fruit bat, breeding, Swaziland.

INTRODUCTION

Wahlberg's epauletted fruit bat, *Epomophorus wahlbergi*, is a common and widespread fruit bat in the eastern parts of southern Africa, with a distribution extending from equatorial Africa through to southern South Africa (Volpers & Kumirai 1995; Monadjem *et al.* 2010). Yet despite its abundance, relatively little is known about its breeding biology, particularly at higher latitudes (Monadjem *et al.* 2010). For example, during extensive mammal surveys in the former Transvaal province of South Africa, Rautenbach (1982) did not collect a single pregnant or lactating female of this species.

As breeding in bats is generally associated with peak food abundances (Okia 1974), clinal differences in the timing of parturition of bats has been recorded in species with distributions spanning widely across latitudes, including E. wahlbergi (Bernard & Cumming 1997). Close to the equator, this species has two birth periods in February-March and in October-December (Bergmans 1979; O'Shea & Vaughan 1980), or an extended period from October to January (Wickler & Sieber 1976; Bernard & Cumming 1997), similar to other congeneric species in this region (Okia 1974). Further south in Malawi and Zambia this species has been described as 'aseasonally polyoestrus' with births from September to March (Happold & Happold 1990). In southern Africa, this species has been described as 'seasonally polyoestrus' (Skinner & Chimimba 2005). Although Taylor (1998) reported that in the KwaZulu-Natal province of South Africa 'breeding occurs throughout the year with peaks in July and in the summer'. However, this statement was based on an unpublished dataset by C. Sapsford, and further details were not presented (Taylor 1998). In Zimbabwe, gravid females have been recorded in June and December (Smithers & Wilson 1979), suggesting an extended breeding season. By contrast, in Kruger National Park, South Africa, parturition has been recorded in November–December (Pienaar *et al.* 1980).

This study aimed to elucidate the breeding season of *E. wahlbergi* in Swaziland based on the capture of 340 individuals netted over a 21-month survey in the northeast of the country. We hypothesized that females would give birth over an extended period of at least six months as in Malawi, Zambia and Zimbabwe (Smithers & Wilson 1979; Happold & Happold 1990), since we except the phenology of fruiting trees to be similar these two areas.

METHODS

This study was conducted in northeastern Swaziland, within the largest protected area network in the country covering an area of almost 500 km². Three protected areas share common boundaries here: Hlane Royal National Park, Mlawula Nature Reserve and Mbuluzi Game Reserve, forming part of the Lubombo Conservancy. A detailed description of this site appears in Monadjem & Reside (2008), and a summary is provided below. The topography of the area is relatively flat and alti-

^{*}Author for correspondence. E-mail: ara@uniswa.sz

tude varies between 150 and 250 m above sea level. The climate is subtropical with hot, wet summers and cool, dry winters. The vegetation is dominated by Acacia savanna, bisected by riparian forest along rivers (Roques et al. 2001). The phenology of fruiting trees has not been studied in Swaziland specifically however information on the fruiting season of some plant species, occurring in southern Africa and important to pteropodid bats, has been reviewed in Cumming & Bernard (1997). The latter study showed that trees fruited throughout the year, with a peak in the wet summer months (October-January). Furthermore, the species Ficus sycomorus, which is thought to constitute an important part of the diet of E. wahlbergi (Monadjem et al. 2010), fruits aseasonally and individual trees may fruit at any time of the year (Cumming & Bernard 1997).

The data presented in this paper were collected as part of the bat community study of Monadjem & Reside (2008), and the description below is based on the latter paper. The study was conducted between October 2004 and May 2006, covering every month of the year. Nineteen sites were sampled; ten in riparian forest and nine in open savanna. Neighbouring sites were at least 2 km apart. In general, sites were sampled for two consecutive nights, and resampled at least once. Eighty metres of four-shelf mist nets (each one covering an area of 3.5×10 m) were set at ground level. One canopy net of 7×10 m (two nets placed one above the other) was hung from branches within the canopy. Nets were opened prior to sunset and closed after 5 hours.

Captured bats were categorized as either adults or subadults. Subadults were distinguished by the incomplete ossification of the epiphyses. Females were classed as pre-parous, pregnant, lactating, or post-lactating (i.e. not currently pregnant or lactating, but having bred at least once previously). Pregnancy was judged by palpation. Males were classed as breeding if descended testes were visible. Body mass (g) was measured with Pescola scales (Forestry Suppliers Inc., U.S.A.) and forearm length was measured with dial callipers (Bergeon, Switzerland) to 0.1 mm. The tip of the thumbclaw of each individual was clipped so that previously caught individuals could be identified within the two-night sampling session. Three voucher specimens of this species from the area have been deposited in the Durban Natural Science Museum (museum numbers: DM5847, DM7171 and DM7901). The externally similar species *Epomo-* phorus crypturus (but see Taylor & Monadjem 2008) is extremely rare in Swaziland, having only been captured on two prior occasions (Monadjem 1998; Monadjem et al. 2010). Only a single individual was captured during this study (DM8035), and this species will not be discussed any further.

The number of sampling nights per month was not uniform throughout the year (see Table 1), hence the data were standardized by dividing by the number of sampling nights.

RESULTS

A total of 340 individual *E. wahlbergi* were captured during this survey, of which 99 were subadults, 65 were adult males, and the remaining 176 were adult females. This species was captured throughout the year, although none were captured in June or November, possibly as a result of low sampling effort at this time (Table 1).

Subadult bats were present in most months, with an apparent bimodal pattern between January and May, and again in August to October (Table 1; Fig. 1). The absence of subadults in June may have been as a result of low sampling effort; no adults were caught during this month either (Table 1). However, 14 adults were captured in July, suggesting that the absence of subadults may have been real. The forearm length of subadults varied between months, increasing from January to May, and again from August to October (Fig. 2), supporting the bimodal distribution pattern of subadults. The forearm length of adults remained the same throughout the year, being longer in males than females (Fig. 2). The forearm lengths of subadults in August were larger than those captured in January (but similar to those in February) (Fig. 2), suggesting that the bats first became volant in July.

By contrast, just four pregnant females were recorded; these were in the months of March, July and September (Table 1). A total of 17 lactating females were recorded between December and May, suggesting a unimodal pattern of reproduction (Table 1). Males in apparent breeding condition (distended testes) were present throughout the year.

DISCUSSION

Despite the large numbers of *E. wahlbergi* captured during this study, only a small proportion was visibly pregnant. This is most likely as a result of us not being able to confidently distinguish pregnant females by palpation. This species has a long gesta-

Category	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Subadults	1	8	2	32	9	0	0	15	21	11	0	0
Total adults	0	27	6	36	14	0	14	88	24	15	0	17
Adult males	0	17	1	6	1	0	5	22	7	0	0	6
Adult females	s 0	10	5	30	13	0	9	66	17	15	0	11
Scrotal	0	11	1	6	1	0	4	16	4	0	0	6
Pregnant	0	0	2	0	0	0	1	0	1	0	0	0
Lactating	0	3	0	12	1	0	0	0	0	0	0	1
Post-lactating	g 0	4	1	14	8	0	1	29	12	7	0	0
Total	1	35	8	68	23	0	14	103	45	26	0	17
Netting night	s 1	6	11	8	17	1	2	6	11	10	2	1
Bats/night	1.0	5.8	0.7	8.5	1.4	0	7	17.2	4.1	2.6	0	17.0

Table 1. Numbers of Epomophorus wahlbergi captured monthly in northeastern Swaziland.

tion period covering five to six months (Acharya 1992), and palpation may only have been effective for determining pregnancy at the end of this period, perhaps only the last two to four weeks. By contrast, lactating females were relatively easy to identify and this may be the reason for the more than four-fold increase in the number of lactating, compared with pregnant, females identified.

The data from subadults strongly suggests a bimodal breeding season. Subadults are present throughout the year, and they vary in size (as measured by forearm length) following a bimodal distribution with smaller-sized subadults present in January–March and August. Subadults were

larger in August than in January (Fig. 2), constituting evidence that they appeared as newly volant earlier in July. The year-long presence of subadults is not surprising since it is estimated that they take 15 months to reach adult size (Acharya 1992).

By contrast, based on the presence of lactating females, it would appear that breeding occurs in a restricted season, and is not distributed throughout the year. Lactating females were present between December and May, with an apparent peak between February and April. Post-lactating females began to appear in February and greatly outnumbered lactating females by May. The presence of small-sized subadults (with shorter

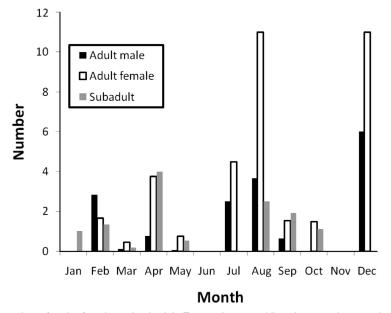


Fig. 1. Monthly number of male, female and subadult *Epomophorus wahlbergi* captured per netting night in north-eastern Swaziland.

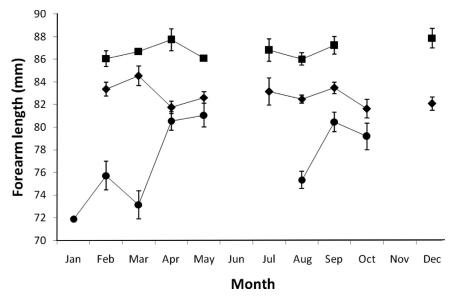


Fig. 2. Monthly variation in forearm length of male (■), female (♦) and subadult (●) *Epomophorus wahlbergi* captured in northeastern Swaziland.

forearms) at this time is further corroboration for this.

There may be considerable errors associated with the detection of pregnancy by palpation or lactation by visual inspection (Thomas & Marshall 1984), but not with the measurement of forearm length (as a measure of age). For this reason, we are inclined towards the bimodal model of births based on the forearm data of subadults, rather than the unimodal model based on pregnancy and lactation. If newly volant bats were present in January and July (as argued above), and assuming a three-month lactation period (Sowler 1980), then this points to parturition having taken place in October-November and April-May. Subtracting a further five months for pregnancy (Thomas & Marshall 1984; Acarya 1992), indicates mating to have occurred in May-June and November-December.

Whether individual *Epomophorus wahlbergi* in Swaziland are capable of producing offspring during both peaks is not known. However, from these data, it is clear that the only way that this would be possible, would be for a female to mate immediately upon parturition. Such post-partum oestrus has been observed in African Molossidae (McWilliam 1987; Van der Merwe *et al.* 1987) and Pteropodidae (Thomas & Marshall 1984). Individual *Epomops franqueti* and *Micropteropus pusillus* in a West African tropical savanna produced offspring at six-month intervals, and births coincided with

peaks in fruit availability following each of two rainy seasons per year (Thomas & Marshall 1984). However, such a relationship is unlikely to hold at higher latitudes where just a single rainy season occurs. In fact, Rousettus aegyptiacus breeds bimodally in tropical Africa, but unimodally in South Africa (Happold & Happold 1990). The two birth peaks in Swaziland coincide with the onset of the rains (October-November) and the beginning of the dry season (April–May). In our study, newly volant bats would be flying during the peak of the rainy season (January-February) and the middle of the dry, cold winter (July-August). The first peak, during the rainy season, coincides with fruit availability (Cumming & Bernard 1997), but the second peak does not. It would be interesting for future researchers to investigate whether survival of newly volant subadults varies with these two seasons.

Our results suggest that data on scrotal *versus* abdominal position was not a useful indicator of breeding status of males. In this study, scrotal males were present throughout the year; however, the reproductive condition of these males need to be ascertained by testes size and/or weight (Okia 1974).

ACKNOWLEDGEMENTS

This is the 19th communication of the All Out Africa Research Unit (www.alloutafrica.org). We thank Mduduzi Ngwenya, Andy Bamford and All

Out volunteers for assistance in the field. The Director of All Out, Kim Roques, provided logistical support in the field. Ngwane Dlamini, Senior Warden, Swaziland National Trust Commission, provided permission for us to work at Mlawula. Three anonymous reviewers greatly improved earlier versions of this paper.

REFERENCES

- ACHARYA, L. 1992. Epomophorus wahlbergi. Mammalian Species 394: 1–4.
- BERGMANS, W. 1979. Taxonomy and zoogeography of the fruit bats of the People's Republic of Congo, with notes on their reproductive biology (Mammalia, Megachiroptera). *Bijdragen tot de Dierkunde* **48**: 161–186.
- BERGMANS, W. 1988. Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 1. General introduction; materials and methods, results; the genus *Epomophorus* Bennett, 1836. *Beaufortia* 38: 75–146.
- BERNARD, R.T.F. & CUMMING, G.S. 1997. African bats: evolution of reproductive patterns and delays. *Quarterly Review of Biology* **72**: 253–274.
- CUMMING, G.S. & BERNARD, R.T.F. 1997. Rainfall, food abundance and timing of parturition in African bats. *Oecologia* **111**: 309–317.
- HAPPOLD, D.C.D. & HAPPOLD, M. 1990. Reproductive strategies of bats in Africa. *Journal of Zoology, London* **222**: 557–583.
- MCWILLIAM, A.N. 1987. Polyoestry and postpartum oestrus in *Tadarida (Chaerephon) pumila* (Chiroptera: Molossidae) in northern Ghana, West Africa. *Journal of Zoology, London* 213: 735–739
- MONADJEM, A. 1998. *Mammals of Swaziland*. The Conservation Trust of Swaziland and Big Game Parks, Mbabane.
- MONADJEM, A. & RESIDE, A. 2008. The influence of riparian vegetation on the distribution and abundance of bats in an African savanna. Acta Chiropterologica 10: 339–348
- MONADJEM, A., TAYLOR, P., COTTERILL, F.P.D. & SCHOEMAN, M.C. 2010. Bats of Southern Africa: A Biogeographic and Taxonomic Synthesis. Wits Univer-

- sity Press, Johannesburg, South Africa.
- OKIA, N.O. 1974. The breeding pattern of the eastern epauletted bat, *Epomophorus anurus* Heuglin, in Uganda. *Journal of Reproduction Fertility* 37: 27–31.
- O'SHEA, T.J. & VAUGHAN, T.A. 1980. Ecological observations on an East African bat community. *Mammalia* 44: 485–496.
- PIENAAR, U. DE V., RAUTENBACH, I.L. & DE GRAAF, G. 1980. *The Small Mammals of Kruger National Park*. National Parks Board of South Africa, Pretoria.
- RAUTENBACH, I.L. 1982. Mammals of the Transvaal. Ecoplan, Pretoria.
- ROQUES, K.G., O'CONNOR, T.G. & WATKINSON, A.R. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*: **38**: 268–280.
- SKINNER, J.D. & CHIMIMBA, C.T. 2005. The Mammals of the Southern African Subregion. Cambridge University Press, Cambridge.
- SMITHERS, R.H.N. & WILSON, V.J. 1979. Check List and Atlas of the Mammals of Zimbabwe Rhodesia. Museum Memoir 9: 1–193. The Trustees of the National Museums and Monuments of Rhodesia, Bulawayo.
- SOWLER, S.G. 1980. Tooth eruption in known age specimens of *Epomophorus wahlbergi*. South African Journal of Wildlife Research 10: 112–117.
- TAYLOR, P.J. 1998. The Smaller Mammals of KwaZulu-Natal. University of Natal Press, Pietermaritzburg.
- THOMAS, D.W. & MARSHALL, A.G. 1984. Reproduction and growth in three species of West African fruit bats. *Journal of Zoology, London* 202: 265–281.
- VAN DER MERWE, M., GIDDINGS, S.R. & RAUTEN-BACH, I.L. 1987. Post-partum oestrus in the little free-tailed bat *Tadarida* (*Chaerephon*) pumila (Microchiroptera: Molossidae). *Journal of Zoology, London* 213: 317–327.
- VOLPERS, W. & KUMIRAI, A. 1995. Ecological aspects of the distribution of *Epomophorus* fruit bats (Mammal., Chiropt.) in Zimbabwe. *Verhandlungen der Gesellschaft für Ökologie* 24: 89–92.
- WICKLER, W. & SIEBT, U. 1976. Field studies on the African fruit bat *Epomophorus wahlbergi* (Sundevall), with special reference to male calling. *Zeitschrift für Tierpsychologie* **40**: 345–376.

Responsible Editor: J.H. van Wyk