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Survival and roost-site selection in the African bat *Nycteris thebaica* (Chiroptera : Nycteridae) in Swaziland

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ABSTRACT. Survival and mortality of African bats is poorly known. A banding study of a population of *Nycteris thebaica*, roosting in 15 road culverts in north-eastern Swaziland, was initiated in 1998. Since then, a total of 799 bats have been banded including five cohorts of same-aged individuals of known age. Cohort life-tables and survivorship curves were calculated using these data. For both males and females, survivorship was low in the first year, but increased thereafter. Approximately 15% of females and 10% of males banded as juveniles in 1998 and 1999 survived to three years of age. Of female bats banded as adults in July 1998 (n = 39), 23% had survived to January 2003 (4.5 years). The corresponding value for males (n = 6) was zero. Of 28 male bats banded in 1998, only one (4%) was recaptured after four years. Female values probably reflect true survival and mortality, whereas, dispersal and movement complicate the values for males. Female *Nycteris thebaica* did not randomly select roosting sites. The 15 culverts were occupied by six discrete groups of female bats. The presence of male bats at the study site was irregular, with movements of 9 km having been recorded by one particular individual.

KEY WORDS : *Nycteris thebaica*, survival, roost selection, Africa.

INTRODUCTION

The ecologies and life histories of African bats are relatively poorly known. For many species, even basic distributional information is highly fragmented and far from complete. To date, most bat studies in Africa have focused on distribution, taxonomy, reproduction and to a lesser extent on diet, domiciles and echolocation. Limited information is available on other biological aspects of African bats including longevity, survival and the behavioural and ecological aspects of roost-site selection. Some notable exceptions are VAN DER MERWE (1989) who showed that *Miniopterus schreibersii natalensis* (A. Smith, 1834) could survive up to 13 years in South Africa, LAVAL & LAVAL (1977), O'SHEA (1980) and HAPPOLD & HAPPOLD (1990, 1996) who investigate roost-site selection and other aspects of social behaviour in *Pipistrellus nanus* (Peters, 1852). Other species of Sub-Saharan Africa microchiropterans whose roosting behaviour have been studied include *Myotis bocagii* (Peters, 1870) (BROSSET, 1976), *Coleura afra* (Peters, 1852) (MCWILLIAM, 1987), *Lavia frons* (E. Geoffroy, 1810) (WICKER & UHRIG, 1969) and *Tadarida pumila* (Cretzschmar, 1830-1831) (MCWILLIAM, 1987).

The microchiropteran bat *Nycteris thebaica* E. Geoffroy, 1818 is widespread in Africa, and tolerates a wide range of environmental conditions (SMITHERS, 1983), roosting in caves, mine adits and various other hollow sites (CHURCHILL et al., 1997; TAYLOR, 1998; TAYLOR, 2000). In Swaziland, it regularly roosts in road culverts where adult females significantly outnumber adult males (MONADJEM, 1998; MONADJEM, 2001). Females are present in significant numbers throughout the year, but it is not known whether these individuals regularly move between culverts or use one or a few culverts exclusively.

Nycteris thebaica often uses different day and night roosts (TAYLOR, 1998). Night roosts are generally associated with feeding (BOWIE et al., 1999; SEAMARK & BOGDANOWICZ, 2002), while day roosts appear to function as resting sites.

The main objectives of this study were to : 1) determine the age-specific survival of *Nycteris thebaica* in Swaziland, and 2) investigate daytime roost-site selection in this species.

METHODS

This study was conducted at Mlawula Nature Reserve (26E 11'S; 31E 59'E, 160 m above sea level) in the lowveld of northeastern Swaziland. Mlawula Nature Reserve typically experiences hot, wet summers (October to March) and cool, dry winters (May to August). Mean annual rainfall is approximately 500-600 mm, but rainfall can vary dramatically between years.

The road leading to the main entrance of the reserve is tarred and is situated within the reserve. It is approximately 3 km in length and passing beneath this road are 15 culverts 60-100 cm wide and up to 50 m long. *Nycteris thebaica* has been known to be using these culverts as daytime roosts for, at least, the past 15 years (MONADJEM, 2001). The bats roosting within these 15 culverts formed the basis of this study. A small number of *Nycteris thebaica* was also captured in culverts passing under the railway track within 10 km of the main study area. Bats were captured in the culverts by pushing a "shield" (a piece of chipboard with the diameter of the culvert) through the culvert into a large sweep net placed over the entrance. The other end of the culvert was blocked to prevent bats that had manoeuvred past the shield from leaving the culvert. The process was repeated until all bats had been captured. In the first year of study this technique was not fully developed and occasionally many bats escaped. From August 1999, however, very few bats escaped. All captured bats were sexed, aged and were fitted with metal bat-bands which were attached around the forearm. Three age classes were identified : juveniles, sub-adults and adults. Juveniles were defined as being dependent on their parents and were easily identified by size and pelage, which was greyer than that of the adults. Sub-adults were identifiable by pelage colour (which was still greyer than that of the adults) only in February and probably March, and represented individuals born in the previous breeding season i.e. November. By July the bats were more than 7 months of age, and could no longer be differentiated from older bats (MONADJEM, 2001).

Culverts were surveyed in July, October and December 1998. From August 1999, culverts were surveyed four times per year in July/August, October, December/January and February. In 1998, only two culverts were surveyed. From August 1999 all 15 culverts were surveyed, and all bats captured, during each survey.

Cluster analysis, conducted by the computer program "Primer" (CLARKE & GORLEY, 2001), was used to identify clusters of roost sites based on the adult males and females utilizing them. Dendrograms were generated based on Bray-Curtis similarities computed on the number of times each bat was recorded roosting in each culvert. Counts were square-rooted so as to down-weight the contributions of a few individuals recorded many times in relation to individuals recorded just once.

RESULTS

A total of 799 bats have been banded since 1998 and there have been 1835 recaptures. Of these, 380 were banded as juveniles. Numbers of juveniles banded varied between years, but the ratio of juveniles to adult females did not differ significantly between the years ($\chi^2 = 3.930$, degrees of freedom = 4, $P > 0.05$; Table 1). Between 1998 and the end of 2000, adults formed a significant proportion of new bats banded. From 2001 onwards, however, a decreasing number of bats were first captured as adults (Fig. 1). Juveniles comprised only 45% of all new bats in the first three years of the study, but 57% in 2001 and 81% in 2002.

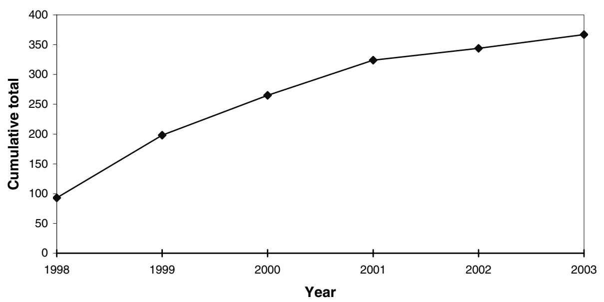

Fig. 1. – Cumulative total number of new (i.e. unbanded) adult *Nycteris thebaica* cap-

The sex ratio of juveniles did not deviate significantly from parity. In total, 196 female and 181 male juveniles were banded, with three unsexed individuals. Juvenile sex ratio also did not differ significantly between years ($÷^2$ = 4.359, degrees of freedom = 4, $P > 0.05$; Table 1).

TABLE 1

Numbers of juveniles banded per year, including juvenile sex ratio and productivity of adult females. Totals do not add up for the years 1999, 2001 and 2002 as single unsexed individuals were banded in these years.

Year	Number of juveniles banded			Juvenile sex ratio (male/ female)	Offspring per adult female
	Male	Female	Total		
1998	13	6	19	2.0	0.8
1999	39	47	87	0.8	1.1
2000	53	55	108	1.0	1.0
2001	36	41	78	0.9	0.8
2002	40	47	88	0.8	0.8

Survivorship curves were similar in shape for male and female bats banded as juveniles (Fig. 2). However, male survival was lower than that of females. Juvenile survival was lowest in the first six months, thereafter levelling off and remaining similar throughout adult life. Approximately 15% of females and 10% of males banded as juveniles in 1998 and 1999 survived to three years of age. Of female bats banded as adults in July 1998 (n = 39), 23% had survived to January 2003 (4.5 years). The corresponding value for males (n = 6) was zero. Of 28 male bats banded in 1998, only one (4%) was recaptured after four years. Adult bats captured in 1998 would have been born at the latest in November 1997 making them over five years old when recaptured in 2003.

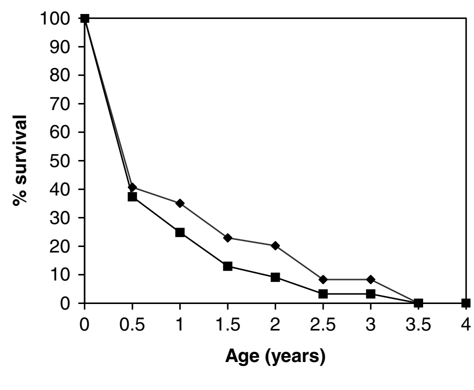

Fig. 2. – Survivorship curves for male (square) and female (diamond) *Nycteris thebaica* banded as juveniles.

Approximately a third of all juvenile females survived to one year, while only a quarter of juvenile males survived to the same age (Table 2). However, this was not statistically different ($\chi^2 = 1.301$, degrees of freedom = 1, $P > 0.05$). Survival to one year varied between years (males : $\chi^2 = 21.416$, degrees of freedom = 3, $P < 0.05$; females : $\chi^2 = 9.582$, degrees of freedom = 3, $P < 0.05$), with highest survival of females and males recorded in 1998 and 1999, respectively. Survival was lowest for both sexes in 2001.

TABLE 2

Minimum estimates of first year survival of juvenile *Nycteris thebaica*.

Year	Proportion juvenile females surviving (n)	Proportion juvenile males surviving (n)	Total number surviving	Overall proportion
1998	0.50	0.15	5	0.26
1999	0.38	0.54	38	0.44
2000	0.38	0.19	31	0.29
2001	0.15	0.11	10	0.13
Mean ± SE	0.35 ± 0.07	0.25 ± 0.10		0.28 ± 0.06

Bats were recorded roosting in 13 of the 15 culverts, with some culverts regularly supporting large numbers of bats (Table 3). Adult bats did not utilize these day roost sites randomly. Adult females tended to be captured in the same culvert on consecutive surveys, occasionally being recorded in neighbouring culverts. This is illustrated in the cluster analysis presented in Fig. 3. Neighbouring roosts cluster together in this analysis, demonstrating similarity in the female "community" using these roosts. Six major groupings are apparent, suggesting that females live in groups whose adult female composition is fairly stable (Fig. 3a). A similar pattern is shown by male bats, however, neighbouring roosts do not necessarily cluster together (Fig. 3b), suggesting greater movement between nonadjacent culverts for males than for females.

Fig 3 (a)

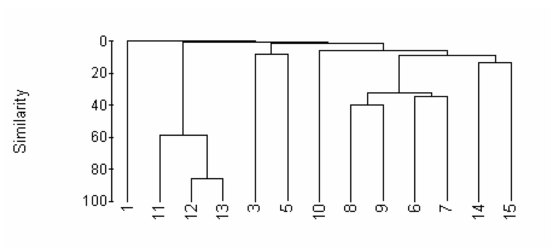

Fig 3 (b)

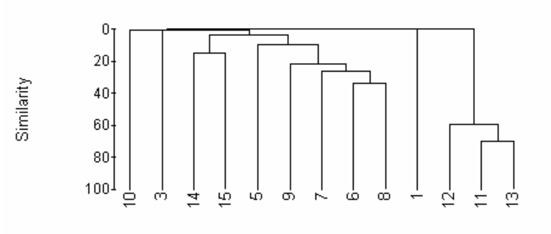

Fig. 3. – Cluster analysis showing relationships between culverts based on : a) female and b) male *Nycteris thebaica* roosting in the 15 culverts. The numbers refer to culvert numbers presented in Table 3. The six female groups are as follows : group 1 (culvert 1), group 2 (culverts 3 & 5), group 3 (culverts 6, 7, 8 & 9), group 4 (culvert 10), group 5 (culverts 11, 12 & 13), group 6 (culverts 14 & 15).

TABLE 3

Total number, mean number and adult sex ratio (male :female) of bats recorded in each of the 15 culverts, and rates of occupancy. Culverts 6 and 7 were surveyed 19 times each; all remaining roosts were surveyed 16 times (see Methods).

	Culverts														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Proportion of visits occupied.	0.50	0	0.31	0	0.25	0.26	0.42	0.69	0.81	0.25	0.38	0.31	0.31	0.31	0.88
No. of bats.	48	0	65	0	92	216	210	345	373	33	19	13	16	41	364
No. of bats/visit when occupied.	6	-	13	-	23	43	26	32	29	8	3	3	3	8	27
Adult sex ratio.	0.21	-	0.45	-	0.62	0.18	0.14	0.24	0.23	0.18	0.20	0.25	0.83	0.44	0.23

DISCUSSION

The proportion of new (unbanded) adults decreased over the duration of the study, demonstrating that levels of immigration into the study population are low. This suggests that emigration from the study area may be correspondingly low. Similar low levels of dispersal have been reported for other species of microchiropteran bats (O'DONNELL, 2000; SWIFT, 1998). Thus, the recapture rates of banded bats in this study are thought to reflect survival.

Juvenile sex ratio did not deviate from parity. The sex ratio of the 1998 cohort, though biased toward males, was not statistically significant and probably a result of the small sample size, which in turn was due to the fact that only two out of 15 culverts were surveyed in that year. The female-biased adult sex ratio (MONADJEM, 2001), therefore, must be a result of differences in survival and/or dispersal after weaning. Rates of recapture were higher for females than for males. Whether this is due to greater mortality among males or whether a greater proportion of males disperse from natal roost sites is not known. However, the sex ratio of immigrant (unbanded) bats is not different from that of resident (banded) bats (male :female = 0.41 and 0.47, respectively; $\chi^2 = 0.830$, $P > 0.05$), suggesting that the skewed sex ratio may be due to differential survival rates. Greater female survival has also been reported for *Chalinolobus tuberculatus* (O'Donnell, 2002) and *Plecotus auritus* (Swift, 1998).

Nycteris thebaica is long-lived with relatively high rates of adult survival. More than a fifth of the adult females captured at the beginning of the study survived at least five years. Comparable results for other species of African bats are severely limited. *Miniopterus schreibersii natalensis* has been shown to survive at least 13 years but survival rates were not estimated (Van Der Merwe, 1989).

Mortality rates, in contrast, were high in the first year after birth and varied between years. The high survival rate of females born in 1998 may have been due to the small number of juveniles sampled in that year. The apparently low survival of males and females born in 2001 is probably an artifact of methodology. Survival to one year was indicated not only by recaptures after exactly one year, but also subsequent recapture of individuals one-and-a-half, two or more years later. Thus an individual recaptured for the first time after two years, would have been registered as being alive after one year, even though it was not captured at that time. For this reason, the survival values for this cohort may increase with subsequent sampling. Excluding 2001 values, average first year survival was 0.42 for females and 0.29 for males. This is slightly lower compared with estimates for *Chalinolobus tuberculatus* from New Zealand (O'Donnell, 2002), but in the range of estimates for microchiropterans from the Northern Hemisphere such as *Eptesicus fuscus* (Mills et al., 1975), and *Myotis myotis* (Zahn, 1999).

Aldridge et al., (1990) and Churchill et al., (1997) provided limited data on the roosting habits of *Nycteris thebaica*, while Fenton et al., (1987), based on a sample of five adults, showed that *Nycteris grandis* may exhibit roost fidelity. In contrast, this paper is the first to report on roost occupancy and fidelity for any Nycteridae based on a large number of banded individuals surveyed over several breeding seasons. Female *Nycteris thebaica* exhibited roost site fidelity returning to the same culvert or neighbouring set of culverts. This is despite the relative proximity of the fifteen culverts. *Nycteris thebaica*, therefore, appears to be a sedentary species with females forming groups of fairly stable composition.

The formation of groups of stable composition has also been observed in other African bats including *Myotis bocagii* (Brosset, 1976), *Coleura afra* (McWilliam, 1987), *Tadarida pumila* (McWilliam, 1988) and in non-African species such as *Chalinolobus tuberculatus* (O'Donnell, 2002). Roost fidelity has been observed in several African microchiropterans including *Hipposideros commersoni* (Vaughan, 1977), *Rhinolophus hidebrandti* and *Tadarida midas* (Fenton & Rautenbach, 1986), *Coleura afra* (McWilliam, 1987), *Tadarida pumila* (McWilliam, 1988) and male *Pipistrellus nanus* (Happold & Happold, 1996). In contrast, *Scotophilus leucogaster* (Fenton, 1983) and *S. viridis/S. borbonicus* (Fenton et al., 1985) regularly switch day roosts.

Male *Nycteris thebaica* exhibited less roost site fidelity than females. Movement between roosts was greater in males than females. Males, therefore, appeared not to be tied down to one particular culvert or group of adjacent culverts. This was illustrated by the fact that a male *Nycteris thebaica* originally banded at a different location was recaptured at this study site, representing a distance of approximately 9 km.

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REFERENCES

Aldridge, H.D.J.N., M. Obrist, H.G. Merriam & B. Fenton (1990). Roosting, vocalizations, and foraging by the African bat, *Nycteris thebaica. J. Mammal.*, 71 : 242-246.

Bowie, R.C.K., D.S. Jacobs & P.J. Taylor (1999). Resource use by two morphologically similar insectivorous bats (*Nycteris thebaica* and *Hipposideros caffer*). *S. Afr. J. Zool.*, 34 : 27-33.

Brosset, A. (1976). Social organization in the African bat, *Myotis bocagei. Zeitschrift fur Tierpsychologie*, 42 : 50-56.

Churchill, S., R. Draper & E. Marais (1997). Cave utilization by Namibian bats : population, microclimate and roost selection. *S. Afr. J. Wildl. Res.*, 27 : 44-50.

Clarke, K.R. & R.N. Gorley (2001). *Primer v5 : user manual.* Plymouth Marine Laboratory, Plymouth.

Fenton, M.B. (1983). Roosts used by the African bat, *Scotophilus leucogaster* (Chiroptera : Vespertilionidae). *Biotropica*, 15 : 129-132.

Fenton, M.B., R.M. Brigham, A.M. Mills & I.L. Rautenbach (1985). The roosting and foraging areas of *Epomophorus wahlbergi* (Pteropodidae) and *Scotophilus viridis* (Vespertilionidae) in Kruger National Park, South Africa. *J. Mammal.*, 66 : 461-468.

Fenton, M.B., D.H.M. Cumming, J.M. Hutton & C.M. Swanepoel (1987). Foraging and habitat use by *Nycteris grandis* (Chiroptera : Nycteridae) in Zimbabwe. *J. Zool., Lond.*, 211 : 709-716.

Fenton, M.B. & I.L. Rautenbach (1986). A comparison of the roosting and foraging behaviours of three species of African insectivorous bats (Rhinolophidae, Vespertilionidae, and Molossidae). *Can. J. Zool.*, 64 : 2860-2867.

Happold, D.C.D. & M. Happold (1990). The domiciles, reproduction, social organization and sex ratios of the Banana Bat, *Pipistrellus nanus* (Chiroptera : Vespertilionidae) in Malawi, Central Africa. *Zeitschrift fur Saugetierkunde*, 55 : 145-160.

Happold, D.C.D. & M. Happold (1996). The social organisation and population dynamics of leaf-roosting banana bats, *Pipistrellus nanus* (Chiroptera : Vespertilionidae), in Malawi, east-central Africa. *Mammalia*, 60 : 517-544.

Laval, R.K. & M.L. Laval (1977). Reproduction and behaviour of the African Banana Bat, *Pipistrellus nanus. J. Mammal.*, 58 : 403-410.

McWilliam, A.N. (1987). The reproductive and social biology of *Coleura afra* in a seasonal environment. In : Fenton, M.B., P. Racey & J.M.V. Rayner (eds), *Recent advances in the study of bats.* Cambridge University Press : 324-350.

McWilliam, A.N. (1988). Social organization of the bat *Tadarida (Chaerephon) pumila* (Chiroptera : Molossidae) in Ghana, West Africa. *Ethology*, 77 : 115-124.

Mills, R.W., G.W. Barrett & M.P. Farrell (1975). Population dynamics of the big brown bat (*Eptesicus fuscus*) in southwestern Ohio. *J. Mammal.*, 56 : 591-604.

MONADJEM, A. (1998). *Mammals of Swaziland*. The Conservation Trust of Swaziland and Big Game Parks, Mbabane.

MONADJEM, A. (2001). Sexual dimorphism, sex ratio and preliminary recapture rates of *Nycteris thebaica* (Nycteridae : Chiroptera) in Swaziland. *Durban Mus. Novit*, 26 : 49-52.

O'DONNELL, C.F.J. (2000). Cryptic local populations in a temperate rainforest bat *Chalinolobus tuberculatus* in New Zealand. *Anim. Conserv.*, 3 : 287-297.

O'DONNELL, C.F.J. (2002). Timing of breeding, productivity and survival of long-tailed bats *Chalinolobus tuberculatus* (Chiroptera : Vespertilionidae) in cold-temperate rainforest in New Zealand. *J. Zool., Lond.*, 257 : 311-323.

O'SHEA, T.J. (1980). Roosting, social organization and annual cycle in a Kenya population of the bat *Pipistrellus nanus*. *Zeitschrift fur Tierpsychologie*, 53 : 171-195.

SEAMARK, E.C.J. & W. BOGDANOWICZ (2002). Feeding ecology of the common slit-faced bat (*Nycteris thebaica*) in KwaZulu-Natal, South Africa. *Acta Chiropterologica*, 4 : 49-54.

SMITHERS (1983). *The mammals of the southern African subregion*. University of Pretoria, Pretoria.

SWIFT, S.M. (1998). *Long-eared bats*. T & AD POYSER, Natural History, London.

TAYLOR, P.J. (1998). *The smaller mammals of KwaZulu-Natal*. University of Natal Press, Pietermaritzburg.

TAYLOR, P.J. (2000). *Bats of southern Africa*. University of Natal Press, Pietermaritzburg.

VAN DER MERWE, M. (1989). Longevity in Schreibers' long-fingered bat. *S. Afr. J. Wildl. Res.*, 19 : 87-89.

VAUGHAN, T.A. (1977). Foraging behaviour of the giant leaf-nosed bat (*Hipposideros commersoni). East African Wildlife Journal*, 15 : 237-249.

WICKER, W. & D. UHRIG (1969). Verhalten und okologische nische der gelbflugelfledermaus *Lavia frons* (Geoffroy) (Chiroptera, Megadermatidae) *Zeitschrift fur Tierpsychologie*, 26 : 726-736.

ZAHN, A. (1999). Reproductive success, colony size and roost temperature in attic-dwelling bat *Myotis myotis*. *J. Zool., (Lond.)*, 247 : 275-280.