

# Group composition and social events of the banana bat, *Neoromicia nanus*, in Mpumalanga, South Africa

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The social structure of banana bats (*Neoromicia nanus*) was studied in relation to reproductive events over an annual cycle in banana plantations in Mpumalanga Province, South Africa. Banana plantations were visited at monthly periods over a year, and social group composition was investigated. Group composition varied considerably over the annual cycle, and was linked to reproductive status. Mixed-sex groups began to form during February, lasted until October, and were most frequent during mid winter (July). During the lactation period (Oct–Jan), females formed maternity colonies composed of lactating females and juveniles. Three kinds of leaf tubes were identified according to the size of the opening: small (0–20 mm), medium-sized (21–115 mm) and large (115 mm-unfolded leaf). Bats occupied mainly medium-sized leaf tubes. Average daily temperatures were high, even during the winter period (Jun–Aug), with humidity in the leaf tubes >80% throughout the year. Although high humidity may play a role during hibernation to restrict dehydration, low ambient temperatures are important to sufficiently lower their body temperatures in order to lower metabolic rate and thus reduces energy requirements.

**Key words:** banana bat, *Neoromicia nanus*, sex ratio, mating strategies, social structure.

## INTRODUCTION

The banana bat, *Neoromicia nanus*, occurs throughout Africa south of the Sahara, except in the arid zones (Happold & Happold 1990; Bernard *et al.* 1997; Taylor 2000). Throughout its range it commonly roosts in the banana and plantain stems, commonly choosing the long narrow tubes formed by the unfolded terminal leaves (Rosevear 1965; Laval & Laval 1977; Happold & Happold 1990, 1996)

Parental investment in bats is high compared to other small mammals (Hayssen & Kunz 1996). Female bats invest long time periods in gestation and lactation and suckle their young until they are nearly adult in size (Kunz 1987).

Lactation is the most energetically expensive period for female mammals and is associated with some of the highest sustained metabolic rates in vertebrates (Loudon & Racey 1987; Mellish *et al.* 2000), and in insectivorous bats lactation is considerably more costly than pregnancy (Racey & Speakman 1987). Bats also have an energetically expensive mode of locomotion, which during lactation accounts for 66% of energy requirements (Kurta *et al.* 1989). Although the costs of reproduc-

tion remain relatively low during pregnancy, they increase dramatically during lactation when they are estimated to be 50% greater than those in other pregnant animals (Kurta *et al.* 1989). Bats have developed strategies to offset these high energetic costs. For example, many chiropteran species have extended gestation periods (Mutere 1967; Fleming 1971; Racey 1973, 1979; Hayssen & Kunz 1996). The period from mating to conception is also regularly extended by timing delays, which include sperm storage (Racey 1979), delayed implantation (Mutere 1967), delayed development (Fleming 1971) and slowed foetal growth (Racey 1973). Terrestrial mammals meet these energetic requirements for lactation by increased food intake (Vernon 1988) as well as mobilization of body reserves accumulated during pregnancy (Bauman & Elliot 1983). Lactating bats which are dependent on aerial foraging would not gain much by such strategies as the energetic cost of flight would make any increase in body weight disadvantageous (Wilde *et al.* 1999). Furthermore, the metabolic load of lactation cannot be significantly met by mobilizing body stores accumulated during pregnancy (Racey & Speakman 1987). The principal mechanism for energy conservation thus appears to be the bat's ability to enter torpor during

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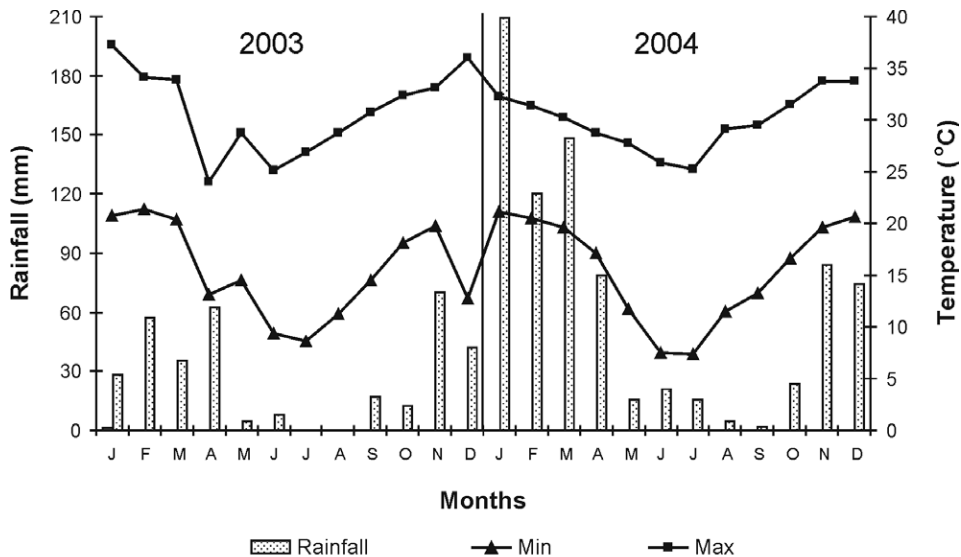


Fig. 1. Mean monthly rainfall with mean maximum and minimum daily temperatures.

pregnancy (Racey & Swift 1981) and lactation (Racey & Speakman 1987; Wilde *et al.* 1999). Furthermore, because flight is energetically expensive, the production of high fat milk may play an important strategy to minimize the cost of flight and at the same time maximize energy transfer to the pups (Kunz *et al.* 1995). Stern *et al.* (1997) found a high degree of variability in milk composition at the same stage of lactation intraspecifically, and predicted that for bats individual differences in milk yield will influence both pup growth and mortality.

Bats spend a significant period of their lives roosting (Kunz 1982) and the availability and abundance of suitable roosts are essential for the success of bat populations (Humphrey 1975; Fenton 1983). Environmental factors such as the abundance, distribution and duration of suitable roosts may, however, change throughout the year in such a way as to reduce the benefits of group living (Lott 1991), which results in intra-annual fluctuation in group composition. As bats show little fidelity to foliage roosts that are abundant and temporary (Kunz 1982), banana bats have to seek new roosts on a regular basis because banana leaves remained furled for only relative short periods.

The present study provides a description of the social behaviour of the banana bat over an annual cycle in the subtropical region of Mpumalanga, South Africa. The purpose of the present study was to determine changes in group formation over the annual cycle and how they are linked with the

timing of reproductive events. Our specific objectives were: (1) to describe the characteristics and availability of roosts used by the banana bat throughout the year and (2) to obtain information about the composition and social behaviour of the banana bats during the various months of the year.

#### MATERIAL AND METHODS

We conducted fieldwork in four commercial banana plantations on the farm Laughing Waters about 25 km south of Malelane (altitude 271 m) in the Mpumalanga Lowveld, South Africa (25°30'S 31°30'E). Each plantation is divided into several blocks or patches by service roads, with banana plants (mainly the dwarf Cavendish cultivar of *Musa acuminata*) spaced in rows 1.5 m apart separated by footpaths. The study area is situated in the Lowveld plains and has a mild to hot subtropical climate with hot, wet summers and cool, dry winters (Fig. 1).

Visits to banana plantations were conducted at monthly intervals (January to December) during 2003, except for June 2003 (data were collected instead in June 2004). During systematic walks in the banana plantations, we counted all the banana plants on each side of the footpath as well as their unfurled leaves (leaf tubes) (Table 1), and checked each for the presence of bats. Unfurled leaves were categorized into small (0–20 mm), medium-sized (21–115 mm) and large (116 mm–unfurled leaf) size classes, based on the diameter of the

**Table 1.** Number of banana plants counted in the rows as well as the number of small, medium-sized and large leaf tubes found on them.

Months	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
No. of plants	4 767	6 304	8 233	8 818	16 910	6 158	6 138	5 341	4 943	6 614	4 723	6 656
No. of small leaf tubes	709	1 211	1 195	1 755	2 096	1 272	1 202	680	1 334	1 878	999	1 718
No. of medium leaf tubes	335	465	548	585	1 114	556	565	364	649	480	344	648
No. of medium leaf tubes*	359	317	405	572	331	148	184	123	126	493	487	207
No. of large leaf tubes	177	252	279	3802	687	244	250	203	290	277	173	140

\*Number of medium-sized leaf tubes checked randomly throughout the plantations.

opening of the leaf tube. Furthermore, in the rest of the plantations medium-sized leaves (preferred by the bats) were also randomly checked for the presence of bats. Humidity within the leaf tubes was recorded by randomly selecting 10 medium-sized leaf tubes within the plantation. Means  $\pm$  S.E. were then calculated for a three-day period on each visit. Humidity (Fig. 2) was recorded with a portable Ama-digit digital Temp/Humidity meter.

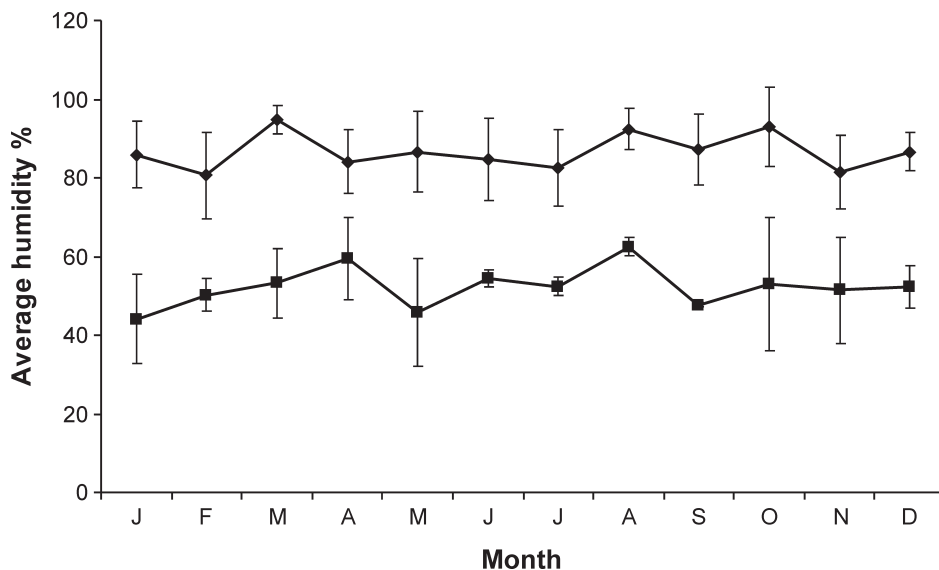
When bats were present, the opening was covered with a small net bag, and the leaf gently squeezed from bottom to top to force the bats out. The bats in each leaf tube were counted, sexed and classed as adults or juveniles, and designated to a specific roosting group (see below). Those that were not collected for histological studies (Van der Merwe & Stirnemann 2007) were released. Roosting groups were divided into one of seven social categories: (1) single males, (2) mixed groups of one male and one female, (3) mixed groups of one male and 2–7 females, (4) single

females, (5) groups of females without males, (6) groups of males without females (7) groups of two males and two or more females (Table 2). Groups 6 and 7 were not considered in the results because only on two occasions were two males found together and only on one occasion were two males found with two females in the same leaf tube. Histological studies of the reproductive tracts (Van der Merwe & Stirnemann 2007) provided reproductive information used in this paper. Weather data were obtained from the South African Weather Service in Pretoria. Average monthly rainfall (mm) for the Malelane area for the months October to February to show the normal rainfall pattern for those months were taken between 1938 to 2008.

## RESULTS

### Roosts

Almost all bats (99%) occupied medium-sized leaf tubes with an average length and opening



**Fig. 2.** Relative humidity (%) outside (■) and inside (◆) the leaf tubes ( $\pm$ S.E.)

**Table 2.** Roosting composition of male and female *Neoromicia nanus* in relation to major events in the reproductive cycle (reproductive information taken from Van der Merwe & Stirnemann 2007). Values indicate the total number of bats found in each of the social roosting groups, while percentages indicate the contribution that a specific social roosting group makes to the composition of the male and female groups.

Month	Reproductive event	Total <i>n</i>	Single males	Single females	Female groups	1 Female: 1 male		Female group: 1 male	
						F	M	F	M
Jan	Lactation	96	32 100%	51 80%	13 20%	0 0%	0 0%	0 0%	0 0%
Feb	Post-lactation Juv. weaned	140	51 78%	47 63%	12 16%	13 17%	13 20%	3 4%	1 2%
Mar	Post-lactation	167	80 83%	39 55%	14 20%	15 21%	15 16%	3 4%	1 1%
Apr	Post-lactation Copulations No ovulation	169	70 75%	23 30%	12 16%	15 20%	15 16%	26 34%	8 9%
May	Copulations No ovulation	94	34 65%	16 38%	2 5%	13 31%	13 25%	11 26%	5 10%
Jun	Copulations No ovulation	15	3 60%	5 50%	2 20%	1 10%	1 20%	2 20%	1 20%
Jul	Copulations No ovulation	106	16 32%	10 18%	0 0%	27 48%	27 54%	19 34%	7 14%
Aug	Ovulation Fertilization Implantation	73	24 77%	24 57%	10 24%	6 14%	6 19%	2 5%	1 3%
Sep	Pregnant	50	15 75%	10 33%	14 47%	4 13%	4 20%	2 7%	1 5%
Oct	Pregnant Parturition Lactation	146	56 78%	20 27%	18 24%	6 8%	6 8%	30 41%	10 14%
Nov	Pregnant Parturition Lactation	244	62 100%	58 32%	124 68%	0 0%	0 0%	0 0%	0 0%
Dec	Lactation	202	112 100%	57 63%	33 37%	0 0%	0 0%	0 0%	0 0%

diameter of 1240.3 mm ( $\pm 155.8$  S.D.) and 77.9 mm ( $\pm 27.2$  S.D.), respectively. Bats occasionally roosted in large leaf tubes (opening  $> 115$  mm) (36 bats, 1% occupancy of leaf tubes examined), but almost never in small leaf tubes (opening  $< 20$  mm) (2 bats; 0.01% occupancy).

Examination of 85 605 banana plants (Table 1; Fig. 3) revealed that suitable leaf tubes (medium-sized tubes) were available throughout the year and that there was never a scarcity of such leaves. As these leaf tubes unfolded and became unsuitable for occupancy, bats moved to new leaf tubes. In the study area bats were never found to occupy anything else other than the rolled banana leaves. Wild strelitzias (*Strelitzia caudata* or *S. nicolai*),

which can also accommodate banana bats, were not found in the study area. On each visit to the banana plantations, 17–35% of medium-sized leaf tubes were found to be occupied. With the exception of five cases, all bats were clinging to the sides of the leaf tubes with their heads facing towards the opening. The number of bats observed during the various months is illustrated in Table 2 and Fig. 4.

### Roosting groupings

Banana bats appeared to be active throughout the year with no indication of prolonged hibernation during the colder months (June and July). Average monthly ambient temperatures are illus-

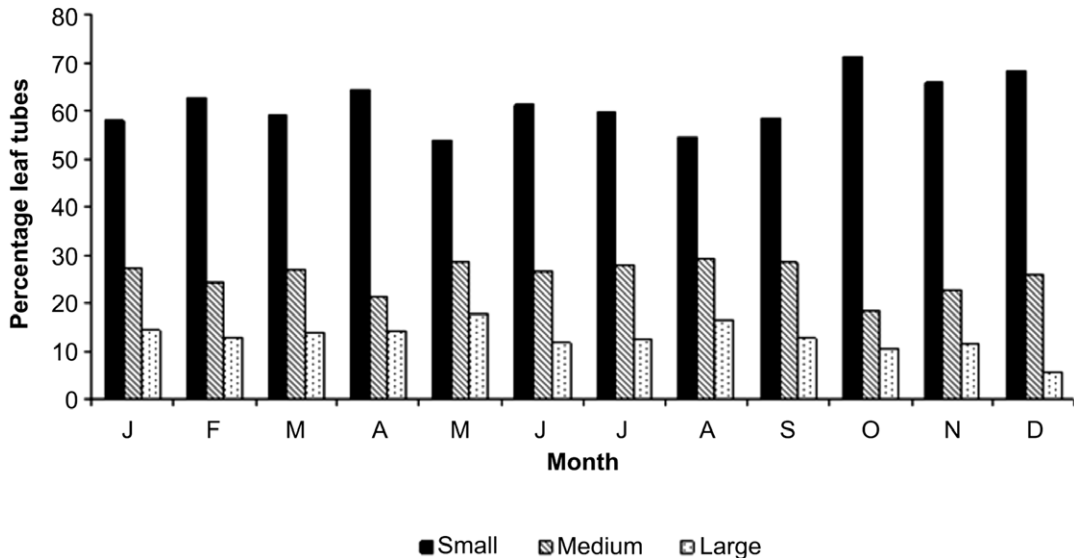


Fig. 3. Percentage of small, medium-sized and large leaf tubes available throughout the year.

trated in Fig. 1. Humidity within the leaf tubes was always above 80% which on average was 34.5% ( $\pm 5.9$  S.D.) higher than on the outside (range 24.7–41.7%) (Fig. 2).

Seasonal changes in sex ratio, age structure and size of roosting groups were observed (Table 2). The latter varied between one and 11. Group composition was made up of various combinations of males, females and juveniles. Throughout the year adult male banana bats roosted solitarily or in groups with one or more females. In nearly all the cases examined, adult males avoided roosting together irrespective of the breeding season. From February to October mixed groups, consisting of a single male and one to seven females, formed. The number of female bats found roosting in mixed groups with males increased significantly from February to July (Table 2; chi-square test  $\chi^2 = 64.13$ , d.f. = 4,  $P < 0.001$ ; with June excluded from analyses due to the small sample size). In July, 82% of all female specimens examined were in mixed groups composed of one male and one female or one male and a group of females (Table 2). The great increase of females in mixed groups during July was just prior to the ovulation and fertilization period in August (Table 2), and numbered twice as many females roosting with males as during any of the other months (Table 2).

Females were pregnant from August to late October/November. From August to November female groups without the presence of a male increased slightly (Table 2). The presence of

males in male–female groups decreased to 0% immediately following parturition in November, and lasted until February. At the start of the lactation period (November), most females roosted together (68%). However, as the lactation period progressed, a significant decrease in females grouping together, with a corresponding increase in females roosting alone was observed ( $\chi^2 = 52.86$ , d.f. = 2,  $P < 0.001$ ). In January, 80% of the females roosted alone (Table 2).

## DISCUSSION

The rolled leaves of banana plants are available in abundance relative to bat densities (LaVal & LaVal 1977) and a surplus of rolled leaves was always available (Happold & Happold 1990, 1996). In the present study area *Neoromicia nanus* occupied less than 35% of the suitably-sized leaves available (medium-sized leaf tubes), indicating that group formation is not the result of a shortage of furled leaves.

LaVal & LaVal (1977) mentioned that it was not clear from their study why some adult bats form groups, when most of them choose to roost singly, and roost sites are in abundance. Happold & Happold (1990) gave three reasons why furled banana leaves provide suitable roosting conditions for banana bats: the leaves are available perennially; the humid microclimate within the furled leaves, caused by transpiration, limits dehydration during the day; and intraspecific competition for suitable leaves is limited.

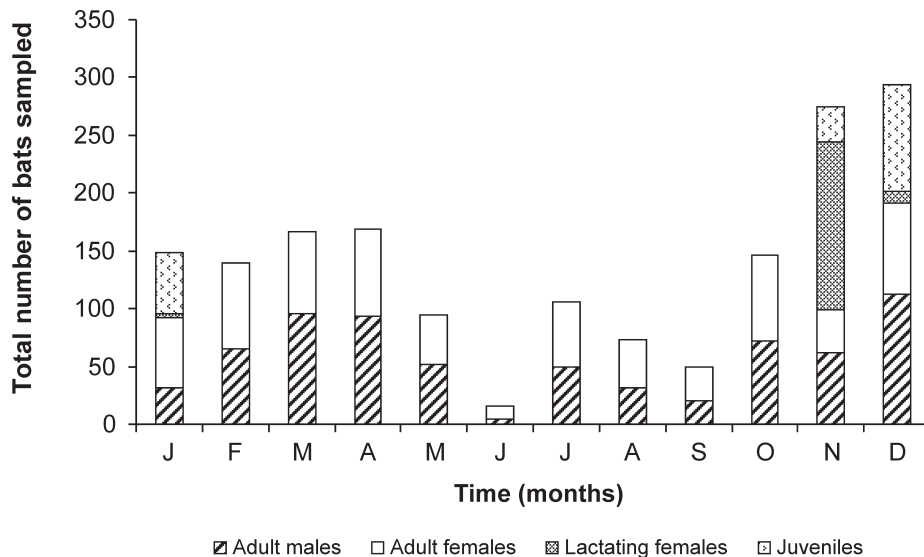


Fig. 4. Total numbers of males, lactating and non-lactating females and juveniles caught each month.

Banana bats must move around to seek suitable furred leaves on a regular basis, and during lactation have to fly around carrying twins or singletons while seeking new furred leaves. This is because banana leaves are suitable roosts for only 1–3 days before they unfurl (Happold & Happold 1990, 1996). In KwaZulu-Natal, LaVal & LaVal (1977) found that furred leaves are only suitable for a few days and when the opening diameter exceeds approximately 160 mm, they are no longer utilized by the bats. Findley & Wilson (1974), in southwestern Costa Rica, found that groups of the Neotropical disk-winged bat (*Thyroptera tricolor*) that roost in the rolled leaves of the banana family Musaceae or related plants, change roost sites nearly every day, as the leaves are in the favourable size range (opening 50–100 mm) for only about 24 hours. In northeastern Costa Rica the same species occupies mainly the rolled leaves of *Heliconia* and *Calathea* plants. Here the duration that they can utilize a leaf as shelter is also relatively short (average 8–16 h; maximum 28–60 h, depending on the plant species) (Vonhof & Fenton 2004). Although we did not mark leaf tubes, we noticed that they become unsuitable for bat occupancy within a few days. We also did not find adult bats in the same tubes from which we had collected them the previous day. If there were juveniles in the leaf tubes that we disturbed, we found that they had been removed by the next day. Another factor that may limit a leaf's use is the accumulation of fresh guano on the inner

surface of the leaf which may soil the bat's fur, causing it to avoid the leaf (LaVal & LaVal 1977).

Except for possible daily torpor, the banana bats in Mpumalanga did not appear to hibernate. During all the months (January to December) when the plantations were visited, the bats became active immediately and either rapidly crawled deeper into the leaf tube or flew out. Because they can only stay in a leaf tube for a few days, banana bats have to fly around seeking suitable leaf tubes throughout the year. LaVal & LaVal (1977) also mentioned never having found banana bats in torpor in KwaZulu-Natal.

Smithers (1983) stated that banana bats hang head down in the furred banana leaves, but our study revealed that, with the exception of five individuals, the bats usually roosted with their heads facing towards the leaf opening. Similarly, *Thyroptera tricolor* arrange themselves in the head-up position in unfurred leaves (Kunz 1982).

It is noteworthy that the formation of roosting groups in the banana bat is closely related to the reproductive cycle and, with the exception of a few differences (see Van der Merwe & Stirnemann 2007), is very similar to those described for the banana bat in Malawi (Happold & Happold 1990, 1996; Bernard *et al.* 1997). Similar to the study of Bernard *et al.* (1997) no males were found roosting with the females during the lactation period (Table 2). The duration of the various reproductive events in the Malawi and Mpumalanga bats appears to be very similar; however, mating in

Malawi occurs between mid-June and early July, followed by sperm storage in both males and females (Bernard *et al.* 1997), while it takes place between late April to late August in the study area, with no apparent sperm storage in either males and females (Van der Merwe & Stirnemann 2007). It would appear that the various reproductive events in the study area occurs two to three weeks earlier than in Malawi, rather than more or less a month as reported during a previous study (Van der Merwe & Stirnemann 2007). Small discrepancies between the results of this study and that of Bernard *et al.* (1997) can perhaps partly be attributed to small sample sizes, time of the month that collections were made, and inconsistencies between the two studies. Mating is an obligatory social event and central to the organization of any species, and variation in social structure can lead to different mating systems between populations of the same species (Clutton-Brock 1989).

Female banana bats give birth at the end of October and in November in Mpumalanga (Van der Merwe & Stirnemann 2007). During lactation, female banana bats form maternity roosting groups, while males roost alone. In other bat species clustering during the major feeding season (maternity season) serves to conserve heat and to maintain the body temperature of the bats higher than that of the external environment (Twente 1955). The microclimate within maternity roosts can be modified substantially by the metabolic heat generated by roosting bats (Sedgeley 2001). Increases in roost temperatures can be as much as 7°C, and there is a significant positive correlation between the number of bats occupying a roost, maximum daily roost temperature, and energy savings (Willis & Brigham 2007). This higher body temperature is necessary in order that digestion and assimilation may proceed efficiently (Twente 1955). Lactation coincides with warmer ambient temperatures (Lewis 1996), and energy invested by lactating females in other activities such as social contact and grooming represents a relatively small part of maternal investment (Kunz 1987). Furthermore, bats in groups are found to have lower energy expenditure than single individuals (Herreid 1963), and clustering provides distinct energetic advantages in terms of reduction of metabolic rates (Trune & Slobodchikoff 1976). Through clustering behaviour and the selection of roost sites bats can markedly alter the microclimate to which the young are exposed (Tuttle 1975). Warmer roost temperatures promote faster prena-

tal growth rates and may be a selective advantage if it results in earlier parturition (Racey 1973). Such conditions also appear to promote rapid post-natal growth, minimize heat loss from suckling and reduce the maintenance cost to females during the costly period of lactation (Kunz 1987; Kurta & Kunz 1987).

In the present study there was a significant decrease in females roosting together during the lactation period (Nov–Jan), with a significant increase in females roosting alone during the same period (Table 2; see Results section). During this period ambient temperatures were highest (Fig. 1) with humidity >80% in the leaf tubes (Fig. 2). It is therefore unlikely that female banana bats form roosts for thermoregulatory energy-saving benefits. During all months of the year, with the exception of September and November, more females roosted alone than in groups. During this period females were pregnant or lactating (Table 2).

Although the mean maximum and minimum temperatures in the study area (Fig. 1) tended to be higher than those in the Malawi study, monthly rainfall in Malawi was much higher (see Bernard *et al.* 1997). Rainfall in the study area, especially during the summer months of 2003, was well below average for that area (normal range: Oct 46.8 ± 31.5 S.D.; Nov 92.9 ± 56.7 S.D.; Dec 94.2 ± 59.2 S.D.; Jan 103.5 ± 75.7 S.D.; Feb 97.3 ± 89.5 S.D.). Bats from temperate latitudes give birth only during the summer months (Oxberry 1979), when insect food supply is at a peak due to the high rainfall (Taylor 1963; see Racey 1982). Cumming & Bernard (1997) showed that insect abundance peaks approximately a month after peak rainfall, and that African microchiropterans give birth roughly a month before the peak in rainfall. Thus, according to them, insect abundance peaks approximately two months after microchiropteran parturition, and with an average six-week lactation period, the timing of parturition is such that young bats are weaned just before the period of maximum insect abundance. In a study on the greater spear-nosed bats, Porter & Wilkinson (2001) found that only 40% of the variability in birth dates could be explained by environmental factors, and that social events influencing the timing of reproduction could help to coordinate reproduction. Below-average rainfall in the study area during 2003 may have had a negative effect on insect numbers, which in turn may have adversely affected the bats, especially young inexperienced bats having to compete for food with experienced

adult bats. It is expected that the 2003 season may have led to the starvation of many bats. During the 2004 rainy season, the rainfall was higher than during 2003, which would have been more beneficial to the bats, due to higher insect numbers (Fig. 1)

Red bats (*Lasiurus borealis*), like most foliage-roosting bats, change roosts frequently (Miller 2003). Lewis (1996) found that 25 of 43 species of bats frequently change roosts. Lewis (1996) mentioned that pallid bats (*Antrozous pallidus*) frequently switch diurnal roost sites and also have a variety of cooperative social behaviours, many of which are associated with the care of developing offspring, and furthermore suggested that roost switching is likely to increase the costs of maintaining group stability expected with cooperative social behaviours. According to Lewis (1996), roost switching is not correlated with daily variations in weather conditions or with structural characteristics of the diurnal roosts, although switching may allow bats to maintain familiarity with several roosts that vary in microclimate. Movement from an established living area has several potential costs, including time and energy spent to find a suitable home site, exposure to predators while searching for a site, and for adults with dependent offspring, additional costs of carrying or leading the new young to the new site (Alcock 1989). In small enclosed roosts such as the rock crevices occupied by pallid bats, there are few opportunities for the bats to adjust to climatic changes by moving within the roost (Kronwiter 1988) which may make periodic roost changes advantageous.

Females 'baby sit' crèches of juveniles while other females forage (Beck & Rudd 1960). The same has been observed for *Anoura geoffroyi* (Galindo-Galindo *et al.* 2000) and *Myotis thysanodes* (O'Farrell & Studier 1973). Maintaining social bonds between roost mates requires greater energy for searching and communication than would be needed simply to locate any group of roosting bats (Lewis 1996). In KwaZulu-Natal LaVal & LaVal (1977) found no evidence of group continuity in the banana bat and mentioned that the bats find their roost partners (if any) by chance. This latter statement of LaVal & LaVal (1977), however, places doubt on their assumption that there is a possibility of group nursing or 'baby sitting' in banana bats. They further mentioned that most of the recaptured bats were in the original patch, within 10 m to 100 m of the leaf where they were banded. Although we did not band any bats, it is

likely that they remain in the same plantations (older plantations). Only occasionally single banana bats were found in younger plantations nearby or in areas surrounding the older plantations.

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