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The domiciles, reproduction, social organisation and sex ratios of the Banana Bat *Pipistrellus nanus* (Chiroptera, Vespertilionidae) in Malawi, Central Africa

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Abstract

Investigated were the domiciles, reproduction, social organisation and sex ratios of the Banana Bat, *Pipistrellus nanus*, in Malawi. The bats were taken from furled banana leaves at fortnightly or monthly intervals from September 1984 to June 1985. The furled leaves were ephemeral domiciles lasting one to three days. A surplus of domiciles was always available. Females were monoestrus with the birth of twins in November and lactation lasted about eight weeks. The testes in males were scrotal from April to October, and attained maximal size in May. During lactation adult males roosted singly, while females with their young roosted singly or in maternity groups. Post-lactating females roosted singly or with groups of subadults and/or other post-lactating females, and the adult males continued to roost singly. In April, by which time the testes of all males have become scrotal, all bats were assumed to have reached sexual maturity and they began to live in harems (one adult male with one or more females). An equal number of males and females were born, but females outnumbered males for at least seven months of the year. The data from Malawi are compared with data from Kenya (O'Shea 1980), South Africa (Laval and Laval 1977), and elsewhere. Geographical variation in domiciles and reproduction, and the relationships between different aspects of the biology of *P. nanus*, are discussed.

Introduction

The Banana Bat, *Pipistrellus nanus* (Peters, 1852) occurs throughout Africa south of the Sahara, except in the arid zones. Throughout its range, it commonly roosts in the ephemeral furled leaves of bananas and other musaceous plants (Brosset 1966; Kingdon 1974; Laval and Laval 1977; Rosevear 1965; Verschuren 1957). Less commonly, it has been found in permanent domiciles such as thatch (O'Shea 1980; Rosevear 1965). Reproductive strategies of two kinds have been observed: aseasonal polyoestry (Anciaux de Faveaux 1972; Verschuren 1966) and seasonal monoestry (Laval and Laval 1977; O'Shea 1980). *Pipistrellus nanus* has been found singly, in pairs, in small groups and in colonies of up to 150 individuals (Laval and Laval 1977). In many parts of the geographical range, males outnumber females (O'Shea 1980; Verschuren 1957, 1966, 1982) but in South Africa adult males and females occur in equal numbers (Laval and Laval 1977).

Although many authors have described various aspects of the biology of *P. nanus*, two recent studies have concentrated on domiciles, reproduction, social organisation and sex ratios, and the relationships between them. The first study (Laval and Laval 1977) dealt with a population roosting in ephemeral furled leaves in the temperate climate of South Africa. The second (O'Shea 1980) dealt with a population roosting in permanent sites in thatch in the equatorial climate of Kenya. The present study deals with a population roosting in furled leaves at Zomba, in the southern region of Malawi. This locality has a highland tropical climate, and lies midway between Kenya and South Africa. The data

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from Kenya, Malawi and South Africa (and elsewhere) are compared to show the extent of geographical variation in some of the characteristics of *P. nanus*, and to investigate the ways in which domiciles, reproduction, social organisation and sex ratios might be interrelated.

The Study area

Malawi is located in Central Africa, from 9° 50′ S to 17° 00′ S, and from 33° 00′ E to 36° 00′ E. It lies in the southern savanna biotic zone as defined by DAVIS (1962). A brief description of the physiographic features and vegetation of this country is given in HAPPOLD et al. (1987) and further details are given by PIKE and RIMMINGTON (1965) and JACKSON (1969).

Malawi has a hot wet season from November to early April, a cool dry season from April to July, and a hot dry season from August to October. The duration of each season varies with latitude. The mean annual rainfall is 775–2164 mm, depending on locality, with most of the rain falling between November and March. Temperature regimes range from extremely hot in the Shire Valley to cool on the high plateaux. Further information about the climate of Malawi is given by PIKE and RIMMINGTON (1965), TORRANCE (1972) and MALAWI GOVERNMENT (1982).

This study was carried out principally at Zomba (15° 23′ S, 35° 19′ E; 800–900 m). This small town at the base of Zomba Plateau, has traditional and European-style buildings interspersed in a mosaic of ornamental gardens, maize and vegetable gardens, groves of bananas, plantations of exotic *Eucalyptus*, riverine forest, and *Brachystegia* woodland. Climatic data for Zomba are given in Fig. 1. The bats were collected from groves of bananas in and near Malonje Village in Zomba, and from the ornamental gardens of several colonial-style houses in the older part of Zomba. Additional data were obtained from Liwonde National Park (15° 02′ S, 35° 15′ E; 500 m) in the Upper Shire Valley, Lengwe National Park (16° 13′ S, 34° 46′ E; 100 m) in the Lower Shire Valley, and six other localities (HAPPOLD et al. 1987).

Material and methods

Banana Bats were taken from furled banana leaves, and caught in mistnets (details in HAPPOLD et al. 1987). At Zomba, the bats were taken from furled leaves in one of two ways. From September to November, the bats were collected by Malawian boys who folded the leaves to block the exit, and then took the bats out by hand. The bats were then placed in one bag and brought in for examination. From 12 December onwards, the authors and two of the boys used a 2 m long "butterfly-net" on a long pole, which was placed over each furled leaf. In this way, it was usually possible to capture all occupants of each leaf, and group compositions were recorded.

Samples were collected fortnightly from October to January (while females were pregnant or rearing young), and monthly from February to mid-June. Sample sizes were 8–45 bats. Adults were usually weighed to nearest 0.1 g (dead) or to nearest 0.5 g (live), and measured to nearest 0.5 mm. Details and results are given in HAPPOLD et al. (1987). To enable comparison with *P. nanus* from Kenya (investigated by O'SHEA 1980), 43 specimens (including both sexes) were examined for the presence of tail glands (paired oval glandular structures on either side of the tail on the anterior fourth of the interfemoral membrane). Reproductive condition was assessed by abdominal palpation and by examination of the nipples and external genitalia, or by autopsy.

Results

Domiciles of *P. nanus* in Malawi

Within Malawi, *P. nanus* has been found in furled banana leaves (this study), among the curled up leaves of *Uapaca kirkiana* (B. MORRIS unpubl.), and two were found, singly, in deserted nests of Weaver Birds (*Ploceus* sp.) by Tarwina Kapunda and Elwin M'banga (this study).

Pipistrellus nanus was found in furled banana leaves from 1 m to about 4 m above the ground. The diameter of the entrance to leaves was 3–24 cm, and the minimum diameter at the base was approximately 3 cm. The percentage occupancy of leaves having different entrance diameters was as follows:

Diameter 3– 6 cm (n = 9): none occupied
Diameter 7–12 cm (n = 32): 22 % occupied

Diameter 13–18 cm (n = 31): 42 % occupied
Diameter 19–24 cm (n = 42): 73 % occupied

Banana leaves unfurl rapidly and are therefore ephemeral domiciles. Rates of unfurling vary. In December, a sample of 17 leaves showed that seven were suitable for occupation for only one day, seven for two days, and three for three days. Furled banana leaves were available from August to June (this study), and are said to be available throughout the year. At no time during this study were all suitable leaves occupied. From December to March, 38–50 % of the suitable leaves examined were occupied by one or more bats. At the beginning of June, suitable leaves were less numerous and 90 % were occupied, but by mid-June they were more abundant, and only 50 % were occupied. No quantitative data are available for July to November. No other species of bats were found in the furled leaves at Zomba or elsewhere in Malawi, and no other vertebrates or invertebrates were found competing with *P. nanus* for furled leaves.

Torpor

At the end of December (mid wet season), some bats in furled leaves were torpid but others were not torpid. In June (cool dry season) all bats taken from furled leaves were torpid. Data are not available for other months. Daytime torpidity in *P. nanus* occurs in Kenya (O'Shea 1980), but not in Natal (Laval and Laval 1977). Since Kenya is tropical and hot, and Natal is temperate and cool, these observations are the opposite of what might be expected.

Litter-size

All pregnant females from Zomba (n = 23) had twin foetuses. Thirteen of these females were autopsied and each had one foetus (near end to term) in each uterine horn.

Male reproductive chronology at Zomba

Observations on the position and size of testes show that they descend in April, reach maximum size (5 × 3 mm) in May, start to decline in size in June, and become abdominal no later than mid-October (Figure and Table 1). Adult males did not roost with adult females from October to April, but were roosting with adult females by 1 June. This suggests that copulation occurs in May–June, but this has not been confirmed by other evidence. In all males, the testes reached maximum size and were scrotal by May indicating that males reach reproductive maturity when they are about six months old.

Female reproductive chronology at Zomba

Female *P. nanus* were conspicuously pregnant when this study began in early October; they gave birth during the first three weeks of November, and stopped lactating approximately eight weeks later during the first two weeks of January (Table 1). No females were pregnant between mid-November and mid-June when this study was curtailed, indicating that in Malawi, females are monoestrous. In mid-June, females which had lactated in November to January had nipples with a slightly raised rim, and could be distinguished from the seven-month old females which had not yet bred. In October, the difference in nipples was still apparent and distinguished primiparous females from those which had bred in the previous year(s). This indicates that females breed at least twice, but the longevity of the species is not known. Although it is assumed that copulation probably occurs in May–June (see above), the gestation period of *P. nanus* in Malawi cannot be determined without knowing if sperm storage in the uterus, or delayed implantation,

Table 1. **The reproductive condition of 302 male and female *Pipistrellus nanus* collected from Zomba, Malawi, October 1984 to June 1985**

Date	Sample Size (males, females)	Males			Females			
		Testes Abdominal	Testes Scrotal	Young Born November 1984	Pregnant	Lactating	Post-lactating	Young Born November 1984
6–9 Oct	6, 4	5	1	0	4	0	0	0
20 Oct	7, 7	7	0	0	7	0	0	0
31 Oct	6,12	6	0	0	12	0	0	0
16 Nov	16,15	16	0	+	7	8	0	+
25 Nov	5, 3	5	0	+	0	3	0	+
2 Dec	10,14	2	0	8	0	6	0	8
14 Dec	9, 9	6	0	3	0	2	0	7
21 Dec	0, 3	0	0	0	0	2	0	1
30 Dec	15,25	6	0	9	0	13	0	12
12 Jan	2,14	1	0	1	0	1	4	9
27 Jan	6,14	4	0	2	0	0	8	5
2 Mar	3,11	1	0	1	0	0	6	5
30 Mar	5,25	2	0	3	0	0	6	19
28 Apr	8,12	0	8^a		0	0	7	5
1 Jun	6,15	0	6^a		0	0	8	7
16 Jun	3,12	0	3^a		0	0	9	3

+ = neonates present but not sexed; ^{a} includes young males born November 1984 which could no longer be distinguished from older males

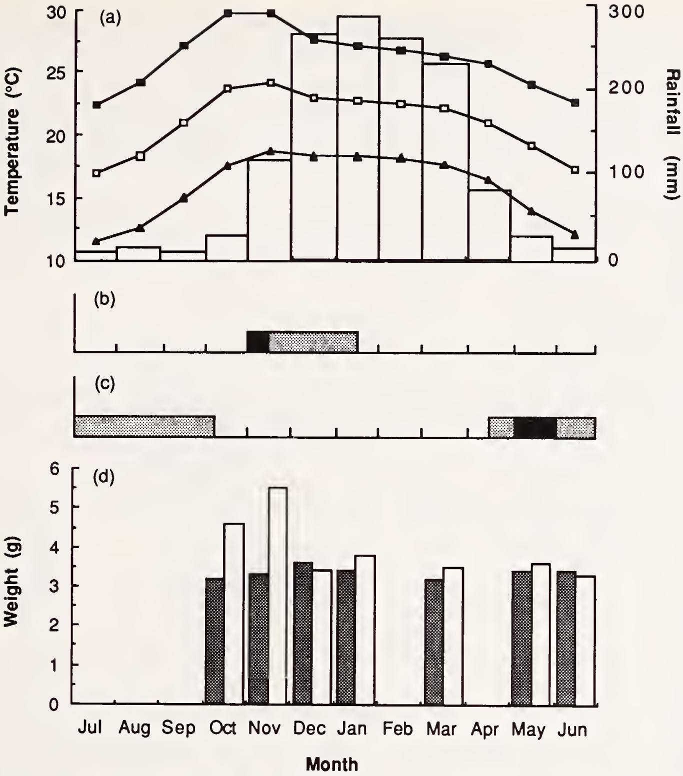
occur. Another possibility is that sperm produced in May is stored in the male epididymes until copulation occurs several months later (followed by the immediate onset of developmental gestation in the female), but the sudden change in roosting behaviour (see above) mitigates against this suggestion. Laval and Laval (1977) in Natal, and O'Shea (1980) in Kenya, were not able to resolve this problem, although O'Shea found that changing patterns of social behaviour suggested that copulation was occuring in May, well in advance of the period of developmental gestation.

In September and October, all females were pregnant showing that females attain reproductive maturity during their first year. One hundred percent pregnancy in large samples of females ($n > 20$) has also been recorded in Kenya (O'Shea 1980), Zimbabwe (Smithers and Wilson 1979) and Natal (Laval and Laval 1977).

Reproductive chronology is related to climate in Malawi: developmental gestation occurs during the dry season, and lactation coincides with the first half of the wet season when small flying insects (assessed qualitatively) are most abundant. Corroborative evidence that conditions are most favourable at this time comes from the monthly mean weights of adult males (see Fig.) which (although the differences were not significant [$F = 1.717$, $p < 0.25$]), were lowest at the end of the dry season, and increased during the first two months of the wet season. The monthly mean weights of adult females reached a peak in January, although the females were still lactating at the beginning of this month (Fig.).

Reproduction of *P. nanus* elsewhere in Malawi

The reproductive condition of 17 *P. nanus* from six other localities in Malawi (Happold et al. 1987), and the data recorded for five *P. nanus* in the literature (Kershaw 1922; Lawrence and Loveridge 1953) and for two specimens in the Museum of Malawi, Blantyre, are consistent with the data from Zomba. This indicates that throughout Malawi, in diverse habitats, *P. nanus* is monoestrous with the birth of twins at the beginning of the wet season.



The reproductive chronologies and mean weights of adult *Pipistrellus nanus* in relation to climate at Zomba, Malawi. (a) Climate: histogram = mean monthly rainfall; ■ = mean monthly maximum temperature; □ = mean monthly temperature; ▲ = mean monthly minimum temperature. (b) Reproductive chronology of females: black = births; stipple = lactation. (c) Reproductive chronology of males: stipple = testes scrotal; black = testes scrotal and at maximal size (see also Table 1). (d) Weights of adults: stipple = males; white = females. No samples in July to September, February, and April. Climatic data from Malawi Government (1982)

Social organisation

From December to June, 66 furled leaves were examined without any of the occupants escaping before they were counted: 38 % were occupied by single bats and 62 % were occupied by groups of 2–10 bats (Table 2). Seasonal changes in mean group size and the range of group sizes were apparent.

From December to June, 59 leaves were examined without any of the occupants escaping before they were aged and sexed (Table 3). These leaves were occupied by single adult females, single adult males, single young, or by groups whose compositions are given in Table 3. Seasonal changes in social organisation were conspicuous, and three distinct phases were observed during the study period. These can be referred to as the lactation phase, the post-lactation phase and the harem-formation phase.

During the lactation phase (30 December and 12 January) the adult males (n = 6) invariably roosted singly, 58 % of the lactating females (n = 12) roosted only with their own young, and 42 % roosted in maternity groups comprising one or two other lactating females and their young. The two single adult females observed on 12 December (Table 3) were post-lactating.

Table 2. **Group sizes of *Pipistrellus nanus* taken from 66 furled banana leaves at Zomba, Malawi, and their frequency of occurrence**

Date	Group Size										Mean Group Size
	1	2	3	4	5	6	7	8	9	10	
30 Dec 1984	8	4	3				1			1	2.5
12 Jan 1985	5	1		2			1				2.4
27 Jan 1985	6	4		1	1						2.1
2 Mar 1985	2		1	1		1					3.0
30 Mar 1985	3	1	2	1	1				1		3.2
1 Jun 1985	2	2	1	1		1		1			3.4
16 Jun 1985	1	2	1		1				1		3.7

Table 3. **Composition of groups of *Pipistrellus nanus* taken from 59 furled banana leaves at Zomba, Malawi, and their frequency of occurrence**

Date	Singles			Group Compositions				
	Single adult male	Single adult female	Single young[a]	One adult female with young	2–3 adult females with or without young	2 or more young	One adult male with one or more females	Two adult males with one or more females
30 Dec 1984	5	0	1	6	1	1	0	0
12 Jan 1985	1	2	2	1	1	0	0	0
27 Jan 1985	4	0	2	1	2	2	0	0
2 Mar 1985	1	1	0	0	2	0	0	0
30 Mar 1985	2	2	0	2	1	3	0	0
1 Jun 1985	0	1	0	0	1	0	4	1
16 Jun 1985	0	1	0	0	2	0	3	0

[a] From 30 Dec to 12 Jan, young = mostly unweaned juveniles; from 27 Jan to 30 Mar, young = subadults; from 1 Jun to 16 Jun, all bats were adults.

During the post-lactation phase (27 January to 31 March), adult males continued to roost singly. Post-lactating females (n = 16) roosted singly (19 %) or with groups of subadults and/or other post-lactating females (81 %). Subadults (n = 36) occasionally roosted singly (5 %), but usually roosted with other subadults and/or post-lactating females (95 %).

In April–May, the testes of all males descended, all bats were assumed to have reached reproductive maturity, and the harem-formation phase began. During this phase (1 June and 16 June), all of the males (n = 9) and 95 % of the females (n = 38) roosted in groups of 2–9 bats. Eleven intact groups were examined, and seven (64 %) of these were harems (one adult male with one or more females). One group comprised two males with two females, and three groups comprised only 2–3 females. O'Shea (1980) pointed out that the harems of *P. nanus* in Kenya, unlike those of many other species, were small and highly labile. The stability of the harems observed in Malawi was not investigated.

If data from the post-lactation and harem-formation phases are combined, some aspects of the social organisation of *P. nanus* in Malawi (this study), Kenya (O'Shea 1980) and South Africa (Laval and Laval 1977) can be compared. These phases are combined because O'Shea was not able to make observations during lactation. From 27 January to 16 June, 38 furled leaves at Zomba were examined without any of the occupants escaping before they were aged and sexed. Fourteen of the leaves contained single bats, one contained two newly weaned males, and 23 contained females in groups; of these, 14

(61 %) were harems, 8 (35 %) were females only, and one (4 %) was females with two adult males. The total number of bats examined was 106: 25 males and 81 females. Fourteen (13 %) were found singly and 92 (87 %) were found in groups. The 14 single bats comprised 7 (50 %) males and 7 (50 %) females. The 92 bats roosting in groups comprised 18 males (72 % of all males) and 74 females (91 % of all females). These data, and the equivalent data from South Africa and Kenya, are summarised in Table 5 (see Discussion).

Table 4. **Sex ratios in samples of *Pipistrellus nanus* from Zomba, Malawi**

Date	Sample	Total Males	Total Females	Ratio M:F
	JUVENILES (unweaned)			
2 Dec	Week 5	8	8	1:1
Dec–Jan	Weeks 7–11	13	29	1:2.2
	ADULTS + SUBADULTS			
Oct	Adults only	18	19	1:1
Nov	Adults only	22	23	1:1
Dec	Adults only	15	20	1:1.3
Jan	Adults only	5	14	1:3
Mar	Adults + Subadults	7	36	1:5
Apr	Adults + Subadults	8	12	1:1.5
Jun	Adults + Subadults	9	17	1:2
Total		84	141	1:1.7

Sex ratios

The ratios of males to females in the samples of *P. nanus* collected at Zomba (Table 4) show that although equal numbers of males and females are born, females outnumber males for at least seven months of the year.

Discussion

This study has dealt with the domiciles, reproduction, social organisation and sex ratios of *P. nanus* in Malawi. When the data from Malawi are compared with the data from Kenya (O'SHEA 1980) and South Africa (LAVAL and LAVAL 1977), it can be seen that some aspects of the biology of *P. nanus* show geographical variation (Table 5). The differences help to elucidate some of the ways in which domiciles, reproduction, social organisation and sex ratios are interelated.

The furled-leaf domicile and its implications

Pipistrellus nanus commonly roosts in the furled terminal leaves of bananas and plantains *(Musa)*, strelitzias *(Strelitzia nicolai)* and other musaceous plants (BROSSET 1966; KINGDON 1974; LAVAL and LAVAL 1977; ROSEVEAR 1965; VERSCHUREN 1957). Musaceous plants are abundant in moist habitats throughout most of Africa south in the Sahara, and *P. nanus* appears to be most abundant where musaceous plants are available. However it also exploits other domiciles such as the fruits and dead leaves of musaceous plants (KINGDON 1974; ROSEVEAR 1965), palm leaves, thatch (O'SHEA 1980; ROSEVEAR 1965), holes and cracks in buildings, roofs, and road culverts (ROSEVEAR 1965; SHORTRIDGE 1934). The domiciles are of two types, some being permanent and some being ephemeral. The use of both permanent and emphemeral domiciles has been recorded in diverse parts of the very extensive geographic range of *P. nanus*, and there is no evidence that the choice of domicile

Table 5. **A comparison of some characteristics of the domiciles, reproduction, social organisation, sex ratios, and related biology of *Pipistrellus nanus* from populations in Kenya (O'Shea 1980), Malawi (this study) and South Africa (Laval and Laval 1977)**

Characteristic	Kenya	Malawi	South Africa
Domicile	Permanent	Ephemeral	Ephemeral
Reproductive strategy	Seasonal monoestry	Seasonal monoestry	Seasonal monoestry
% twin births	100 %	100 %	Approx. 50 %
Mean group size ± SD (incl. solitary bats)	1.4 ± 0.9	2.8 ± 2.2	2.8*
Range group size	2–12	2–10	2–6*
% adults roosting in groups	49 %	87 %	28 %
% males roosting in groups	33 %	72 %	24 %
% females roosting in groups	79 %	91 %	34 %
% males of solitary bats	91 %	50 %	61 %
Roost site fidelity in males	High	Not possible	Not possible
Roost site fidelity in females	Low	Not possible	Not possible
Territoriality in males	High	nd, presumed absent	Absent
Competition for roosts by males	Present	nd, presumed absent	Absent
Group formation	Not random	nd	Random
Group composition	Labile	nd, presumed labile	Labile
Sex ratio in adults (M:F)	2:1	1:1.7	1:1
Sex ratio in juveniles (M:F)	1:1	1:1	1:2
Differential mortality	Greater in females	Greater in males	Greater in females
Daytime torpidity	Present	Present	Absent
Tail glands	Present	Absent	Absent

Data on social organisation excludes the period when females were giving birth and lactating, except where indicated by an asterisk. nd = no data

is related to climate. Throughout its range, the exploitation of permanent domiciles is uncommon. It might be relevant that 43 *P. nanus* from banana leaves in Malawi (this study), and *P. nanus* from banana leaves in Ivory Coast and some other parts of Africa (T. J. O'Shea, pers. comm.), did not have tail glands whereas those roosting in permanent domiciles in Kenya (O'Shea 1980) and Ivory Coast (T. J. O'Shea, pers. comm.) did have these glands. This discrepancy raises doubts about the taxonomic relationship between the leaf-roosting bats and those roosting in permanent domiciles (T. J. O'Shea pers. comm.).

Only two other species of bats in Africa are known to regularly exploit furled musaceous leaves for domiciles. *Myotis bocagei* (Vespertilionidae), which occurs in the rainforest and in some parts of the southern savanna, frequently roosts in the furled leaves of *Musa* and also in clusters of banana fruits and in dead banana leaves (Brosset 1966, 1976). The other species, *Myzopoda aurata* (Myzopodidae), is an extremely rare species found only on Madagascar (Hill and Smith 1984). One specimen of *Myotis welwitschii* from Livingstonia (Malawi) was found in a furled banana leaf by R. C. Wood (Ansell and Dowsett 1988) but this species is generally thought to hang from trees and low bushes.

Pipistrellus nanus has enlarged pads on the thumbs and soles which probably contribute to its ability to climb very easily over the slippery surfaces of banana leaves (Brosset 1966; Lang and Chapin 1917). Enlarged pads do not occur in *M. bocagei* or *M. welwitschii*, and therefore *P. nanus* is apparently the only species on the African mainland which is specialised, in both behaviour and anatomy, to roost in the furled leaves of musaceous plants. Therefore, although *P. nanus* may compete for food with syntopic species which are very similar in size and aspect ratio, it does not compete with these species for furled-leaf domiciles. This is probably one of the reasons why *P. nanus* has such a widespread distribution in Africa, and why it has been able to find an ecological niche in a wide variety of bat communities. On the mainland, competition for furled leaves might be expected between *P. nanus* and *Myotis bocagei*, but has not apparently been documented. Furthermore, in Gabon (Brosset 1976), South Africa (Laval and Laval 1977) and Malawi (this study), where *M. bocagei* or *P. nanus* roosting in furled leaves have been studied in detail, only some of the available furled leaves have been occupied, suggesting that the availability of domiciles is not a limiting factor. Both *M. bocagei* and *P. nanus* feed mainly on Lepidoptera, Coleoptera and Diptera (Fenton and Thomas 1980; Whitaker and Mumford 1978), but *M. bocagei* is a larger species (FA = 39.3, WT = c. 7 g.; Happold et al. 1987) and can eat larger insects with harder integuments (D. C. D. Happold and M. Happold, unpubl.). Consequently, *M. bocagei* is unlikely to compete with *P. nanus* for the same species of insects.

Bananas and plantains *(Musa)* are not endemic to Africa. They originated in Malasia, and appear to have been introduced to Africa, via Madagascar, during the first 500 years A.D. (Simmonds 1962). Simmonds suggested that, in Africa, bananas spread up the Zambesi valley and the Great Rift Valleys and then across central Africa to West Africa. The present geographical range of *Musa* in Africa covers all but the most southern part of the range of *P. nanus*. The distribution and domiciles of *P. nanus* prior to the introduction of *Musa* to Africa are not known. Verschuren (1957) suggested that *P. nanus* may have roosted in ensete (*Ensete ventricosum* and other species), a banana-like plant sometimes called "wild banana" or "false banana". *Ensete* is endemic to Africa. It was utilised and/or cultivated in Ethiopia possibly as early as the Upper Pleistocene (Brandt 1984), and is distributed throughout most of the range of *P. nanus* in west, east, central and southern Africa and Madagascar (Simmonds 1962), Alternatively, *P. nanus* may have roosted in permanent domiciles before bananas became widespread.

In southern Africa *P. nanus* extends beyond the southern limit of the ranges of *Musa* and *Ensete*, into the range of *Strelitzia nicolai* which occurs mainly in the coastal forests of Natal and some parts of Cape Province. Where *Musa* and *Ensete* are absent, *P. nanus* roosts in furled *Strelitzia* leaves (Laval and Laval 1977). The distribution of *P. nanus* in southern Africa (Smithers 1983) appears to be restricted to habitats having either *Musa, Ensete* or *Strelitzia*. There is some evidence that *P. nanus* prefers *Musa* to both *Ensete* and *Strelitzia* (Laval and Laval 1977; Verschuren 1957). Laval and Laval concluded that *P. nanus* prefers *Musa* because they produce more leaves in closer proximity.

The furled leaves of musaceous plants are advantageous domiciles for *P. nanus* for at least three reasons. Firstly, they are available throughout the year although leaf production may fall off during colder periods (Simmonds 1959; this study). Secondly, the microclimate inside the furled leaf is undoubtedly very humid because of transpiration, and this would reduce the likelihood of bats becoming dehydrated during the day, and thirdly, there appears to be minimal competition for furled musaceous leaves on the African mainland.

The main disadvantage of furled musaceous leaves is that they unfurl rapidly, and are only suitable as domiciles for a few days. During the hot wet season, when leaves unfurl most rapidly, females have to carry non-volant young to a new domicile every 1–3 days, but they are aerodynamically well adapted to do this. The mean wing-loading in non-pregnant adult *P. nanus* is 0.05 g/cm^2 (derived from weights and aspect ratios given by Happold and Happold 1988), but when maximally loaded with two non-volant young, the wing-loading increases to 0.14 g/cm^2. Mean wing-loadings in non-pregnant adult bats of 33 other species from Malawi ranged from 0.05 to 0.22 g/cm^2, and 11 of these had wing-loadings above 0.1 g/cm^2 (Happold and Happold unpubl.).

Reproduction

The data currently available for *P. nanus* elsewhere in Africa can be summarised as follows:

1. South Africa, Natal, two localities at 28°55′ S and 30°24′ S, evergreen coastal forest,

rainfall unimodal with wet season October–April. Reproduction concluded to be monoestry with the birth of twins or (less often) singletons in November and early December (Laval and Laval 1977).

2. South-west Africa, Ovamboland, 17° 20′ S. "A female contained twin foetuses in October" (Shortridge 1934).
3. Zimbabwe, 16–20° S, southern savanna woodland, rainfall unimodal, wet season November–April. Females not pregnant in July (n = 17); some females pregnant in August; all females pregnant (with twins) in September (n = 26) (Smithers and Wilson 1979).
4. Kenya, Bushwhacker's Safari Camp, 2° 18′ S, dry thornscrub and bushland, rainfall bimodal with peaks during November–December and March–April, main dry season May–October. Reproduction was monoestry with the birth of twins (n = 16) in November. Mating assumed to occur from May to late August (O'Shea 1980).
5. East Africa, 5° N–12° S, rainforest and savanna, rainfall bimodal but varies with locality. "Breeding is apparently not seasonal as females with young have been collected at all times of the year" (Kingdon 1974).
6. Zaire, 5° N–5° S, rainforest and savanna, rainfall generally bimodal but varies with locality: no details available. "On rare occasions two young are born. We had at least one female in August with two embryos, though in December and January, single young were observed" (Lang and Chapin 1917).
7. Zaire, Parc National de la Garamba, 3° 40′ N–4° 40′ N, Guinea savanna, rainfall bimodal with peaks in April and November, main dry season December–February. Concluded to breed throughout the year (Verschuren 1957) but this was based on the limited observations that no females were pregnant or lactating in April and May, and that 44 specimens at the end of July included only two juveniles less than one month old. Verschuren also concluded that *P. culex* (now a synonym of *P. nanus* [see Hayman and Hill 1971]) gave birth in March because a colony of three females with seven non-volant young was found in mid-April.
8. Zaire, Parc National Albert, 1–2° N, rainforest and savanna, climate practically constant throughout year. Specimens were captured throughout the year (n = 362). Eighty-five were females of which only 10 were pregnant: one in February, one in May, four in July, three in August, and one at end of October. Only five juveniles were obtained: these were found in February, July, August and October. No cases of twin births were noted (Verschuren 1966).
9. Rwanda, 1–3° S. Details of habitat not available. Reproduction concluded to be aseasonal polyoestry (Anciaux de Faveaux 1972, quoted by Laval and Laval 1977).
10. Rwanda, Parc National de la Kagera, c. 1° 30′ S. Details of habitat not available. "No twin births were recorded" (Verschuren 1965 in Verschuren 1966).
11. Gabon, c. 1° N, rainforest, rainfall bimodal with peaks in February–June and September–December, and some rain in all months (Charles-Dominique 1971). Bats were collected from January–August 1965, November 1965 and January 1966. Pregnant females, and females with young of different ages were found in July–August, and in January–April. The number of young was one (n = 3) or two (n = 3). It was concluded that *P. nanus* in Gabon breeds throughout the year (Brosset 1966).
12. Rio Muni, c. 1–2° N, rainforest, rainfall bimodal with peaks March–May and September–December, main dry season June–August. Three specimens included a lactating female in August, and a male with scrotal testes 5 × 3 mm in November (Jones 1971).
13. Ghana, 6° 10′ N, rainforest, rainfall bimodal with peaks in May–June and September–October, dry season November–February. Lactating females with one and two young were obtained in March; no data for other months (Jeffrey 1975).
14. Liberia c. 4–8° N, rainforest, no climatic data given. Data for *Pipistrellus stampflii* (now a synonym of *P. nanus*, see Hayman and Hill 1971; Rosevear 1965). Females

were found with two embryos and with two young. It was concluded that twin births were more common in *P. stampflii* from Sierra Leone to Liberia, than in *P. nanus* from further east in West Africa (Kuhn 1962 in Rosevear 1965).

15. Senegal, Parc National du Niokolo-Koba, c. 11° N–12° 30′ N, Sudan savanna, rainfall unimodal, wet season May–September. Two females in late February were not lactating (Poché 1975).
16. Senegal, Parc National du Niokolo-Koba (see above) and Missira (no details available). Nine females in May were not pregnant (Verschuren 1982).

Several conclusions can be drawn from these data, but a comprehensive account of geographical variation in the reproduction of *P. nanus* must await further data. The data from Zimbabwe, Malawi and Kenya suggest that twinning is the norm throughout the southern savanna, in tropical and subtropical localities. The frequency of twin births in South Africa appeared to be approximately 50 %, but since this was based on counts of non-volant young, it was considered to be an underestimate. In marked contrast, no twin births were recorded in some parts of Zaire and Rwanda. The limited information from elsewhere indicates that both singleton and twin births occur in some parts of Zaire, Gabon, Ghana and Liberia, but the relative frequencies are not known.

The data from South Africa, South-west Africa and Zimbabwe, and from this study in Malawi, are consistant with the view that *P. nanus* in the southern half of the southern savanna biotic zone has an austral reproductive cycle characterised by monoestry and parturition in November at the beginning of the wet season. In the northern part of the southern savanna zone (Kenya), the austral cycle persists with parturition in November at the beginning of the first peak in the bimodal wet season. Births occur a little earlier in Kenya and Malawi than in Natal, but in all of these localities, developmental gestation occurs during the dry season, and lactation coincides with the early part of the wet season. Although Kenya and Malawi are tropical, and Natal is temperate, each has a prolonged dry season when conditions are least favourable with respect to the abundance of insects. In Kenya at 4° 15′ S, the abundance of insects increased about tenfold from October to December (McWilliam 1982, in Racey 1982), and an increase in the abundance of insects at the beginning of the wet season has been noted qualitatively in Malawi (this study), and South Africa (van der Merwe et al. 1986).

Data from localities in the northern savanna are very limited. Extrapolating from the southern savanna data, one would expect a boreal cycle characterised by monoestry and parturition in June at the beginning of the wet season. However, this does not seem to occur in Senegal, and it is clear that the reproductive chronology of *P. nanus* in northern savanna habitats needs investigating.

Aseasonal parturition occurs in some of the localities in or near the tropical rainforest zone (see sources 6, 7, 8 and 11), but it is not possible to tell if *P. nanus* is monoestrus with highly unsynchronised parturition, or polyoestrus. None of these sources record simultaneous pregnancy and lactation, and this mitigates against continuous polyoestry with a post-partum oestrus. In Parc National Albert, only 12 % of the 85 females captured throughout the year were pregnant which strongly suggests monoestry. In contrast, *P. nanus* in Rwanda appears to be polyoestrous and breeds continuously (Anciaux de Faveaux 1972, quoted by Laval and Laval 1977).

The combination of all these observations suggests that *P. nanus* exemplifies at least two reproductive strategies. First, it concentrates reproductive effort by having two young once per year in habitats where conditions fluctuate and are most favourable only once during the year. Second, it dilutes reproductive effort by usually having one young, but maybe more than one pregnancy per year, in habitats which are comparatively stable throughout the year.

Relationships between domiciles, reproduction, social organisation and sex ratios

Throughout its geographic range, *P. nanus* sometimes roosts singly, sometimes in small groups, and occasionally in large groups. Group size is obviously determined to some extent by the size of the domicile. In furled leaves, group sizes range from 2–6 (mean 2.8) in Natal (Laval and Laval 1977), 2–10 (mean 2.8) in Malawi (this study), 2–3 in Rwanda (Anciaux de Faveaux 1972), and 2–3 in Zaire (Verschuren 1957). O'Shea (1980) found groups of 2–12 (mean 1.4) roosting in the spaces (some very constricted) between leaflets of palm fronds in roofing thatch in Kenya. A very unusual record is that of a colony of 150 *P. nanus* in thatch in the Kruger National Park in Natal: this appeared to be a maternal colony (Laval and Laval 1977). Laval and Laval (1977) suggested that grouping may be more general in the tropics, and this is supported by the observations that the proportion of bats roosting in groups is only 28 % in South Africa, but 87 % in Malawi (both populations roosting in furled leaves) and 49 % in Kenya (population roosting in thatch) (Table 5).

The social organisation of *P. nanus* roosting in ephemeral furled leaves in Malawi (this study) appears to be very similar to that of *P. nanus* roosting in ephemeral furled leaves in South Africa (Laval and Laval 1977). Some minor differences (related to the lower incidence of group roosting in South Africa) are listed in Table 5, but in both places the social organisation is characterised by the following features: 1. the bats roost singly or in small groups, 2. roost-site fidelity is negligible, 3. lactating females roost alone with their young, or in small maternity groups, 4. adult males roost singly while females are rearing young, and 5. adult males almost never roost together. Other characteristics revealed by Laval and Laval (1977) but not investigated in the Malawian study are: 6. male territoriality does not occur, 7. group formation is random, and 8. group cohesion is negligible except between females and their unweaned young. The study by Laval and Laval (1977) on the South African bats did not reveal seasonal trends in group size or group composition, except for showing that mean group size was largest in November, when only maternity groups were encountered. In contrast, seasonal trends in group size and group composition were evident in Malawi, and two distinct phases (post-lactation and harem-formation) in social organisation were recognised in the five months following weaning of the young. The harem-formation phase was not seen in Malawi until June, but there is no data for May. In South Africa, the harem-formation phase was not recognised in May and there are no data for June, but it seems likely that this phase would have been observed in South Africa if data had been collected in June.

The social organisation of *P. nanus* roosting in permanent thatch in Kenya differs mainly because roost fidelity is possible. O'Shea (1980) found that males showed greater roost fidelity than females, and they defended their roost sites against invasion by other males. In contrast, the females gathered in small groups of labile composition attracted to the most vocal males. Males competed for the best roost sites and also for females, and the resulting mating system is one based on resource defence polygyny. O'Shea observed that females left the domiciles in his study area just prior to giving birth and he assumed they had gone elsewhere to establish a maternal colony. The main differences between the social behaviour of *P. nanus* in South Africa, Malawi and Kenya are summarised in Table 5, together with differences in other biological characteristics.

Some of the differences in social behaviour seem to be causally related to the differences in domiciles. When *P. nanus* roosts in ephemeral furled leafs, roost fidelity is almost negligible (Laval and Laval 1977; this study) but when *P. nanus* roosts in permanent thatch, roost fidelity is possible and is shown to a high degree by males (O'Shea 1980). There also appears to be a relationship between the evolution of male territoriality in *P. nanus* and the exploitation of permanent domiciles (O'Shea 1980): male territoriality occurs in the Kenya thatch-roosting population but not in the leaf-roosting population in South Africa. Furthermore, in the Kenya population, males compete for roost sites

(O'Shea 1980) whereas in both South Africa and Malawi, empty banana leaves were always available and competition for leaves was not observed.

Other differences in social behaviour are probably coincidental. When *P. nanus* exploits ephemeral domiciles, the formation of groups is random and group cohesion is not maintained except between females and their unweaned young (Laval and Laval 1977). When permanent domiciles are used, group formation is non-random and is influenced by several aspects of social behaviour: again group cohesion is not maintained (O'Shea 1980). However, as O'Shea (1980) pointed out, both non-random group formation, and maintenance of group cohesion, have been recorded in other leaf-roosting bats (e.g. *Myotis bocagei* [see Brosset 1976] and *Thyroptera tricolor* [see Findley and Wilson 1974]), and therefore, random group formation and the lack of group cohesion can not be consequences of roosting in ephemeral domiciles.

Brosset (1976) recorded a predominance of females in populations of *M. bocagei* roosting in furled leaves in Gabon. These bats formed harems and Brosset noted that harems seem to exist in species where adult females largely outnumber adult males. However, in *P. nanus*, harems (albeit small and labile) have been observed in populations exploiting both furled leaves and thatch, and in populations where males outnumber females, where females outnumber males and where the sex ratio is balanced (Table 5). In Malawi, females outnumbered males for at least seven months of the year (Table 4). In contrast, males outnumbered females in Senegal (Verschuren 1982), Parc National Albert in Zaire (3.2 males:1 female, n = 362) (Verschuren 1966), Parc National de la Garamba in Zaire (1.6:1) (Verschuren 1957), Burundi (Niort 1970 quoted by Laval and Laval 1977), and Kenya (2:1) (O'Shea 1980). In South Africa, Laval and Laval (1977) found equal numbers of adult males and females (n = 186), but the ratio was 0.5:1 (n = 54) in juveniles.

The apparent shift from the predominance of males in West Africa, East Africa and Zaire, to the predominance of females in Malawi and the balanced sex ratio in South Africa calls for further investigation, and one of the first objectives must be to ascertain the cause(s) of bias in each situation. Adult sex ratios can only be altered by differential maturation rates, unbalanced ratios at birth, or differential mortality (e.g. Wilson 1975). In both Kenya (O'Shea 1980) and Malawi (this study), the sexes mature at the same time, and in Malawi (and probably in Kenya), the sex ratio at birth was equal. This means that differential mortality is the most likely factor contributing to the biassed ratio in both Kenya (O'Shea 1980) and Malawi. Differential mortality also appears to contribute to the balanced sex ratio observed in adult *P. nanus* in South Africa because the ratio in juveniles (Laval and Laval 1977) is biassed in favour of females. O'Shea (1980) suggested that since females in the Kenya population roosted in groups more often than males roosted in groups, predation at roost sites (especially when bats were torpid) would result in a greater mortality of females. He also concluded that females were unlikely to experience a constant mortality factor imposed by the stress of birth and rearing of two young because, if this was so, it would lead to a greater frequency of singleton births. In support of this hypothesis, O'Shea outlined the differences between his observations and those of Laval and Laval (1977) in South Africa. In South Africa, females roosted socially 43 % of the time (as opposed to 79 % in Kenya), the predictability of roost site locations was minimal, and the bats did not enter torpor. Sex ratios were unbiassed, and the frequency of singleton births, based on post-partum counts of young, was about 50 % (as opposed to 0 % in Kenya). The data from Malawi, however, contrasts with that for South Africa in spite of the fact that ephemeral domiciles are exploited in both places. In Malawi, the proportion of females roosting socially (91 %) was even higher than in Kenya, the bats entered torpor, sex ratios were biassed in favour of females, and the frequency of singleton births was 0 %. These data (summarised in Table 5) suggest that there are no consistent relationships between sex ratios, domiciles, torpor, twinning, and roosting singly, with the exception that the absence of torpor was associated with a reduced incidence of twinning and a reduced incidence of females roosting in groups. Since huddling is a means of conserving body heat, the absence of torpor is not likely to be causally related to the reduced incidence of roosting in groups. On the other hand, the absence of torpor might impose a level of stress on pregnant females which makes the bearing of twins less advantageous.

The overall conclusion from the comparison of data on *P. nanus* from diverse part of its range, is that the domiciles, reproduction, social behaviour, torpor, and sex ratios show considerable variation. While some of the differences appear to be causally interelated, others appear to vary independently. As a result, *P. nanus* has an unusual degree of flexibility which has undoubtedly contributed to its ability to exploit many diverse habitats, and to inhabit most of Africa south of the Sahara.

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Zusammenfassung

Aufenthaltsorte, Fortpflanzung, soziale Organisation und Geschlechterverhältnisse bei der Bananen-Zwergfledermaus Pipistrellus nanus (Chiroptera, Vespertilionidae) in Malawi, Zentralafrika

Es wurden Aufenthaltsorte, Fortpflanzung, soziale Organisation und Geschlechterverhältnisse der Bananen-Zwergfledermaus, *Pipistrellus nanus,* in Malawi untersucht. Die Fledermäuse wurden in der Zeit von September 1984 bis zum Juni 1985 alle vierzehn Tage oder monatlich aufgerollten Bananenblättern entnommen. Die aufgerollten Blätter stellten vorübergehende Aufenthaltsorte für ein bis zwei Tage dar. Es gab immer einen Überschuß an möglichen Aufenthaltsorten. Weibchen waren monöstrisch und warfen im November Zwillinge. Die Laktationszeit dauerte acht Wochen. Von April bis Oktober waren die Hoden der Männchen ins Skrotum descendiert. Sie erreichten ihre maximale Größe im Monat Mai. Während der Laktationszeit ruhten die Männchen alleine, die Weibchen mit ihren Jungen hingegen ruhten allein oder in Muttergruppen. Weibchen nach der Laktation ruhten alleine oder mit Gruppen subadulter Tiere und/oder anderen Weibchen, die nicht mehr laktierten. Die erwachsenen Männchen ruhten weiterhin allein. Es wurde angenommen, daß im April, in dem die Testes aller Männchen ins Skrotum descendiert waren, alle Fledermäuse ihre sexuelle Reife erreicht haben. Jeweils ein erwachsenes Männchen lebte mit einem oder mehreren Weibchen im Harem zusammen. Es wurden jeweils die gleiche Anzahl Männchen und Weibchen geboren, die Zahl der Weibchen übertraf aber die der Männchen in wenigstens sieben Monaten des Jahres.

Die Daten aus Malawi werden mit denen aus Kenia, Südafrika und anderen Lokalitäten verglichen. Die geographischen Unterschiede in den Aufenthaltsorten und in der Reproduktionsbiologie, wie auch die Beziehungen zwischen verschiedenen Aspekten der Biologie von *P. nanus* werden besprochen.

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