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Z. Säugetierkunde **63** (1998) 65–78
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ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Effects of bat-bands and banding on a population of *Pipistrellus nanus* (Chiroptera: Vespertilionidae) in Malawi

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SMITHSONIAN
JUL 2 4 1998
LIBRARIES

Receipt of Ms. 26. 03. 1997
Acceptance of Ms. 29. 08. 1997

Abstract

This study provides information about the effects of flanged metal bat-bands, and the procedures associated with banding and frequent censusing, on a population of *Pipistrellus nanus*, a particularly small vespertilionid bat. The bats were censused at their roosts in a banana plantation, at intervals of approximately two weeks, for 10 months; 120 bats were banded and 75 were recaptured (447 recaptures). The best data came from a cohort of 64 adults (banded during the first six censuses), 25 of which were recaptured 9–15 times. Band-status (the effect of the band on the bat) was recorded each time a bat was captured. We recognised four classes of band-status ranging from class 1 (band-free with no injuries, observed on 66% of occasions) to class 4 (band-immobile with an unhealed wound, observed on 11% of occasions). Analyses of the results showed that (a) the majority of bats were in class 1 on most occasions, but some had injuries (classes 2–4) which often improved or deteriorated unpredictably; (b) the band-status changed in relation to time after banding, following an unexplained pattern; (c) band-status was not affected by seasonal changes in climate, or by the sex of the bat; (d) banding did not affect flight and foraging, or mass, or "survival" in the population; and (e) roosting behaviour was not adversely affected. Bats banded when we were inexperienced (census 1) were more prone to injuries than bats banded when we had improved our banding technique. Banding enabled us to study the social behaviour and reproduction of this species and we believe that the results justified banding one small population of this common, widespread species. We predict that other species of small vespertilionids may respond similarly to banding, but extrapolation to species in other families is probably not justified. We recommend that flanged bat-bands should be fitted as loosely as possible, that new bat-banders should be trained by experienced banders, and that banding of bats is permitted only when there are very good scientific reasons for the banding and when harm to individual bats and populations is likely to be minimal.

Key words: *Pipistrellus*, Chiroptera, Bat-bands, banding, techniques

Introduction

Banding of bats, with numbered bands so that individuals may be recognised if recaptured, has been conducted for many years (Barclay and Bell 1988; Greenhall and Paradiso 1968; Roer 1995), and has often yielded valuable information. However, bat-banding has limitations and disadvantages which make its usefulness controversial – both scientifically and ethically. For example, bats must be handled when the band is fitted and

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usually have to be recaptured to obtain further data. Both procedures may interfere with the behaviour and well-being of the bats. In addition, bands may cause injuries ranging from trivial to potentially fatal (Bels 1952; Cockrum 1956; Cranbrook and Barrett 1965; Dwyer 1965; Herreid et al. 1960; Hitchcock 1957).

Originally, bats were banded on the hind-foot with conventional bird-bands but, in 1939, Trapido and Crowe (1946) began banding on the forearm, and this method has been widely used ever since (Greenhall and Paradiso 1968). However, bird-bands placed on the wing frequently caused extensive injuries and therefore, about forty years ago, a special flanged metal band ("bat-band") was designed specifically for bats with the object of minimising band-caused injuries (Hitchcock 1957). Bat-bands have been shown to cause fewer injuries than bird-bands (Dwyer 1965; Herreid et al. 1960), but they do cause some injuries, and the banding procedures may still cause distress and the disruption of normal behaviour. Very often, data obtained by banding cannot be fully interpreted unless the effects of the bands and banding procedures are known. In order to assess the effects of the bands and banding the following conditions must be satisfied: the bats must be recaptured frequently over a suitably long period, the fate of bats which are not recaptured must be known, and any changes in behaviour which may be attributable to the bands and banding procedures must be documented. In the field, this is practically impossible. Nevertheless, valuable information about the effects of bands and banding can be obtained if a large percentage of the banded bats are recaptured frequently over a long period, and if it is possible to compare the health and behaviour of banded and unbanded bats (other factors being equal). We were able to obtain this sort of information while studying a population of banana bats, *Pipistrellus nanus* (Peters, 1852) banded with flanged metal bands (Bernard et al. 1997; Happold and Happold 1996). Banana bats are very small vespertilionids with a mass of 2.5 to 5.0 g (mean 3.2 ± 0.5 g, excluding pregnant females) and mean forearm length of 31.5 mm. During the day, they usually roost in the furled leaves of banana plants, and all occupants of a furled leaf can be captured easily (Happold and Happold 1990).

This study provides detailed information and analysis of the effects of flanged metal bat-bands on the welfare and biology of this particularly small vespertilionid bat, and on the procedures associated with banding. The study also considers the situations and conditions for which bat-banding may be justified.

Material and methods

The study was conducted in an isolated plantation of 138 clumps of banana plants on Kapalasa Farm near Namadzi (15°31′ S, 35°11′ E; ca. 1 000 m a. s. l.) on the Shire Highlands of Malawi in east-central Africa. The bats were censused at their roosts in the plantation using a modified butterfly net, and it was usually possible to capture every bat which was roosting in the plantation on the day of a census (Happold and Happold 1996). Each bat was weighed to the nearest 0.5 g, and its reproductive condition, roosting associates, band number, and band-status (including injuries and bite marks) were recorded. The bats were released near a swimming pool adjacent to the plantation, usually at dusk when it was still light enough to observe their flight and behaviour. On some occasions, echolocation calls associated with foraging and feeding were recorded and analysed with an Anabat II bat-detector, tape-recorder, Anabat II zero crossings analysis interface module and Anabat II software (Titley Electronics, P. O. Box 19, Ballina, N. S. W. 2478, Australia). The calls of banana bats were recognised by their "shape", and by their minimum and characteristic frequencies. The flight and foraging behaviour of the banded bats was compared with that of unbanded banana bats.

When first captured, each bat was banded by placing a numbered metallic bat-band around the right forearm. We used 2.2 mm alloy bat-bands [Code: IBR 3505, from Lambournes Ltd, Shallowford Court, off High Street, Henley-in-Arden, Solihull, West Midlands B 95 5 BY, England.]. Each band was roughly circular, with outwardly curving flanges at the open end. All edges of the band were rounded

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and smooth, and contact between the wing membrane and the band was through the two smooth, broad surfaces of the flanges. The average mass of each band was 0.037 g (manufacturer's information), equivalent to 1.2% of the mean mass of the species (excluding pregnant females) and 1.5% of the mass of the lightest individuals which were banded.

All bands were fitted by one person (D. C. D. H.) although the body and outstretched wing of the bat were supported firmly by M. H. whose hands rested on a bench while the band was being fitted. Neither authors had previous experience at banding bats although they had consulted bat-banding literature and several bat-banders prior to the study. During the first census, the band was carefully placed around the forearm and then squeezed once only (by applying pressure on either side of the band with thumb and index finger) until the gap between the flanges were almost closed. The band was then moved along the forearm to ensure that it slid smoothly over the wing membrane and, in a few cases only, it was necessary to prize the flanges further apart. This method is referred to as Technique A. Approximately half of the bats banded during Census 1 were recaptured at Census 2 (two weeks later) and 38% (n = 32) had bands which had become immobile. Because this was unsatisfactory, we adopted Technique B which aimed at maximising the gap between the flanges. This was achieved by closing the gap by very small increments until it was closed just enough to prevent the band falling off. After each squeeze, the band was gently pulled outwards to ensure that it could not be detached, and then moved up and down the forearm to ensure that it could not slide over the joints. If necessary, the band was given a small extra squeeze and tested again. Technique B usually involved 2–4 squeezes to fit each band satisfactorily.

Censuses were conducted on 18 occasions, at intervals of approximately two weeks, for a period of 41 weeks from late August 1993 to mid-June 1994, except for a period of six weeks (16 November to 29 December) while the females were giving birth and suckling non-volant young. At each census, except Census 6, all furled leaves on the 138 clumps of bananas were examined. Census 6, on 15 November, was terminated when a lactating female was captured.

As in Happold and Happold (1996) this study is divided into four periods. These periods, and the censuses within each period, were:

Period 1: the hot dry season when all females were pregnant; late August to mid-November (censuses 1–6).
Period 2: the hot wet season, when females give birth and lactate and males are in the early stages of spermatogenesis; mid-November to end of April (censuses 7–14).
Period 3: the first half of the cool dry season; spermatozoa are released into the epididymides, and mating begins at the end of the period; May and June (censuses 15–18).
Period 4: the second half of the cool dry season; sperm are stored by both sexes, mating presumably continues, and ovulation and fertilisation occur at the end of the period; July to late August (no censuses).

Bats were assigned to cohorts depending on when they were first caught and their age (adult, young of the year). These cohorts were:

Cohort 1: adult bats banded during Period 1, no young present (n = 84),
Cohort 2: young bats banded in Period 2 (n = 20),
Cohort 3: adult bats banded in Period 3 (n = 21).

Throughout this study, the bands were not damaged by the bats, and therefore the term "band-status" (used below) refers solely to the physical effects of undamaged bands on the wings of the bats. Four classes of band-status were recognised. During each census, the band-status for each captured bat was entered on a conventional calendar of catches (longitudinal data) and on a second calendar of catches laid out according to the number of weeks after the bat was banded (cross-sectional data). Both data sets were analysed using, where appropriate, non-parametric statistics (Kruskal-Wallis and Mann-Whitney U tests). Mean values ± one standard deviation are given where relevant.

During the last census, no bats were banded (although five new bats were captured), and bands were removed from all recaptured bats. Bands were removed very easily by prizing the flanges apart with the thumb-nails while supporting the band with the index fingers. A second person held the bat with its wing outstretched during this procedure.

In addition to the censuses of bats in the Kapalasa plantation, banana bats were caught in mist-nets located at seven localities within a 1.5 km radius from the plantation. Others were taken from furled leaves in the nearest banana plants to the Kapalasa plantation (0.2 to 1.5 km away) and in plantations at Zomba (20 km away). Most of these bats were not banded and they enabled us to compare banded and not-banded bats.

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Rainfall and daily maximum and minimum temperatures were recorded throughout the study. Further climatic details are given in Happold and Happold (1990).

Results

Between 27 August 1993 and 13 June 1994, 125 banana bats (50 males, 75 females) were captured in the banana plantation and, of these, 120 were banded. Cohort 1 contained 84 adults (30 males, 54 females) of unknown age which were banded between 27 August and 15 November 1993 (Period 1). Cohort 2 contained 20 young of the year (born about 15 November) which were banded between late December 1993 and March 1994 (Period 2); no new adult bats were caught in Period 2. Cohort 3 contained 21 adults (young of the year which had reached adult size or adults born in previous years) which were banded in April–June (Period 3). The 84 bats of Cohort 1 provided the best data on the effects of the bands and banding procedures for the following reasons. (1) Sixty-four of these bats were recaptured. (2) The number of times males were recaptured ranged from 0–15 (mean 7.2 ± 4.5, $n = 30$), and the number of times females were recaptured ranged from 0–15 (mean 3.6 ± 4.5, $n = 54$). (3) The number of weeks between the first and final times a bat was caught in the plantation ranged from 2–41 weeks with 41 weeks being the maximum possible; however, for 61% of the bats, the range was 28–41 weeks. (4) Twenty-five bats which were recaptured nine or more times over at least 34 weeks provided longitudinal data. (5) The masses of banded and unbanded bats could be compared. Some data were also obtained from the bats of Cohort 2.

Band Status

Description of band-status

Band-status was recorded for each bat on each occasion when it was recaptured (447 recaptures, 75 bats). Four classes of band-status (the effects of undamaged bands on the wings of the bats) were recognised:

Class 1. Band free with no evidence of any injury (past or present).

Class 2. Band free but with slight chafing or inflammation, and/or evidence of more severe injury in the past.

Class 3. Band immobile but surrounded by a wound which was healed. Class 3 status was the result of swelling and/or abrasion which resulted in the band becoming immobilised by dried fluids, scab tissue or, at worst, an over-growth of flesh. Immobile bands were usually found at the proximal end of the forearm.

Class 4. Band immobile but surrounded by a wound which was not healed. Class 4 status differed from Class 3 status only in that the wound was not healed and there was inflammation, swelling and/or suppuration.

Class 1 status was observed on 295 occasions (66% of the occasions on which band-status was recorded). Class 2 status was observed on 47 occasions (11%). On 41 (87%) of these occasions, the chafing associated with Class 2 status was trivial but, on three occasions, a lump was observed at the distal end of the forearm and, on another three occasions, chafing had caused slight suppuration. Class 3 status was observed on 51 occasions (11%). In some cases, the band had punctured the wing membrane (but this did not always result in the band becoming immobile). On three occasions, the band was barely immobile and was easily dislodged and made free; these bands were still free two weeks later. Class 4 status was observed on 47 occasions (11%). Although this condition looked painful we did not observe bats attending their wounds or seeming to notice them. No other injuries attributable to the bands were observed.

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Table 1. The number of individuals of *Pipistrellus nanus* recaptured at selected intervals after banding. See text for definition of Classes. Percentages are given in brackets

Weeks after banding	Sample size	Class 1	Class 2	Class 3	Class 4
2–3 weeks	50	32 (64%)	3 (6%)	4 (8%)	11 (22%)
6–7 weeks	31	23 (74%)	4 (13%)	1 (3%)	3 (10%)
10–11 weeks	10	8 (80%)	2 (20%)	0 (0%)	0 (0%)
18–19 weeks	26	23 (88%)	1 (4%)	1 (4%)	1 (4%)
20–21 weeks	19	13 (68%)	1 (5%)	4(21%)	1 (5%)
30–31 weeks	23	15 (65%)	1 (4%)	4 (17%)	3(13%)
39–39 weeks	20	11 (55%)	3 (15%)	6 (30%)	0 (0%)

Changes in band-status during the study

Cross-sectional analysis of band-status at selected intervals after banding indicated that the percentage of bats in each class changed with time after banding (Tab. 1). The percentage in Class 1 (no injuries) increased steadily from 2–19 weeks and then decreased steadily. Although this trend was matched by the concomitant decrease, and then increase, in bats with some degree of injury (Classes 2–4) during weeks 2–19, the changes within each of these classes were erratic. Table 1 also shows that, irrespective of the time after banding, the majority of bats had free bands (Classes 1 and 2), and, from week 20 onwards, the percentage with free bands remained almost constant (69–73%).

Longitudinal analysis shows how the band-status changes with time for individual bats. The data for 25 bats from Cohort 1 which were recaptured at least nine times and were still members of the Kapalasa population in Period 3 were analysed in this way. The number of recaptures ranged from 9–15 (mean 11.5 ± 1.9). For 12 of these bats (48%), the band-status was invariably Class 1 and these bats appear to have been trouble-free throughout the study. The remaining 13 bats had injuries ranging from Class 2 to Class 4, which lasted from no more than two weeks to as long as 40 weeks. The records of band-status for five individuals are given in table 2 to illustrate a range of scenarios. Male 55 was typical of the 12 bats which were trouble-free. Male 46 was one of two bats for which band-immobility was observed only once. Female 60 was one of four bats which exemplified two separate incidences of band-immobility. Male 41 was one of four bats with intermittent periods of comparatively short-lasting band-immobility. Female 18 had the worst record and was one of three bats with periods of long-lasting band-immobility.

The band-status of an individual bat could remain the same, or it could change from one class to any other class, within the two-week interval between consecutive censuses (Tab. 2). Of particular interest, however, are the changes – and lack of changes – from band-free status to band-immobile status, and vice-versa. Therefore, we analysed every pair of consecutive recaptures (n = 293) for 65 bats which were caught during consecutive censuses. The possibilities, and their frequencies of occurrence, were: band-free to band-free 70%; band-free to band-immobile 11%; band immobile to band-free 8%; band-immobile to band-immobile 11%. It is evident that free bands tend to stay free, and that immobile bands, almost as often as not, become free. It is relevant, also, that 42 (56%) of the 75 bats which were recaptured were never observed with an immobile band and that, for the 33 bats which were observed with immobile bands at sometime during the study, the number of times that the band was observed to change from free to immobile ranged from 1–4.

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Table 2. Records of band status for five bats which illustrate different scenarios, selected from the records of 25 bats from Cohort 1 which were recaptured at least nine times. M = males, F = female. B = census when the bat was banded. – = censuses when the bat was not captured. See text for definition of band status Classes. The band was free in Classes 1 and 2, but immobile in Classes 3 and 4. Bats M41 and F18 were banded by Technique A; bats M55, M46, and F60 were banded by Technique B (details in text).

Bat	Census at which band status was recorded																		% times band immobile	Number of bats with similar records
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18		
M55		B	–	–	1	–	1	1	1	1	1	1	1	1	1	1	1	1	0	12
M46		B	1	–	–	1	–	1	–	4	1	1	1	1	–	2	1	1	9	2
F60		B	1	1	1	4	–	1	1	–	1	1	1	1	4	–	3	1	17	4
M41		B	3	4	1	2	1	2	4	2	3	3	3	1	3	3	–	3	60	4
F18	B	4	4	4	3	–	3	3	3	3	3	3	3	3	4	2	2	3	87	3

The records of band-status for each of the 25 bats from Cohort 1 which were recaptured at least nine times showed that bands were free for 13–100% of the occasions when the bats were recaptured. The numbers of occasions when the band was free were categorised as <25%, 26–50%, 51–75%, and 76–100% of the occasions when the bat was recaptured. The number of bats in each category was 2 (8%), 1 (4%), 5 (20%) and 17 (68%) respectively, and 12 (48%) were trouble-free (Class 1) on all occasions. For 48 bats recaptured 1–8 times, the results were similar: the percentages were 6%, 15%, 10% and 69% respectively, and 63% of these bats were trouble-free on all occasions.

These data, collectively, show that band-status may change frequently. However, the majority of bats were trouble-free on most occasions, and those which had some form of injury on one occasion were likely to show an improvement by the next occasion.

Band-status in relation to banding technique

We compared the severity, onset and duration of injuries observed in bats banded by Techniques A and B. To eliminate variables, such as differences in the age of the bats and the effects of the seasons, we used data from Cohort 1 only. Technique A was more harmful than Technique B: bats banded by Technique A were more prone to injuries and their injuries tended to develop sooner, last longer and be more severe (Tab. 3). The longitudinal records of two bats banded by Technique A (F18 and M41) and three bats by Technique B (M46, M55, and F60) are given in table 2.

Did the banding technique influence the number of times a bat was recaptured? Bats banded during Census 1 (Technique A) were compared with bats banded during Census 2 (Technique B) and, to standardise the maximum number of recaptures possible, we counted recaptures from Census 3 onwards (excluding Census 6 which was incomplete) for both groups. For bats banded by Technique A, the number of recaptures ranged from 0–15 (mean 5.8 ± 4.7, $n = 40$); for Technique B, the number of recaptures ranged from 0–13 (mean 4.7 ± 4.7, $n = 21$). There was no significant difference (Mann-Whitney $U° = 448.5$, $p = 0.66$). Thus the banding technique did not affect the number of times that any bat was recaptured.

Did banding technique influence the number of bats which were "lost" from the Kapalasa population? A bat was considered to be lost from the Kapalasa plantation during Period 1 if it was not recaptured subsequently, or lost during Period 2 if it was not recaptured during any of the four censuses conducted in Period 3. Forty bats (from Cohort 1) were banded by Technique A and, of these, 24 (60%) were lost during Periods 1 or 2. Similarly, forty-four bats (also from Cohort 1) were banded by Technique B and, of these, 23 (52%) were lost. Therefore the number of bats lost from the population was not af-

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Table 3. The prevalence, severity, onset and duration of injuries in bats banded by Techniques A and B (described in Methods). To eliminate effects of age and season, all data are from Cohort 1. Free bands = Classes 1 and 2; immobile bands = Classes 3 and 4.

	Banding Technique A	Banding Technique B
Prevalence and severity of injuries		
Total number of bats banded and recaptured	31	33
Percentage of bats which experienced some band-immobility	61	33
Total number of recaptures	193	211
Percentage of times each class of band status was observed:		
Class 1 (no injuries)	50	81
Class 2	14	6
Class 3	20	7
Class 4 (severest injuries)	16	6
Onset of injuries		
Number of bats observed 2–5 weeks after banding	21	25
Percentage with immobile bands 2–5 weeks after banding	67	24
Duration of injuries		
Number of bats recaptured 9–15 times	10	15
Percentage which were entirely trouble-free (Class 1 only)	30	60
Percentage with Class 4 observed at least once	70	40
Percentage with free bands on:		
more than 75% of occasions	40	87
less than 25% of occasions	20	0

fected by banding technique ($\chi^2 = 0.46$, $p = 0.5$). Further information about losses of bats from the population is given below.

Band-status in relation to time after banding

To analyse how band-status may have changed with time after banding, we used the calendar of catches which was laid out according to the number of weeks (in two-week intervals) after the bat was banded. For every interval after banding, we calculated the percentage of bats which had immobile bands: data from all recaptured bats (n = 75) were used. A pattern was evident (Tab. 4). Injuries severe enough to immobilise the bands (classes 3 and 4) often developed very soon after banding with the result that 30% of the bats had immobile bands after 2–3 weeks and 24% had immobile bands after 4–5 weeks. Subsequently, the percentages with immobile bands dropped very markedly during weeks 6–19, but then increased during weeks 20–29 and then increased again during weeks 30–41. This pattern was more conspicuous for the bats banded by Technique A than for those banded by Technique B – mainly because more of the bats banded by Technique A experienced band-immobility, and the first period of immobility occurred earlier (see Tab. 3).

To ascertain why the percentage of bats with immobile bands decreased during weeks 6–19 after banding, we examined the longitudinal records for each bat which was observed during weeks 2–5 and also during weeks 6–19 (n = 42 bats). Sixty-six percent of these bats remained band-free, two percent remained band-immobile but 32% changed from being band-immobile to band-free. A similar analysis showed why the percentage of bats with immobile bands increased after week 20: 34% changed from being band-free (prior to week 20) to band-immobile whereas only 3% changed from band-immobile to band-free (59% remained band-free and 3% remained band-immobile). We cannot explain why band-immobility decreased 6–19 weeks after banding, or why it subsequently increased.

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Table 4. The percentages of recaptured bats with immobile bands (Classes 3 and 4) in relation to time (in two-week intervals) after the bats were banded.

Time after banding (weeks)	Two-week intervals	Number of intervals	Mean number of bats observed in each interval	% bats with immobile bands	
				Mean	Range
2–5	2–3 and 4–5	2	45.5	27.0	24–30
6–19	6–7 to 18–19	7	17.6	5.0	0–13
20–29	20–21 to 28–29	5	22.4	24.8	17–35
30–41	30–31 to 40–41	6	19.3	32.5	28–42

Band-status in relation to climatic conditions

Malawi has three seasons: 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. Climatic averages for Zomba (20 km from Kapalasa Farm) are given by HAPPOLD and HAPPOLD (1990). To investigate changes in band-status in relation to season, we calculated the percentage of bats observed with immobile bands during each of four consecutive censuses in each season (Tab. 5). We also recorded the number of rainy days, total rainfall, mean daily minimum temperatures, and mean daily maximum temperatures for every day between the first and last of the four consecutive censuses in each season (Tab. 5). There was no significant difference in the percentages of bats with immobile bands from season to season (Kruskal-Wallis $H_c = 0.203$, $\chi^2_{0.05,2} = 5.99$, $p = 0.9$) although there were marked changes in rainfall and temperature.

We also tabulated the worst band-status recorded during each season for bats which were recaptured at least once during each season, and then noted the frequencies with which the band-status improved, deteriorated or stayed the same from one season to the next season. For the transition from the hot dry season to the hot wet season, 8 improved, 4 deteriorated, and 10 remained the same. For the transition from the hot wet to the cool dry season, 6 improved, 7 deteriorated, and 11 remained the same. There was no differ-

Table 5. Band status in relation to climatic conditions recorded at Kapalasa Farm from Census 2 to Census 5 (hot dry season), Census 7 to Census 10 (hot wet season) and from Census 15 to Census 18 (cool dry season).

	Season		
	Hot dry	Hot wet	Cool Dry
Number of rainy days	3	29	2
Rainfall (mm)	4	445	9
Minimum temperature °C:			
Mean ± SD	17.9 ± 2.5	19.6 ± 1.9	14.2 ± 2.4
Range	13–22	17–24	10–22
Maximum temperature °C:			
Mean ± SD	29.4 ± 3.2	27.9 ± 1.8	24.6 ± 2.9
Range	22–33	24–33	16–30
Number of bats observed each census	21–36	18–25	20–28
Percentage bats with immobile bands:			
Mean	25.0	22.3	28.5
Range	8–38	6–37	25–31

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ence between the transitions ($\chi^2 = 2.04$, $p = 0.36$) and this is further evidence that band-status was not affected by the seasons.

Band-status in relation to sex

To investigate whether the severity and duration of injuries differed between males and females, we compared the percentage of occasions for which the band was observed to be free for 16 males, and for nine females, which were recaptured at least nine times. The percentages ranged from 22–100% (mean 82.3 ± 26.5) for males, and from 13–100% (mean 73.6 ± 28.3) for females. There was no significant difference between the sexes (Mann-Whitney U° = 87.5, $p = 0.35$).

Responses of the bats

Responses of bats to their bands

Banded bats were observed when they were returned to holding bags after banding, and while they were resting (on the bags or on our hands) prior to being released. We did not observe any bat biting its band or attending to an injury. There was no evidence that the bats chewed their bands at any other time – none of the bands had tooth marks and the band number was always readable although, on a few occasions, cell debris and dried fluids had to be removed from the surface of the band.

Effects of bands on flight and foraging behaviour

Banded bats were usually released at dusk, on the day of the census, before other bats had emerged from their domiciles. The bats were often torpid, and torpid individuals were allowed to warm themselves in our hands or on our arms until they were ready to fly. The banded bats took off strongly and usually spent at least ten minutes flying nearby. During this time, they foraged for flying insects (feeding buzzes were recorded), flew very close to the observers while other unreleased bats were warming up and echolocating, and flew down to a swimming pool (about 4 m diameter) to drink and/or forage. We observed no abnormalities of flight and could not distinguish the flight of the banded bats from that of banana bats which were not banded.

Effects of bands and/or banding on the mass of the bats

During Census 2, we compared the masses of unbanded bats (2.5–3.5 g, $n = 22$) with those of bats which were recaptured after carrying bands for two weeks (2.5–3.5 g, $n = 21$). There was no significant difference between the banded and unbanded bats (Mann-Whitney U° = 269.5, $p = 0.3$). Similarly, there was no significant difference between the masses of the banded females ($n = 14$) and the unbanded females ($n = 10$) (Mann-Whitney U° = 73.0, $p = 0.85$). During Census 3, we compared the masses of unbanded bats ($n = 13$) with those of bats which were recaptured after carrying bands for two weeks ($n = 11$) and for four weeks ($n = 24$). By this time, the females (all in the early stages of pregnancy) were heavier than the males so the comparisons were restricted to bats of the same sex. Again, there was no significant difference between the masses of the bats in each category (for males, Kruskal-Wallis Hc = 2.67, $\chi^2_{0.5,2} = 5.99$, $p = 0.26$; for females, Kruskal-Wallis Hc = 0.85, $\chi^2_{0.05,2} = 5.99$, $p = 0.65$).

Effects of the bands and banding on "survival" in the Kapalasa population

For this investigation, bats were considered to have been lost if they were not recaptured in the Kapalasa plantation after being missing for four or more consecutive censuses. To investigate whether the loss of bats was related to band-immobility (Class 3 and Class 4), we compared the longitudinal records of bats from Cohort 1 which were lost (after being recaptured 3–5 times, $n = 11$) with those which were not lost (after being re-

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captured at least nine times, n = 25). The records for the lost bats were marginally better than those of the bats which were not lost. For example, for the lost bats, the percentage of occasions on which the band was immobile ranged from 0–50% (cf. 0–87% for bats which were not lost); and only 9% of the lost bats had immobile bands on more than half the occasions when recaptured (cf. 16% for bats which were not lost). Furthermore, bat F18 which had the worst record of band-immobility (Tab. 2) was not lost.

Further evidence that band-immobility was unlikely to cause the loss of bats was obtained by analysing the status, when last observed, of all bats in Cohort 1 which were lost (n = 42). Only 4% of these bats had immobile bands, whereas 96% had free bands (Class 1 79%, Class 2 18%).

Although these data suggest that losses are not related to band-immobility, it is possible that some bands may have caused injuries more severe than any which were observed, and that these resulted in the death of the bat. However, while examining furled leaves at Kapalasa, we never found a dead or unfit banded bat. It is also relevant that (a) at other localities, we recaptured three bats which had been lost from the Kapalasa population, and (b) six bats which appeared to have been lost, turned up again after being missing for 24 to 34 weeks.

Losses of bats caused by the procedures of banding and/or censusing were impossible to assess in this study. Losses of male bats from Cohort 1 in Period 1 were very low: 30 were banded, and of these four were never recaptured, four were lost at the beginning of Period 2, and 22 were still being recaptured during Period 3. Evidently banding did not disturb the majority of the males enough to make them permanently abandon the plantation for the duration of the study, even though other roosts were available and were utilised some of the time. The number of times these males were recaptured was high (mean 7.2 ± 4.5), which also suggests that they were not particularly distressed by the censuses. Losses of females (all pregnant) during Period 1 were much greater than the losses of males: 54 were banded, and of these 16 were not recaptured and six others were lost. The females were recaptured less often (mean 3.6 ± 4.5) than the males. The disproportionate loss of females was not a result of females being affected more adversely by the bands because the sexes were affected equally. Possibly the females were more distressed by the banding and the censuses, and responded by abandoning the Kapalasa plantation, but there could be alternative explanations for the disproportionate loss of females (e.g. the occurrence of pregnancy-related mortalities and/or higher predation due to the clumping of females at roosts).

Effects of the bands and/or banding on social behaviour

Throughout most of the year, including during Period 3 when mating begins, male banana bats sometimes roost singly and sometimes in labile groups composed of one (rarely two) males and 1–10 females. During the time of parturition and lactation, females very rarely roost with adult males, but at all other times of the year they usually roost with males and, during Period 3, they almost always roost with males (Happold and Happold 1990, 1997). We were able to compare two aspects of the roosting behaviour of banded bats with that of bats which were not banded; Period 3 was chosen for the comparison because this was the time when male-female relationships were particularly important.

Firstly, we compared the roosting behaviour of females which were banded and not banded. During Period 3, 20 banded females were recaptured 1–4 times, resulting in 50 observations of banded females at their roosts. On all but two occasions, these females were roosting with males, and the band-status of the two females which were found roosting without a male (on one occasion each) was Class 1. Band-immobility was observed on 17 (34%) of the 50 occasions. During the same period, 29 females which were not banded were captured, with their roost associates, at localities other than the Kapalasa plantation. On all but three occasions, these females were found with males. These data indicate that

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the roosting behaviour of females was not adversely affected by censusing, banding or by the status of the bands.

Secondly, we compared the roosting behaviour of males which were banded and not banded. During Period 3, 27 banded males were recaptured 1–4 times resulting in 86 observations of banded males at their roosts. Banded males were found with females on 45% of occasions. During the same period, 23 unbanded males were observed and, of these, 69% were found with females. These data suggest that banded males were found less often with females, but we have no evidence that this was disadvantageous.

Discussion

In recent years, there has been a rapid increase in the number and scope of studies involving bats, and a growing need for bats to be recognisable either as individuals or as members of a particular group. For example, our investigations of the reproductive biology, population dynamics and social behaviour of the banana bat, *Pipistrellus nanus*, could not have been carried out successfully unless the identity of each individual in the Kapalasa population was known. At the beginning of the study, we were inexperienced and we did not know if the bands and/or banding procedures would harm or distress the bats. Before commencing the study, we sought advice from other bat-banders (which was conflicting) and from the literature (which was hard to find and obtain). There is clearly a need for bat-banding information to be accumulated and published in well-known, accessible sources.

During this study, we were able to obtain information about the effects of bands and frequent censusing because banana bats had a high level of fidelity to particularly clumps of bananas in the plantation, and consequently we were able to recapture banded bats many times (Happold and Happold 1996). We were able to follow band-status in the population as a whole, and in individuals who were recaptured at two-week intervals for the best part of a year. Our classes of band-status are very similar to those defined and described by Dwyer (1965) and currently used for bats by the Australian Bird and Bat Banding Scheme. It is possible (and for some species highly probably) that bands also cause some injuries which are fatal, but these are very rarely observed. For the banana bats, survival in the banded population was high, particularly for males and particularly during times of the year when there was neither courtship, immigration or emigration. We obtained no evidence that losses of bats from the population were the result of band-caused mortality, although some bats (particularly pregnant females) might have abandoned their roosts in the Kapalasa plantation because they were distressed by being captured and/or banded. Some banded bats which no longer roosted in the plantation were recaptured elsewhere, proving that at least some losses were not mortalities. Losses did not appear to be related to the band-status of the bats when they were last observed. Band-status did not change as a result of seasonal changes in rainfall and temperature, nor was it related to sex. Most bats remained free of injury for most or all of the time, but injuries could arise unpredictably and also heal themselves unpredictably. Banding did not result in weight-loss, and did not affect the behaviour of the bats to the extent that reproductive processes (such as females rearing their young, and roosting with males during the mating season) were compromised. Consequently, the banding of these bats enabled us to complete our research with satisfactory results.

To what extent does this help other bat-banders to design projects on other species, and interpret the results? At the moment, it is not possible to answer this with certainty, and this again highlights the need for more information so that widespread comparisons can be made. *Pipistrellus nanus* belongs to a cosmopolitan group of genera of small vespertilionids collectively known as the pipistrelles and serotines. There are approximately

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50 pipistrelles in the genus *Pipistrellus*, 33 species of serotines in the genus *Eptesicus* and additional species in other closely related genera (Koopman 1993). All are of similar size or a little larger than *Pipistrellus nanus* and, like *Pipistrellus nanus*, they all have a comparatively narrow propatagium. Furthermore, none of these bats are restless or free-hanging at their roosts and therefore their bands are unlikely to chafe them, or fall over their wrists, during roosting. Provided that these species do not damage their bands by chewing them, the physical effects of the bands are likely to be similar to those of *Pipistrellus nanus*. However, they may respond differently to being disturbed, handled, banded, and recaptured. For example, banana bats do not hibernate but bats which do hibernate can be very seriously disadvantaged if they are disturbed at their hibernacula (Jones 1976; Keen and Hitchcock 1980; Tuttle 1979; all in Barclay and Bell 1988). Another consideration is that banana bats are very common throughout most of Africa, and the banding of one small population was not going to compromise the survival of the species. In contrast, even if all other factors appeared to be similar, the banding of rare pipistrelles and serotines should not be justified solely on the basis that banding with flanged bands proved almost harmless to banana bats.

It is probable that many species of pipistrelles, serotines, and other small vespertilionids can be banded with consequences similar to those described in this study, and therefore banding projects on these species can be planned, and the results interpreted, with reasonable confidence. However, extrapolating from banana bats to larger vespertilionids and to species in other families is probably not justified. For example, some species often damage metal bands by chewing them and, as a result, the edges may become jagged and inflict severe injuries, the band may become crushed so it no longer moves, and the writing on the band may become illegible (Barclay and Bell 1988; Bonaccorso and Smythe 1972; Cranbrook and Barrett 1965; Dwyer 1965; Hitchcock 1957). Similarly, species which have a wide propatagium (e.g. pteropodids, rhinolophids, mormoopids, and phyllostomids) cannot be banded satisfactorily on their wings unless the propatagium is punctured to create a hole to accommodate the band (Barclay and Bell 1988), and Jolly (1988) found that this technique was also superior in the case of the emballonurid *Taphozous georgianus*. Furthermore, some species (e.g. rhinolophids) spend a lot of time hanging upside-down, swivelling from side to side and quivering as they echolocate, and it has been suggested that this may increase the likelihood of the band sliding down the forearm and onto the wrist (Dwyer 1965).

It has been demonstrated that small birds and bats are not seriously disadvantaged unless they carry devices (such as transmitters) which weigh more than 5% of the body weight (Barclay and Bell 1988). Banana bats are particularly small and delicate, but because the mass of each band was only 1.5% of the mass of the lightest individuals (2.5 g), and 1.2% of the mean mass of average individuals (3.2 g), they are unlikely to have been disadvantaged by the mass of the band. Furthermore, female banana bats adjust to changes in mass amounting to as much as 80–90% of the mean mass of the species when they are carrying two foetuses (combined mass 2.5 g at full term), or when transporting non-volant young (individual mass 1–3 g) from one roost to another. In this study, banded females survived pregnancy and lactation without showing any evidence of being less fit than unbanded females.

Some bat banders believe that injuries are caused by careless banding while others believe that many injuries are caused by bats biting their bands (Greenhall and Paradiso 1968). The banana bats did not bite their bands, but some individuals were injured by their bands and the prevalence and severity of the injuries was affected by banding technique in a way which shows that careless banding can indeed result in more injuries. In our case, we were not careless but, at first, we were inexperienced and the outcome was the same – bats banded by our first technique (Technique A) suffered more injuries which developed sooner, became more serious and lasted longer than bats banded by our

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second technique (Technique B). Consequently, we can make two recommendations: (1) flanged metal bands should be fitted as loosely as possible, and (2) new bat-banders should receive training from experienced banders before attempting to work on their own. Bat banding is not as easy as it appears to be.

As information accumulates, it will become increasingly easier to make wise, ethical decisions about which species are safe to band and which investigations are important enough to justify banding. We felt, and still feel, that the information we obtained about the reproduction, population dynamics and social behaviour of the banana bats at Kapalasa justified banding them. We showed that banana bats exhibit roost fidelity despite the ephemeral nature of their roosts, that group membership is highly labile, that multiple matings over a period of 2.5 months are possible, and that there is potential for sperm competition (Bernard et al. 1997; Happold and Happold 1996). We harmed very few individuals, did nothing to jeopardise the survival of the species and, at the end of the study, we removed the bands from as many bats as possible. From our point of view, the banding was justified.

The bats themselves may have a different opinion. We received a letter recently from Malawian friends who are employed on Kapalasa Farm. As a result of our work, they learned a lot about banana bats and wrote, very sensitively, about them: "The bats nowadays are many. Bats are now rejoicing in the new plantations simply because they are missing some-one who can catch them."

Acknowledgements

This study was part of a research project on the small mammals of Malawi undertaken during an Outside Studies Programme granted to DCDH from the Australian National University in 1993–1994. We are particularly grateful to Sven Grüner, the owner of Kapalasa Farm, for allowing us to work on his farm and for his kindness and hospitality during our study. Likewise we are also particularly grateful to our warm-hearted Malawian friends at Kapalasa Farm who helped us in many ways and showed an encouraging interest in our work. We also gratefully acknowledge the assistance of Chancellor College, University of Malawi and the Department of National Parks and Wildlife of Malawi for their support of our studies, and the Australian National University and the Australian Research Council which provided some of the funds for our studies in Malawi.

Zusammenfassung

Auswirkungen von Fledermausklammern und Markierung auf eine Population von Pipistrellus nanus (Chiroptera: Vespertilionidae) in Malawi

Die Arbeit enthält Informationen über den Effekt von Metallklammern und über die Verfahren, die mit Beringung und häufiger Kontrolle verbunden sind, auf eine Population von *Pipistrellus nanus*, einer sehr kleinen Glattnase. Die Tiere wurden über 10 Monate in Intervallen von etwa 2 Wochen an ihren Quartieren in einer Bananenplantage kontrolliert; 120 Bananenfledermäuse wurden markiert und 75 mehrfach wiedergefangen (447 Wiederfänge). Die besten Daten lieferten 64 Adulte (während der ersten 6 Kontrollen beringt), von denen 25 mehrfach (9–15mal) wiedergefangen wurden. Der Effekt der Metallklammern auf die Fledermäuse wurde bei jeder Kontrolle festgehalten. Wir unterschieden 4 Zustandsklassen von 1 (Klammer frei beweglich ohne Verletzung, in 66% aller Fälle beobachtet) bis 4 (Klammer unbeweglich mit offener Wunde, in 11% aller Fälle beobachtet). Die Ergebnisse zeigen, daß (a) die meisten Fledermäuse der Klasse 1 angehörten, einige aber Verletzungen aufwiesen (Klassen 2–4), die sich oft unvorhersagbar verschlimmerten; (b) der Zustand sich ohne erkennbares Muster mit zunehmender Zeit nach der Markierung veränderte; (c) der Zustand nicht vom Klima noch vom Geschlecht abhängig war; (d) die Markierung nicht Flug- und Jagdverhalten, Körpermasse oder Überlebensdauer in der Population beeinflußte; und (e) das Quartierverhalten unverändert war. Fledermäuse, die von uns ohne Erfahrung während der ersten Kontrolle markiert wurden, trugen ein größeres Verlet-

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zungsrisiko als Tiere, die später markiert wurden, nachdem wir unsere Technik verbessert hatten. Mit Hilfe der Beringungsmethode konnten wir das Sozial- und Fortpflanzungsverhalten dieser Art studieren und glauben, daß die dabei erzielten Resultate die Markierung einer kleinen Population dieser häufigen und weitverbreiteten Art rechtfertigten. Wir vermuten, daß andere Arten kleiner Glattnasen in ähnlicher Weise auf Metallklammern reagieren werden, aber eine Ausweitung auf Arten anderer Familien ist wahrscheinlich nicht möglich. Wir empfehlen, daß Metallklammern so locker wie möglich angelegt werden, daß Anfänger von erfahrenen Beringern ausgebildet werden sollten, und daß die Beringung von Fledermäusen nur gestattet werden sollte, wenn sehr gute wissenschaftliche Gründe dafür vorliegen, und wenn ein Schaden für Individuen und Populationen von Fledermäusen unwahrscheinlich ist.

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: Mammalian Biology (früher Zeitschrift für Säugetierkunde)

Jahr/Year: 1998

Band/Volume: 63

Autor(en)/Author(s): Happold D.C.D., Happold Meredith

Artikel/Article: Effects of bat-bands and banding on a population of Pipistrellus nanus (Chiroptera: Vespertilionidae) in Malawi 65-78