



Researching little-known species: the African bat *Otomops martiensseni* (Chiroptera: Molossidae)

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Abstract. Listed as 'vulnerable' by the International Union for the Conservation of Nature, the molossid bat *Otomops martiensseni* occurs widely in Africa and, according to some authorities, in Madagascar. Apart from a few known cave roosts, there are few records of *O. martiensseni*, although around Durban, South Africa, the species is common and roosts in buildings. Originally described as three species, populations of *O. martiensseni* differ significantly in size (length of forearm) between East Africa and Durban or Madagascar, but not between Durban and Madagascar. Seventeen buildings used as roosts by *O. martiensseni* averaged 34.5 ± 15.8 years old. In the Durban area, bats entered roosts by landing and crawling. Roost populations ranged from 7 to 29 individuals, typically consisting of one adult male, several adult females and young (bats with unossified epiphyses), suggesting a harem social structure. The ratio of adult females to young was virtually 1:1, and among young the ratio of males:females averaged 2:1. Radio-tracking showed that individuals used several day and night roosts, and foraged widely in a landscape dominated by sugarcane and urban development. The echolocation and many social calls of *O. martiensseni* are readily audible to human observers, allowing a non-contact, low technology method for monitoring the local distribution and activity of these bats. Although listed as a species of special concern in KwaZulu Natal, these bats appear to be candidates for inclusion on a 'blue' list of species, ones showing stabilized or increased abundance. We recommend that *O. martiensseni* be recognized as a 'flagship' species in the Durban area, representing the resilience of nature.

Introduction

Identifying some species as vulnerable or endangered sets targets in conservation and can be positive because it forces us to identify taxa that need immediate attention (Soulé and Sanjayan 1998). Most of the approximately 950 species of bats are not in the 2000 Red List Rating by the International Union for the Conservation of Nature (IUCN), reflecting a lack of data about their populations and distribution (Hutson et al. 2001). Over a decade ago in Europe, identifying some species of bats as endangered or at risk, resulted in an explosion of basic research (Racey and

Entwistle 2002). The combination of small size, longevity, mobility, and trophic diversity means that bats can be useful organisms for monitoring disturbance (Medellín et al. 2000), although some species exploit human-wrought changes in the environment, persisting and even thriving when other species have gone (Altringham 1996; Medellín et al. 2000). Advancing the conservation of bats must involve both documenting their diversity in specific areas (Simmons and Voss 1998; Lim and Engstrom 2001), as well as obtaining more data about their ecology and behavior (Racey and Entwistle 2002).

Species are fundamental units in conservation. There are several ways to determine viable population size (Mann and Plummer 1999) as well as the relationships between a species' range and its abundance or the number of species in an area (Hanski and Gyllenberg 1997; Kunin 1998; Harte et al. 1999). Sometimes one can predict accurately which endangered species will occur in some fragmented ecosystems (Wahlberg et al. 1996), but the conservation status of any one species might be a poor criterion for setting conservation priorities (Cassidy et al. 2001). An important problem in identifying areas to preserve is that different groups of organisms can give quite different views of which are the important areas and places to protect (van Jaarsveld et al. 1998). Predictions must be based on sufficient basic information about species, their populations, basic biology, and distribution (Pimm and Lawton 1998; van Jaarsveld et al. 1998), information that is lacking for most species of bats. Part of the problem is the difficulty of sampling bats because different techniques (searches for roosts, captures in nets versus traps, or monitoring echolocation calls) present different pictures of local faunas (Simmons and Voss 1998). African bats mirror the overall situation with respect to bat conservation, but the molossid, *Otomops martiensseni* (Matschie), presents a different situation.

In the South African province of KwaZulu Natal, the Provincial government's revised Conservation Ordinance lists of 1999 identify *O. martiensseni* as 'Specially Protected', giving it the same status there as the black rhinoceros, *Diceros bicornis*. In 2000, IUCN classified *O. martiensseni* as 'vulnerable' in their Red List Rating. Although widespread and sometimes locally numerous, it is known from relatively few specimen records other than those from caves in East Africa and Madagascar, and buildings around Durban, South Africa (Smithers 1983; Long 1995; Richardson and Taylor 1995). *Otomops* from Durban had been described as a distinct species (*O. icarus* – Chubb 1917) but Harrison (1957) treated them as a subspecies of *O. martiensseni*. *Otomops madagascarensis* (Dorst 1953) also has been treated as a subspecies of *O. martiensseni* (Freeman 1981; Wilson and Reeder 1993). The combination of large populations, some of which have declined precipitously in some roosts (A.M. Hutson, personal communication), and sparse records from elsewhere makes *O. martiensseni* a species of concern (Hutson et al. 2001).

The main purpose of our study was to examine a southern African population of *O. martiensseni* by: (1) documenting population structure in roosts and assessing morphological variation in the study area and across the species' range; (2) determining the use of roosts and foraging space to consider the impact of either resource on the bats; (3) assessing the practicality of using its vocalizations to monitor distribution, activity, and habitat use. The conservation implications of basic ecological information about *O. martiensseni* are presented and discussed.

Study area

Between 11 and 24 January 2001 we worked in the vicinity of Durban, South Africa (Figure 1). The Durban metropolitan region (in the KwaZulu Natal Province of South Africa) covers some 2297 km², and has a human population of 2.75 million, extending about 90 km along the east coast of South Africa, from Tongaat (29°33' S; 31°8' E) in the north to Umkomaas (30°13' S; 30°48' E) in the south (Figure 2). The Durban region encloses most of the known range of *O. martiensseni* in South Africa (Taylor 2000). Ballito (29°32' S; 31°13' E), the focus of our study, is just north of the Durban metropolitan region (Figure 3).

Outside urban and suburban developments in the region (20–30% of the area) the dominant land use is sugarcane monoculture (ca. 70%). Before intensive settlement and agriculture, this area was covered with a mosaic of evergreen coastal forest along the coast and river valleys and coastal grassland on the hills and higher slopes ('coastal bushveld-grassland', no. 23 – Low and Rebelo 1996). Small remaining patches (1–50 ha) of original forest and grassland remain scattered throughout the study area in the 'savanna' biome (Low and Rebelo 1996, no. 1 – Tongaland–Pondoland regional mosaic).

During our field work, sunrise ranged from 5 h 11 min on 11 January to 5 h 16 min on 23 January and sunset from 18 h 49 min to 18 h 57 min. In this period, at the nearby Mount Edgecombe weather station average daily temperatures ranged from 20.2 to 26.1 °C, with minimum temperatures varying from 17.5 to 23.3 °C and maximum temperatures from 22.8 to 30.3 °C. There was light rain (<5 mm) on two days, 14 and 21 January.

Materials and methods

In the attics of five buildings occupied by colonies of *O. martiensseni* (Taylor et al. 1999), we tried to catch all individuals by hand and placed them in holding bags made of soft cloth. We weighed each captured bat (to the nearest g), measured length of forearm to the nearest 0.1 mm and classified them as adult (fully ossified third digit metacarpal – phalanx I joint – Anthony 1988) or young (unossified third digit metacarpal – phalanx I joint). We extended the right wing of each adult bat and outlined along with the bat's body from nosetip to tailtip either by tracing or by taking a digital photo (Kodak DC 215 digital camera). From these drawings we measured adult wing span (B) and wing area (S) using Image-pro Express software (v. 4.0 – Media Cybernetics). We used these data and body weight (mass \times 9.81) to calculate aspect ratio (B^2/S) and wing loading ($M \times 9.81/S$) as per Norberg (1990). We measured forearms of specimens from East Africa and Madagascar in the collections of the Centre for Biodiversity and Conservation Biology in the Royal Ontario Museum (Toronto, Canada).

In Ballito (Figure 3), we used 10 collars made of fiber tape (Fenton et al. 1998a) and two from cable ties to attach Holohil (Carp, ON, Canada) MD-2C transmitters to 12 adult *O. martiensseni* (2 males, 10 females), 11 from roost 1 (Figure 3; one male, 11 females), one male from roost 7 (Figure 3). When attached, the transmitters

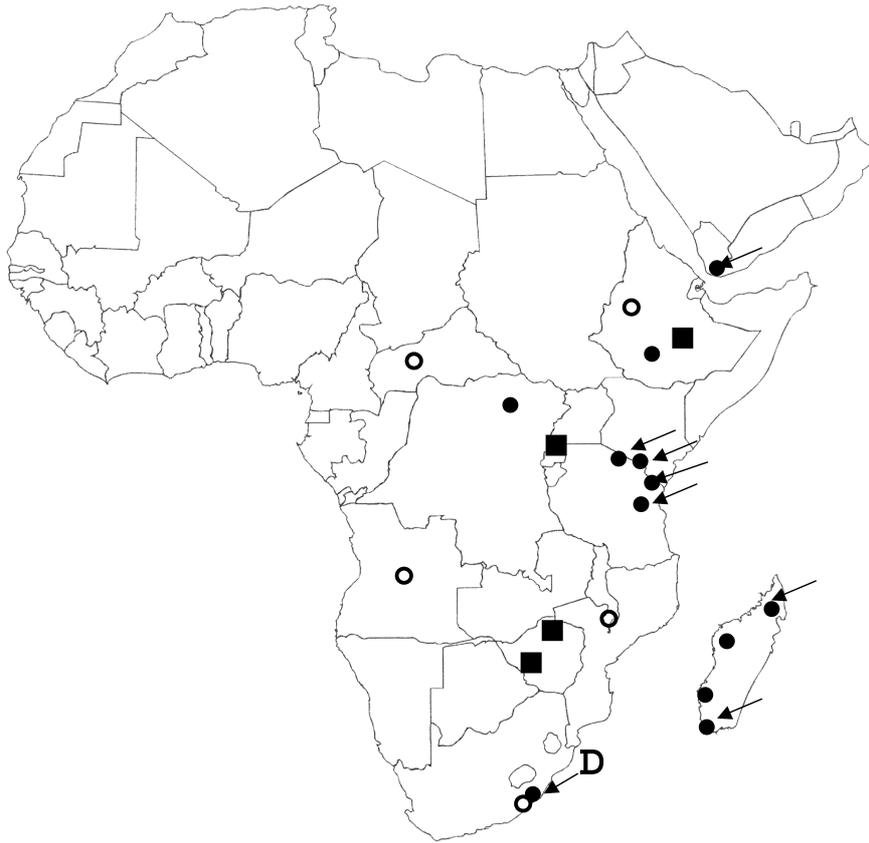


Figure 1. The location of our study area near Durban, South Africa (●←D) and the distribution records of *O. martiensseni*, showing places where these bats were taken in roosts (●), sites where bats were netted (■), along with locations lacking information about the collecting situation (○). The arrows identify roosts (or roosting areas) housing >5 bats. The records are as follows: Angola (Hill and Carter 1941), Central African Republic (Hill 1983), Congo (Verschuren 1957), Kenya (Kingdon 1974), Ethiopia (Hill and Morris 1971; Royal Ontario Museum), Madagascar (Peterson et al. 1995), Malawi (Dowsett and Hunter 1980), South Africa (Harrison 1957; Taylor et al. 1999; specimens in Harrison Zoological Museum), Tanzania (H.F. Baagøe, personal communication, colony of 11 in a hollow tree), Uganda (ROM), Yemen (specimen in Harrison Zoological Museum) and Zimbabwe (Fenton and Bell 1981; Smithers 1983).

and collars ranged from 3.4 to 4.8% of the bats' body masses at capture. To find and follow radio-tagged bats, we used two Lotek (Lotek Engineering Inc., Newmarket, ON, Canada) SRX400 Telemetry Receivers and two Communications Specialists (Orange, CA, USA) Telemetry Receivers Model R1000, all equipped with Lotek H (Model AN-ADH) antennae. One bat carrying an active transmitter for 1 day was designated as one bat-day.

We used pairs of radio receivers and observers in communication by walkie-talkie to locate roosting bats, making daily searches from the highest local points of land.

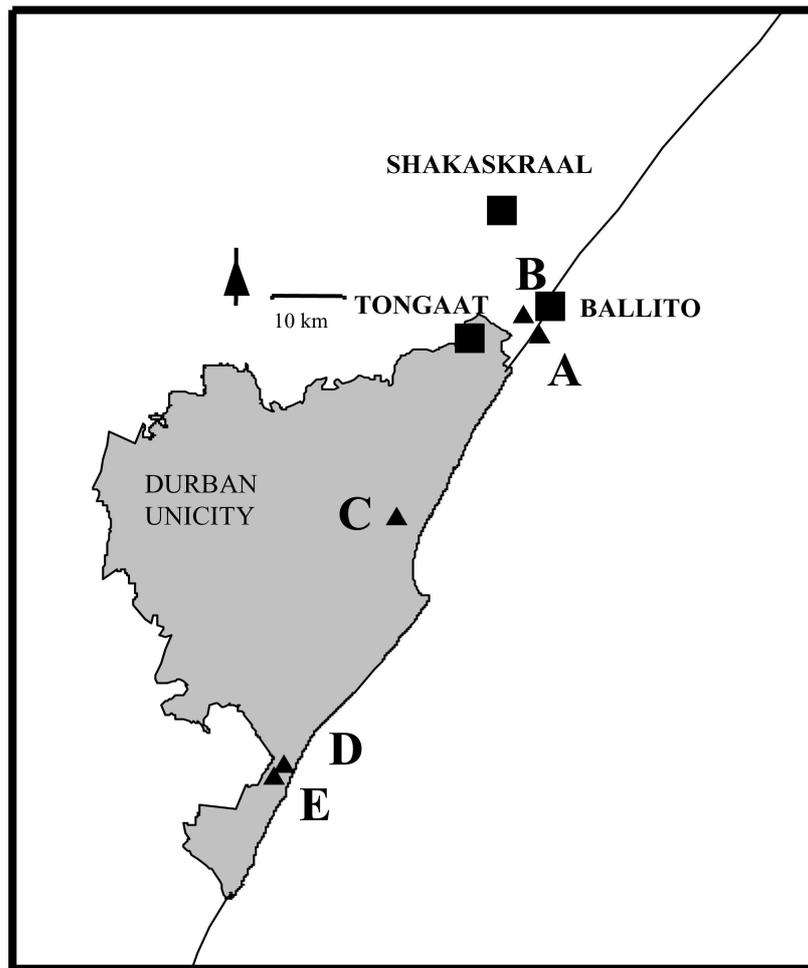


Figure 2. The distribution of five colonies (▲ and letters as in Table 1) of *O. martiensseni* sampled in the Durban area, as well as towns (■) mentioned in the text. Radio-tagged bats from Ballito flew as far north as Shakaskraal, and as far to the southwest as Tongaat.

Between 11 and 13 h on 13 January two observers flew over the study area in a fixed-wing aircraft and scanned for signals from radio-tagged bats. Each day we also monitored the signals from tagged bats from the time they emerged each evening until sunrise, using a combination of one mobile and one stationary receiver to follow bats away from their roosts. Roost positions and distances between roosts were determined using a Garmin GPS 12 Personal Navigator, Software 4.55, accurate to the nearest 15 m. The location of a radio-tagged bat in an attic affected the range of signal detection. For example, the range on one transmitter was not detectable at 770 m from one roost, but detectable at distances twice this when the

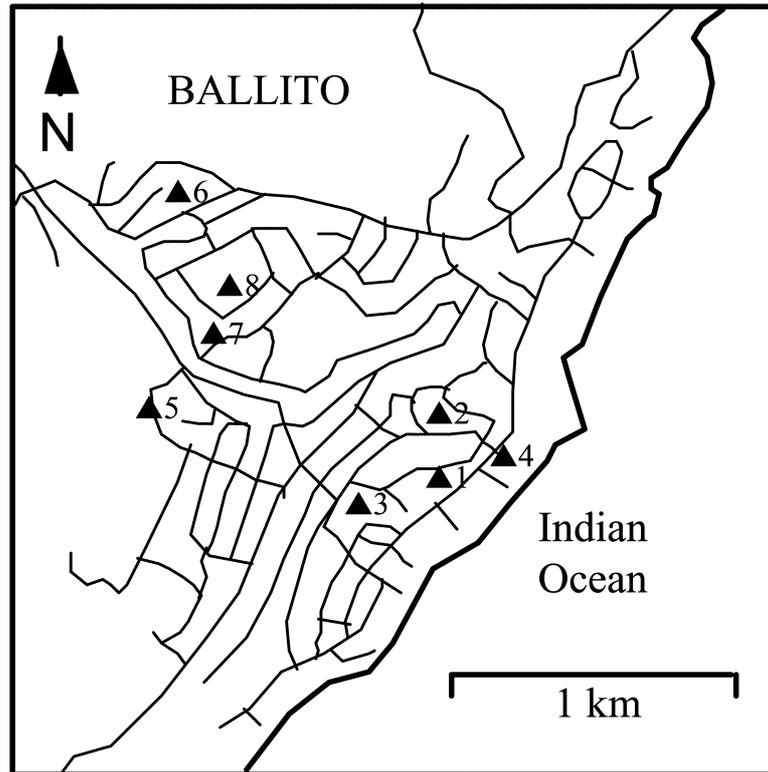


Figure 3. The location of buildings (▲) used by roosting radio-tagged *O. martiensseni* in Ballito. Exact addresses of colonies are on file at the Durban Museum.

bat roosted elsewhere. Bats carrying active transmitters and flying were readily detectable at ranges of up to 3 km, occasionally to ~5 km using the Lotek receivers, but considerably less with the Communications Specialists Telemetry receivers. The range achieved for roosting bats varied, but was usually about 2 km with a Lotek.

We used a Pettersson D980 bat detector operated with 12 s digital expansion to record vocalizations of *O. martiensseni* and then transferred them to BatSoundPro software running on a Dell Inspiron 3800 personal computer. The Pettersson detector and BatSoundPro came from Pettersson Elektronik AB (Uppsala, Sweden). We sometimes used two other systems to record the vocalizations of bats. The high frequency output of the Pettersson detector was recorded on a Racal Store 4D tape recorder operated at 76 cm s^{-1} , and the slowed down recordings were analyzed with BatSoundPro. In this case we used a Tektronix oscilloscope (THS 710 A, 60 MHz Scope/DMM Digital Real-Time 250 MS/s) to monitor recording levels. We also recorded some echolocation calls using an Anabat II bat detector with Anabat Zero Crossing Analysis Interface Module (ZCAIM – Titley Electronics, Ballina, NSW,

Table 1. Morphological variation in *O. maritimensis* captured in five colonies (Figure 2) in the vicinity of Durban, South Africa.

Colony	n	Mass (kg)	Forearm (m)	Wingspan B (m)	Wing area S (m ²)	AR (B ² /S)	WLN m ⁻² (9.81 Mg/S)
A							
Male adult	1	0.033	0.066	0.343	0.146	9.2	22.2
Female lact	7	0.027 ± 0.003	0.063 ± 0.002	0.343 ± 0.15	0.013 ± 0.001	10.6 ± 3.7	19.15 ± 8.79
Female postl	3	0.026 ± 0.002	0.061 ± 0.002	0.384 ±	0.016 ± 0.004	9.07 ± 0.009	15.75 ± 1.04
Female nonrep	1	0.028	0.064	0.367	0.016	8.2	16.8
B							
Male adult	1	0.035	0.065	0.421	0.019	9.2	17.77
Female lact	8	0.031 ± 0.002	0.063 ± 0.002	0.381 ± 0.02	0.016 ± 0.002	9.1 ± 0.004	19.28 ± 2.01
Female postl	2	0.033 ± 0.006	0.064 ± 0.001	0.41 ± 0.009	0.016 ± 0.001	10.3 ± 0.001	19.68 ± 1.39
C							
Male adult	1	0.036	0.067	0.388	0.0164	9.2	21.2
Female lact	4	0.030 ± 0.002	0.064 ± 0.002	0.040 ± 0.032	0.017 ± 0.002	9.3 ± 0.007	17.11 ± 1.69
Female postl	3	0.031 ± 0.002	0.064 ± 0.002	0.24 ± 0.212	0.010 ± 0.009	9.2 ± 0.001	20.74 ± 1.77
D							
Male adult	1	0.032	0.066	0.38	0.0156	9.2	20
Female lact	9	0.032 ± 0.002	0.064 ± 0.002	0.036 ± 0.028	0.014 ± 0.002	9.4 ± 0.006	22.9 ± 3.18
Female postl	1	0.034	0.064	0.324	0.011	9.5	30
E							
Male adult	1	0.038	0.069	0.404	0.019	8.5	19.37
Female lact	1	0.037	0.066	0.466	0.024	9.0	14.97
Female nonrep	1	0.030	0.063	0.419	0.020	8.6	14.4

n – sample size; AR – aspect ratio; WL – wing loading. Means are shown ± 1 standard deviation, and letters refer to colonies identified in Figure 2.

Australia) and a Dell Inspiron 3800 running (not in Windows) Anabat6 software. Both bat detectors use solid dielectric microphones (Simmons et al. 1979).

In BatSoundPro, we sampled at 44 100 Hz (16 bits, mono), used a threshold of 15 and then measured duration from the time–amplitude and frequency change over time displays and frequency information (for the dominant harmonic) from the fast Fourier transform (FFT) power spectrum (size 512, Hanning window), taking – 55 dB as the criterion for identifying highest and lowest frequencies in any call. We used the display showing time–amplitude and frequency–time plots, zooming in on individual calls, identifying them with the cursor, and from there first measuring duration and then acquiring an FFT power spectrum of the selected call.

Means are shown \pm one standard deviation. Statistical tests were done with Statistix® (Analytical Software, Tallahassee, Florida).

Results

Roosts

We sampled bats in five colonies (Figure 2): (A) in Ballito (= 1 in Figure 3), about 30 years old with no indication of how long the bats had roosted there; (B) in Ballito (= 7 in Figure 3), 12–15 years old with bats in the roof for at least 5 years; (C) in Glenhills, of unknown age, but with bats for at least 9 years; (D) in Amanzimtoti, a 20-year old house with no information about how long the bats had roosted there; and (E) in Amanzimtoti, of unknown age where the bats had roosted for at least 2 years. Using radio-tracking (see below), we found bats roosting in an additional six houses in Ballito (Figure 3), all of the same general age (10–30 years) and construction. Records from the Durban Bat Interest Group (Taylor 1999a) show that 17 buildings of known age used as day roosts by *O. martiensseni* averaged 34.5 ± 15.8 years old, ranging from 12 to 70 years. These records also show seven buildings with solitary bats (three males, one female, and three bats of unreported gender). Setting aside these records, and two involving two bats, 24 colonies of *O. martiensseni* averaged 11.2 ± 6.7 individuals.

Roosting bats

Within building roosts, individuals of *O. martiensseni* were alert and active and usually in physical contact with one another (Figure 4). Bats invariably roosted in the attic spaces of houses, either hanging on rafters or on the inside of the outer walls of the buildings, with their venters against a surface. Bats used holes or cracks 4–6 m above ground level as access points to the roosts. None of the openings was large enough for access by a flying *O. martiensseni*. The bats had to land and crawl into the roost or crawl out to take flight.

We captured 84 *O. martiensseni* (six males; 30 lactating females, nine postlactating females, one non-reproductive female, 25 male subadults, 13 female subadults) in five colonies (houses) in the Durban area (Figure 2). The number of bats in a roost



Figure 4. A group of *O. martiensseni* roosting on the rafters in the attic of a house (D in Figure 1).

ranged from 7 to 29 individuals. In each building we captured one male with a well-developed chest (gular) gland, but in one colony one male with fully ossified finger joints lacked a well-developed chest gland. The sex ratio among adult bats was skewed towards females (Table 1) and among the colonies sampled, ranged from 1 male:2 females to 1:11.

Morphology

Adult bats from the five colonies varied in morphology (Table 1). A Kruskal–Wallis one-way ANOVA revealed significant differences in body mass of adult females between the five colonies (KW = 14.35; $P = 0.006$), but none in length of forearm (KW = 4.38, $P = 0.36$). Since the bats were captured in the afternoon at least 8 h after their return from foraging, differences in mass are not obviously attributable to the contents of the digestive tract. Thus, while there were significant differences in wing loading between colonies (KW = 17.30; $P = 0.002$), there were none in aspect ratio (KW = 5.344; $P = 0.25$). Young bats overlapped in size with adults (Table 1). Young males had lengths of forearms averaging 58.6 ± 3.4 mm ($n = 26$, range 48.1–65.5 mm), and body masses 26.4 ± 2.9 g ($n = 26$, range 19–33 g); young females had lengths of forearms averaging 58.2 ± 2.3 mm ($n = 14$; range 52.6–60 mm), and body masses averaging 23.7 ± 2.1 g ($n = 14$; range 19.2–28 g). Two sample t tests revealed that adults were significantly larger than young (males, length of forearm $t = 4.76$; $df = 27$; $P = 0.0001$; body mass $t = 4.82$; $df = 27$; $P < 0.0001$; females, length of forearm $t = 9.41$; $df = 51$; $P < 0.0001$; body mass $t =$

Table 2. Details of day roosts used by radio-tagged *O. martiensseni* in Ballito, KwaZulu Natal Province, South Africa between 11 and 23 January, 2001.^a

Date	Individual bats and roosts											
	male ad	female postl	female lact	female postl	female nr	female postl	female nr	female postl	female lact	female postl	female lact	female lact
	431 ^b	492	576	593 ^c	853	873	887	911 ^d	932	952	991	994
11 Jan	1		1	1	1	1	1	1	1	1	1	1
12 Jan	4		+	-	1	1	1	f	+	+		+
13 Jan	4	1	+	-	4	+	1	f	4	+		+
14 Jan	Shed	2	+	-	+	+	+	+	+	2		+
15 Jan	-	2	2	-	+	+	+	+	+	2		5
16 Jan	-	2	+	-	+	+	+	f	+	2		5
17 Jan	-	2	+	-	1	2	+	+	1	2		5
18 Jan	-	2	+	-	1	2	+	f	1	f		-
19 Jan	-	2	3	-	2	+	+	f	1	f	7	-
20 Jan	-	2	+	-	1	2	+	+	1	f	8	-
21 Jan	-	-	3	-	1	2	2	f	1	f	6	-
22 Jan	-	-	+	-	1	2	-	-	1	f	7	-
23 Jan	-	-	3	-	-	2	-	-	-	-	7	-
n - Bat-days	2	7	12	0	11	12	10	9	10	11	4	6
n - Roosts	2	2	4	0	4	3	3	?	3	3	3	3
Move/stay	1-6	1-6	8-0	5-4	4-5	4-5	2-2		4-5	4-2	3-1	2-2

Bold indicates location and date that transmitters were applied. The '+' indicates a bat with an active transmitter, the '-' a shed transmitter or lost signal, and the 'f' a signal from a bat flying at night. Individual bats are identified by transmitter number. Radio-tagged bats were either adult males (ad) or lactating (lact), postlactating (postl) or nonreproductive (nr) females. The number of bat-days is the number of days a bat carried an active transmitter, and the number of roosts, the minimum number of roosts used. Move/stay identifies the number of times a radio-tagged bat moved between roosts, or spends consecutive days in the same roost. ^aThe first 10 radio-tagged bats emerged from roost 1 on the evening of 11 January, the day they were tagged. ^bShed its transmitter in Roost 4 on 14 January. ^cDisappeared after emergence on 11 January. ^dDetected as it foraged almost nightly between 12 and 21 January, but we never located its day roost(s).

8.31; $df = 51$; $P < 0.00001$). Adult males were significantly larger than females (length of forearm $t = 4.31$; $df = 41$; $P = 0.0001$; body mass $t = 3.03$; $df = 41$; $P = 0.004$), while young males were significantly larger than females only in mass (length of forearm $t = 0.52$; $df = 37$; $P = 0.61$; body mass $t = 2.87$; $df = 37$; $P = 0.007$).

Radio-tracking

Data from radio-tagged bats that we followed for 94 bat-days, provided information about the use of day and night roosts, as well as the areas covered by foraging bats. The radio-tracking data indicate that the bats moved in and out of the area, using several roosts and foraging areas, some of which we located (Table 2). For example, on 13 January from an aircraft we detected signals from two of the bats tagged and released in roost 1 on 11 January. On the night of 13–14 January, however, three radio-tagged bats foraged within range of the receivers. On the morning of 14 January two radio-tagged bats roosted in Ballito, neither in roost 1 (Table 2). Tagged bats from different colonies were never observed roosting in the same houses.

Day roosts ($n = 8$) of tagged bats in Ballito were always in houses and bats used at least 2-day roosts, most three or more (Table 2). A comparison of days when female bats changed day roosts or did not (Table 2) reveals no significant difference in this behavior between four lactating, three postlactating, and one non-reproductive female(s) ($\chi^2 = 2.21$, $df = 2$, $P = 0.33$). The movement of radio-tagged *O. martiensseni* between so many roosts and the failure of known individuals from the two different original roosts to intermingle all suggest that, even when undisturbed, these bats use several roost sites.

The first *O. martiensseni* emerged from their day roosts 15–30 min after sunset. Although pairs of bats occasionally emerged within a minute of one another, emergences were more typically at 5–10 min intervals and on two occasions bats continued to emerge from the day roost 55 min after the first one had departed. Emerging bats did not begin to produce echolocation calls until they were at least 10 m from the entrance.

Otomops martiensseni also used buildings as night roosts, places to roost at night after having emerged from their day roosts. Between 12 and 23 January, we found night-roosting bats on 58 occasions between 20 h and 3 h 59 min. Seven individuals used five night roosts in buildings also used as day roosts, while two bats used more distant buildings. Radio-tagged bats typically used several night roosts, one used 4 of them, one 3, two 2, and two just 1. Although night-roosting bats tended to occupy these roosts later in the night, some were found there from 20 h on (60 min beginning at 20 – 2; 21 – 3; 22 – 8; 23 – 6; 0 – 8; 1 – 15; 2 – 9 and 3 – 7). While three bats used the same buildings as day roosts and night roosts (two postlactating females, one lactating female), four other bats used fewer roosts as night roosts than as day roosts.

Radio-tagged bats sometimes covered considerable distances while foraging and, as with roost use, appeared to move into and out of the Ballito area. One male (no.

991) night-roosted in a building in Tongaat, 6.8 km from the day roost it usually used, and two females (nos. 576 and 583) night-roosted at least 10 km from Ballito between Umhali and Shakaskraal (Figure 1). On the night of 20–21 January, these three bats were at these distant sites through the middle of the night and back in roosts in Ballito by dawn. On the night of 22–23 January one female (576) was again detected north of Ballito between Stanger and Shakaskraal around 04:00 (Figure 2) and was back in a roost in Ballito by dawn (Table 2). After emergence some radio-tagged animals flew about within range of receivers in Ballito for up to 90 min, flying back and forth over the beach as well as generally over Ballito from housing developments to parks. Radio-tagged individuals also flew over the sugarcane fields in the adjoining countryside.

To quantify the comings and goings of radio-tagged bats, we counted the 1-h periods between 20 and 5 h in which we detected signals from them. In total, we detected flying radio-tagged bats in 199 1-h periods between 20 and 5 h, mostly (190) from locations in Ballito, reflecting the focus of our sampling. Flying, radio-tagged bats were most often detected in the first 3 hours after sunset ($n = 91$ 1-h periods) and in the 3 hours before sunrise ($n = 56$). Furthermore, the frequency of detection ranged from 13 to 32 1-h periods in a night. Our contact with signals from bats flying away from their roosts varied from bat to bat and night to night. Signals from three flying bats (431, 593 and 887) were detected <5 times each, and only on one night. Four bats (576, 853, 873 and 932) were detected more than 20 times (21, 29, 32, and 29, respectively) over 7, 10, 9 and 8 days, respectively. The remaining bats (492, 911, 952, 994 and 991) were detected 19, 16, 14, 16 and 19 times, respectively over 7, 7, 7, 5 and 4 days. At night, most bats were >3 km from Ballito most of the time (Figure 3).

Vocalizations

Flying *O. martiensseni* produced many vocalizations that were clearly audible to us. Indeed, some human residents of buildings used as roosts by these bats claimed to be all too familiar with the vocalizations of flying and roosting bats. Analysis of recordings indicated two types of calls differing in patterns of frequency change over time (Figure 5), namely: frequency sweeps (Figure 5A – like those described as echolocation calls of *O. martiensseni* – Fenton and Bell 1981) and lilts (Figure 5B). We also heard calls from other bats flying in the area (Figure 6).

We analyzed 250 frequency sweeps (Table 3), recorded by time expansion from bats flying near roosts or in the general area of Ballito. The sweeps went from about 18 to about 9 kHz in 5–50 ms and had most energy between 10 and 12 kHz (Table 3). Harmonics were uncommon and duration was not a significant predictor of bandwidth ($r^2 = 0.005$; $df = 248$). When there was one bat flying in the airspace sampled by the microphone and the recorded signals were of uniform strength and duration (13–15 ms), interpulse intervals ranged from 600 to 800 ms and the duty cycle was about 2.5%. From over 20 h of monitoring vocalizations we heard no feeding buzzes from *O. martiensseni*. Compared to time expansion, the Anabat

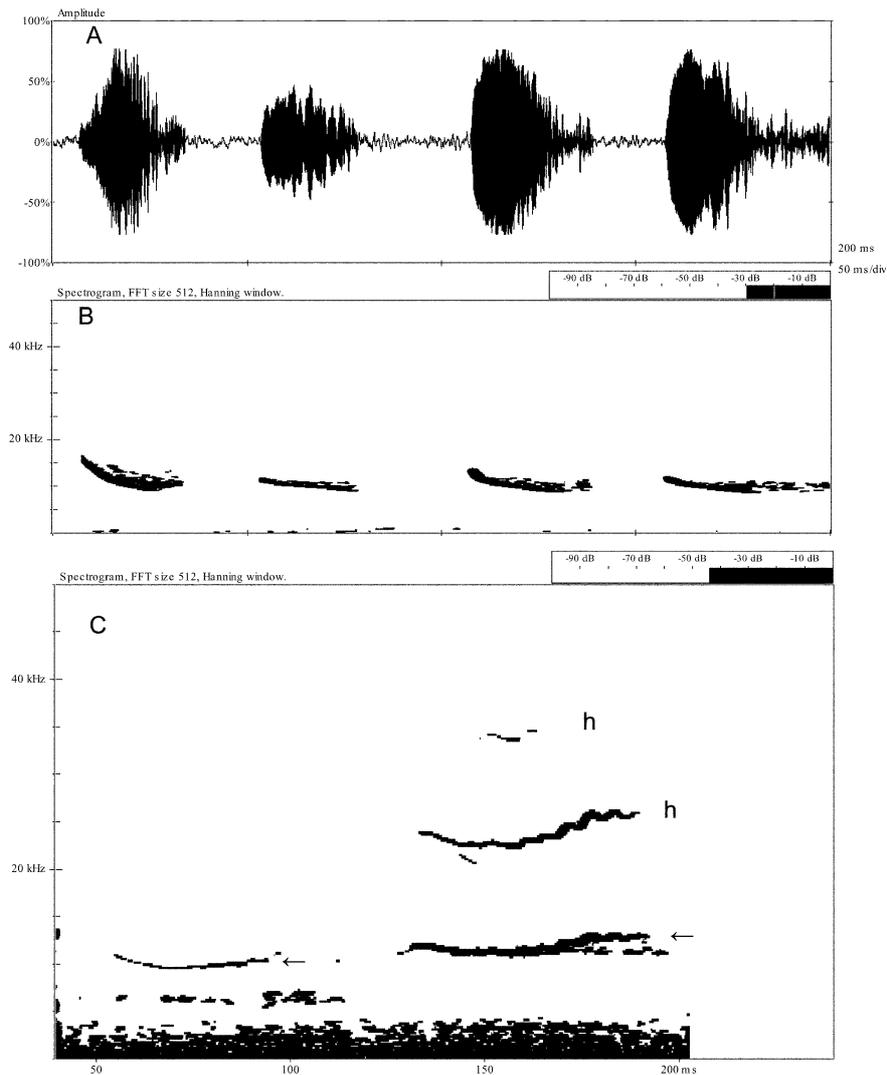


Figure 5. Oscillograms (A) and plots of frequency change over time (B) of frequency sweeps recorded from *O. martiensseni*. Patterns of frequency change over time are shown for two lilt vocalizations (arrows) recorded from *O. martiensseni*. Lilt vocalizations finished with an upward sweep and often included harmonics (h in C).

system presented a slightly different view of *O. martiensseni* frequency sweep calls (Table 3).

The echolocation calls (frequency sweeps; Figure 5A and B) of *O. martiensseni* differed from those of other molossids recorded flying around Ballito. While *Chaerephon pumilus* produced echolocation calls with most energy at 27.1 ± 0.8 kHz, ranging from 30.3 ± 1 to 25.7 ± 0.5 kHz in 12.1 ± 1.5 ms ($n = 10$ calls), in

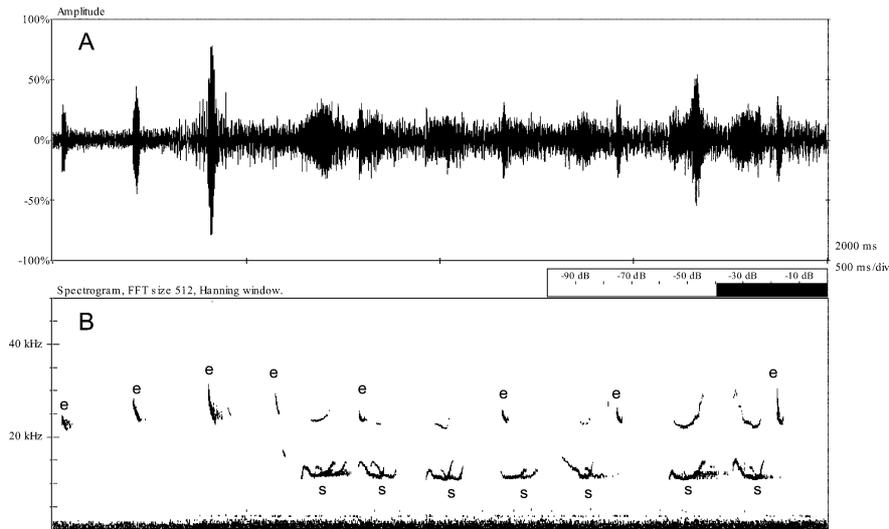


Figure 6. Time–amplitude (A) and frequency change over time (B) presentations of vocalizations of *C. pumilus*, including echolocation calls (e) above the range of human hearing, and social calls (s) audible to human observers, yet distinguishable by frequency from the vocalizations of *O. martiensseni* (compare with Figure 5B and C and data in Table 3).

Tadarida aegyptiaca these values were 21.8 ± 0.8 , 24.5 ± 2.1 to 20.2 ± 0.7 kHz in 17 ± 3 ms ($n = 10$ calls). The vocalizations also differed from the fainter echolocation calls of the emballonurid, *Taphozous mauritanus*, whose calls occasionally sweep to 10 kHz but typically have most energy in the second harmonic (>20 kHz – Taylor 1999b).

Lilt calls (Figure 5C) began the same way as frequency sweeps but finished with an increase in frequency, a lilt, and often included an obvious harmonic (Figure 5C). Lilts were most obvious in calls lasting over 25 ms, and the upward sweep was most conspicuous when recorded signals were played back at reduced speed. Lilts were not obvious when listening in real time to the calls of flying *O. martiensseni*. *Chaerephon pumilus* also produced vocalizations (but not their echolocation calls) that we could hear (Figure 6). Frequency characteristics made sounds we heard from *C. pumilus* in the area (Figure 6) distinguishable from the frequency sweeps or lilts of *O. martiensseni*.

Although the bats tended to emerge individually from roosts, we often heard vocalizations produced by individuals apparently flying together near roosts. On 12 January at roost 1, for example, the radio-tagged and other bats had emerged by 20 h 15 min and then left the area and no *O. martiensseni* were within earshot of this roost. Then, between 21 h 45 min and 22 h 15 min, *O. martiensseni* were back and there was almost constant activity over and around the roost, evidenced by almost continuous vocalizations, and individuals flying up to and then turning away from the entrances to the roost used by the bats. None of this activity involved radio-tagged animals. Before 21 h 34 min and after 22 h 15 min there was virtually no

Table 3. Features of the frequency sweep vocalizations of *O. marriensis* (Figure 5A and C) as recorded by time-expansion and zero-crossing period meter sound analysis and recording systems.

	n	Duration (ms)	Bandwidth (kHz)	Lowest frequency (kHz)	Highest frequency (kHz)	Frequency with most energy (kHz)	Slope (kHz ms^{-2})	Number of calls with harmonics
Time-expansion durations (ms)								
1-9	64	4.48 \pm 2.39	6.04 \pm 1.41	8.27 \pm 2.27	14.31 \pm 1.24	10.22 \pm 0.63	1.18 \pm 1.18	1
10-19	21	17.53 \pm 2.41	5.3 \pm 2.77	9.88 \pm 1.3	15.17 \pm 3.13	13.38 \pm 4.04	0.30 \pm 0.15	1
≥ 20	165	32.5 \pm 10.33	6.6 \pm 2.4	9.0 \pm 1.17	15.7 \pm 2.7	10.63 \pm 1.74	0.23 \pm 0.11	15
All calls	250	24.01 \pm 14.83	6.35 \pm 2.27	8.9 \pm 1.19	15.25 \pm 2.53	10.75 \pm 2.01	0.62 \pm 0.89	17
Zero-crossing								
Period meter	12	10.35 \pm 4.5	6.54 \pm 1.52	10.94 \pm 0.79	17.48 \pm 1.51			

Means are shown ± 1 standard deviation, and n is the number of calls analyzed.

audible activity around the roost. Away from known roost sites (≥ 1 km), we occasionally heard similar bursts of audible activity. The vocalizations produced in these circumstances included frequency sweeps, lilt, and signals with more complex changes in frequency over time (Figure 5). On other nights there was very little audible activity around roosts. For example, on 19 January by 20 h 15 min we heard almost no *O. martiensseni* vocalizations at any locations around Ballito, although by 22 h 30 min we again heard some bats flying in the area. The comings and goings of bats were clear from radio-tracking and monitoring their vocalizations.

Discussion

Roosts

The range of roost structures used by *O. martiensseni* is similar to those reported for the genus. *Otomops martiensseni* sometimes roosts in very large numbers in caves in East Africa (Kingdon 1974) and in Madagascar (Peterson et al. 1995), similar to *O. wroughtoni* in India (Bates and Harrison 1997). *Otomops martiensseni* also roosts in smaller numbers in buildings (Harrison 1957; Richardson and Taylor 1995; this study) and, like *O. formosus* (Chasen 1940), in hollows in trees (Verschuren 1957; H.F. Baagøe, personal communication). Although the original record of *O. martiensseni* from Durban was dead when found in a gutter (Chubb 1917), Harrison (1957) found this species roosting there in buildings. The combination of darkness, a protected environment, and room for individuals to cluster together appears to make a roost attractive to *Otomops* species which may land to crawl into a roost.

Roosting bats

Roost demographics suggest a 'harem' organization, one adult male with a group of reproductive females and their dependent young. The fact that males with well-developed chest glands were with females and young outside the mating season (maximum testicular development in August–September – Mutere 1973) suggests associations not just related to mating. The ratio of adult females to dependent young was almost 1:1 in our study (40 adult females:38 young), unlike the situation in two Kenyan caves where the ratio was 7:1 or 9:1 (Mutere 1973). Mutere (1973) reported that the ratio of subadult males:females ranged from 1:1 in 1 year to 1:4 and 3:1 in others, bracketing the almost 2:1 that we observed (Table 1). Data from large cave aggregations do not include information about smaller roosting groups. In such large roosting aggregations, however, the harem organization also may prevail, as in the neotropical *Phyllostomus hastatus*, where a harem male fathers most young born to females in its group (McCracken and Bradbury 1981). But unlike *P. hastatus*, individual *O. martiensseni* females caught together often roosted in different locations, more like individuals in a colony of *Desmodus rotundus* (Wilkinson

1985). Solitary bats or pairs of bats in building or tree roosts (this study; Verschuren 1957) could be dispersing individuals and/or those unable to attract conspecifics.

Morphology

Our data for aspect ratio and wing loading for *O. martiensseni* bracket those provided by Norberg and Rayner (1987), 9.3 and 14.9 N m⁻², respectively, and are comparable to those for two similar-sized molossids, *T. midas* (aspect ratio 8.9 ± 0.7; wing loading 18.4 ± 0.9 N m⁻² – Fenton and Rautenbach 1986) and *Molossus ater* (8.3–9.1; 17.55–24.15 N m⁻² – Fenton et al. 1998a). While the aspect ratios are within the range reported for the vespertilionid *Lasiurus cinereus* (8.1 ± 1.16 – de la Cueva Salcedo et al. 1995), this bat has lower wing loading (15.62 ± 0.36 – de la Cueva Salcedo et al. 1995) and shows geographic variation in aspect ratio and wing loading between Hawaii and Manitoba (Jacobs 1996).

In length of forearm, the *Otomops* at Durban do not differ significantly from specimens from Madagascar (males two sample $t = -2.03$; $df = 10$; $P = 0.07$; $n = 6$ from each area; females $t = 1.59$; $df = 18$; $P = 0.13$; $n = 10$ from each area), while both of these populations are significantly smaller than those from East Africa (ANOVA, male $F = 40.26$; $df = 2$; $P < 0.001$; female $F = 113.24$; $df = 2$; $P < 0.001$). The *Otomops* we studied showed the same timing of births as those in East Africa (Mutere 1973), an interesting similarity across 31° of latitude when several other species of bats show one pattern of timing north of the equator, and another to the south (Anciaux de Faveaux 1977). Bernard and Cumming (1997) noted that African molossids differ from other bats in their patterns of reproduction, but still show decreases in reproductive season away from the equator. Although Wilson and Reeder (1993) treated the three populations as one species, Peterson et al. (1995) used skull width and wing features to support Dorst's (1953) view that *O. madagascarensis* is distinct. For a similar-sized bat with broader wings (*Myotis myotis* – aspect ratio 6.3; wing loading 11.35 N m⁻² – Norberg and Rayner 1987), which may not be as strong a flier (Norberg 1990), a much narrower body of water (Strait of Gibraltar) than the one between Africa and Madagascar (16 vs. 400 km) appears to be a barrier to gene flow (Castella et al. 2000). The combination of distinctness in morphology and size and the distance between Africa and Madagascar may be used to support the view that the Madagascar and African populations are different taxa.

Radio-tracking

In its day-roosting behavior, *O. martiensseni* differs markedly from African molossids such as *C. pumilus* or *Mops condylurus* which roost in very large numbers, usually in crevices in houses, trees, and bridges (Smithers 1983; Bouchard 1998). Not only are there many fewer individuals in *O. martiensseni* roosts, but the pattern of emergence is quite different. Emerging *C. pumilus* or *M. condylurus* come out of the roost in streams, the *O. martiensseni* emerge individually. Simultaneous

emergences by many individuals reduce the risk of predation on any one (Fenton et al. 1994), but erratic emergences might achieve the same end.

Like many other species of bats (Lewis 1995), *O. martiensseni* switches between day roosts, although the initial moves by radio-tagged animals from roost 1 or 7 may reflect the disturbance of capture and handling. *Nycteris grandis* also abandoned a roost after the disturbance of capture and radio-tagging, but returned within 3 days (Fenton et al. 1993).

Foraging, radio-tagged *O. martiensseni* typically flew >3 km away from their roosts, resembling aerial-feeding *T. midas* in Kruger National Park (Fenton and Rautenbach 1986) or *L. cinereus* in Manitoba (Barclay 1989) and Hawaii (D.S.J., unpublished data), bats of similar size and wing features. Similar-sized gleaning bats have broader wings and may cover large areas (≥ 10 km from roost) while foraging (e.g., *My. myotis* – Audet 1990), although others (e.g., *N. grandis* – aspect ratio 5.2, wing loading 11.35 N m^{-2}) cover much less ground (<3 km – Fenton et al. 1993).

Vocalizations

Calls of flying *O. martiensseni* appear to be a mixture of echolocation and social calls, functioning in communication between group members, like the directive calls of rallying *Antrozous pallidus* returning to day roosts at dawn (Vaughan and O’Shea 1976), calls of *P. hastatus* away from roosts (Boughman and Wilkinson 1998) or those of swifts in ‘screaming parties’ (Lack 1973). The setting in which we heard them does not suggest food-sharing calls (Brown et al. 1991). Echolocation calls can serve a communication function (*My. lucifugus* – Barclay 1982; *Euderma maculatum* – Leonard and Fenton 1984), and be colony (Pearl and Fenton 1996) or individual specific (Masters et al. 1995). In some ‘social’ situations, bats modify echolocation calls by lowering the terminal frequency and increasing call bandwidth (e.g., *Noctilio leporinus* on collision courses – Suthers 1965). In *O. martiensseni* echolocation calls appear to be modified into lilt calls by raising the terminal portion of echolocation calls (cf. Figure 5B and C), and none of the vocalizations we recorded was harsh and broadband like those of *L. cinereus* at feeding sites in Hawaii (Belwood and Fullard 1984). Echolocation or social calls dominated by sounds <20 kHz should carry farther because they are less subject to atmospheric attenuation than sounds >20 kHz (Lawrence and Simmons 1982).

As in *A. pallidus*, when individuals change day roosts, low-frequency vocalizations can be an effective way to locate roost-mates at greater distances. In *A. pallidus* (Trune and Slobodchikoff 1976) and many other bats (e.g., *Noctilio albiventris* – Roverud and Chappell 1991), roosting in contact with conspecifics can reduce the costs of thermoregulation. The presence of groups of *O. martiensseni* flying around day roosts at different times during the night makes it obvious that these vocalizations are more than a means of locating a current day roost. The calls appear to be of more general use in group cohesion, perhaps functioning as others do in *P. hastatus* (Boughman and Wilkinson 1998) or in swifts (Lack 1973).

Farther north in Africa, the calls of *O. martiensseni* might be confused with those of molossids such as *T. midas* (forearm 57–63 mm), whose echolocation calls are

slightly higher in pitch (16–11 kHz over 17.5 ms – Fenton et al. 1998b), sound less piercing, and are less variable. While *T. midas* often alternates frequencies between adjacent echolocation calls (Fenton et al. 1998b), we did not hear this from *O. martiensseni*. Farther north in Africa, other large molossids (FA > 55 mm) such as *T. fulminans* or *T. africana* also can be expected to use lower frequency vocalizations, as reported for *T. lobata* (Peterson 1974). The practicality of identifying these molossids by their calls remains to be determined.

The activity, distribution and behavior of *O. martiensseni* can be monitored without using bat detectors or captures. In some other species echolocation calls are audible and conspicuous to people (e.g., *E. maculatum* – Fullard and Dawson 1997; *T. teniotis* – Rydell and Arlettaz 1994), while in others it is vocalizations functioning in sexual advertising (e.g., epomophorine bats – Bradbury 1977, or *Vespertilio murinus* – Rydell and Baagøe 1998). Field experience indicates that vocalizations of *O. martiensseni* that are audible to trained humans can be used to document its distribution. In October 1979 in the Sengwa Wildlife Research Area in Zimbabwe, one of us (M.B.F.) caught two *O. martiensseni* in mist nets set over the Sengwa River and described their echolocation calls (Fenton and Bell 1981). Similar calls had been heard there in June 1977 when the bats were not captured. One of us (M.B.F.) has not heard the distinctive calls of *O. martiensseni* during extensive field work on bats elsewhere in Zimbabwe and South Africa, areas where we heard and caught *T. midas*.

Recommendations for conservation

We address three fundamental questions regarding the conservation of *O. martiensseni*, including: (1) population; (2) roles of roost and food resources; and (3) use of vocalizations to study the biology and distribution of this species.

(1) Although Harrison (1957) spoke of *Otomops* as rare, Mutere (1973) found that *O. martiensseni* was abundant and sacrificed 4954 of them in his study of reproduction. Apart from the threat posed by biologists, guano mining at caves in East Africa is a disturbance with a negative impact on roosting populations of *O. martiensseni* (Taylor 2000). In the Durban area, *O. martiensseni* is one of the most commonly encountered bats (Taylor et al. 1999) and around Ballito we often heard many *O. martiensseni* at one time. Furthermore, around Durban, *O. martiensseni* appears to be reproducing to capacity (39 of 40 adult females lactating or postlactating). But in this area, timber treatments are commonly used in buildings and they can be lethal to roosting *O. martiensseni* (Taylor 2000).

(2) The *O. martiensseni* we studied only roosted in buildings, and just in some of the buildings available in Ballito and the greater Durban area. While this species forms large aggregations elsewhere in its range, the dispersion of breeding groups around Durban suggests no shortage of roost sites and hints that elsewhere a shortage of roost sites could lead to large aggregations. Similarly, the combination of wide range foraging and the reproductive output of the bats could indicate that food was not limiting. The vocalization behavior and data on movements of tagged

individuals between roosts suggest larger population units than the reproductive aggregations we observed. The erection of new housing developments in the Durban area, particularly along the coast from Durban north to Ballito and beyond suggests a consistent, if not expanding supply of new roosts. Elsewhere in Africa the construction of new housing (Cumming 2000) that does not provide an enclosed attic space may not offer as suitable roosts for *O. martiensseni*. The propensity of *O. martiensseni* to roost and forage in human-disturbed environments and its incidence in the Durban area suggest that its listing as a species of special concern in KwaZulu Natal could be overstated – but not if listing protects the bats from destruction resulting from timber treatments or their eviction by people who do not want bats in their roofs. Meanwhile, declines in populations of *O. martiensseni* in East Africa (Hutson et al. 2001) show that situations vary across a species' range. *O. martiensseni* may be one species that is resistant to declines associated with increasing human populations (Balmford et al. 2001).

(3) Emergence behavior and echolocation calls should allow observers to distinguish *O. martiensseni* from many other molossids. But counts of emerging bats may be less useful in determining the numbers of *O. martiensseni* leaving a roost because of the long times between emerging individuals. The distinctive repertoire of vocalizations that are clearly audible to humans offers a convenient and accessible means for monitoring distribution, activity and habitat use by *O. martiensseni* throughout the night. Listening by trained observers can provide a clear indication of where and when the bats are active. More detailed studies of vocalizations, preferably with real time bat detectors or those operating by time expansion, will increase the information about species' identities. This will be particularly important where *O. martiensseni* is sympatric with other large (length of forearm >55 mm) molossids that use calls with most energy <20 kHz. In any event, the choice of bat-detecting system influences the picture (Table 3) that emerges from the calls (Waters and Walsh 1994; Fenton 2000).

We found roost 7 in Ballito because of press coverage of our field work, demonstrating the importance of communication as well as the fact that some human residents of buildings are well aware of bats they live with. Knowledge about bats of the Durban area is a direct consequence of publicity, public interest in the animals, and the hard work of volunteers who show the flag for bats (Taylor 1999a). In our experience, after seeing an *O. martiensseni* up close, many humans (children and adults) who shared buildings with them were more interested in the bats and more tolerant of them as co-habitants. This is important because of the potential impact of timber treatments on bats (Taylor 2000). People interested in the bats may be more prepared to use less hazardous materials to protect their buildings from termites, wood borers, and other biological ravages. At the same time, drawing attention to the bats could be detrimental, just as establishing protected areas can backfire (Liu et al. 2001).

Our data do not address two unresolved problems about *Otomops* from Africa and Madagascar, namely questions about taxonomy and distribution. Although we follow Wilson and Reeder (1993) and speak of one species (*O. martiensseni*) occurring from East Africa to Madagascar, there may be two or three species in this

complex. The geographic range of *O. martiensseni* is not well documented. Long (1995) indicated its general distribution, but specific records (Figure 1) reveal that apart from some known roosts, most (10/20) records represent one or two specimens.

Otomops martiensseni, a large bat of striking appearance (Figure 4), is made conspicuous by its vocal repertoire. Its ability to find and exploit roosts in urban areas and to thrive in areas of intensive agricultural operations together suggest that it could have a role as flagship species representing the resilience of nature. Indeed, *O. martiensseni* may be a threatened species with stabilized or increasing abundance, a candidate for inclusion on a 'blue' list (Gigon et al. 2000) in KwaZulu Natal.

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