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Author(s): Ara Monadjem, Julie T. Shapiro, Fezile Mtsetfwa, April E. Reside and Robert A. McCleery

Source: *Acta Chiropterologica*, 19(1):175-187.

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

DOI: <http://dx.doi.org/10.3161/15081109ACC2017.19.1.014>

URL: <http://www.bioone.org/doi/full/10.3161/15081109ACC2017.19.1.014>

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Acoustic call library and detection distances for bats of Swaziland

ARA MONADJEM^{1,2,3,5}, JULIE T. SHAPIRO², FEZILE MTSETFWA¹, APRIL E. RESIDE⁴, and ROBERT A. MCCLEERY²

¹*All Out Africa Research Unit, Department of Biological Sciences, University of Swaziland, Private Bag 4, Kwaluseni, Swaziland*

²*School of Natural Resources and Environment and Department of Wildlife Ecology and Conservation University of Florida, Newins-Ziegler Hall, Gainesville FL 32611, USA*

³*Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag 20, Hatfield 0028, Pretoria, South Africa*

⁴*Centre for Biodiversity and Conservation Science, University of Queensland, Brisbane, Queensland 4072, Australia*

⁵*Corresponding author: E-mail: aramonadjem@gmail.com*

Bats are a critical component of most terrestrial systems, yet accurately assessing species richness and abundances remains a challenge. The use of acoustic monitoring has increasingly been used to assess bat communities. Compared with more traditional trapping surveys, acoustic monitoring is relatively easy to use and vastly increases the amount of data collected. However, the ability to accurately identify bat calls from acoustic detectors is limited by the availability of regional call libraries describing the calls of local species. Further, the lack of knowledge of detection distances for different species limits the ability to compare activity levels or abundances between species. We developed an echolocation call library based on zero-crossing recordings with Anabat Express detectors that can be applied broadly to bat acoustic detector surveys across the savanna systems of Swaziland and South Africa, and potentially the broader region of Southern Africa. We also compared detection distances for different species and provide a correction factor that will increase our ability to accurately compare activity between different species.

Key words: acoustic survey, Anabat, Chiroptera, bat call library, Swaziland, detection distance

INTRODUCTION

Bats are a critical component of most terrestrial ecosystems, providing services such as pollination (Jones *et al.*, 2009), seed dispersal (Duncan and Chapman, 1999; Djossa *et al.*, 2008), consumption of agricultural pests (Cleveland *et al.*, 2006; Maine and Boyles, 2015), and serving as bioindicators (Jones *et al.*, 2009). Specifically, bats have been shown to play a major role in southern African agroecosystems (Bohmann *et al.*, 2011; Taylor *et al.*, 2013*b*). However, ecological studies in this region, have been constrained by the difficulty of observing and identifying bats in the field. Traditionally, bats were surveyed in southern Africa using various live-capture methods (Monadjem *et al.*, 2010*a*), which are typically labour intensive (e.g., Monadjem and Reside, 2008) and yield low returns. The advent of acoustic bat detectors has opened up opportunities for remotely surveying echolocating bats without having to capture them (Hayes, 2000).

Acoustic surveys now play a prominent role in studies of bat ecology (O'Farrell *et al.*, 1999; Hayes,

2000), including in Africa (Monadjem *et al.*, 2010*b*). Acoustic studies, however, are limited by the availability of bat echolocation call libraries that allow the discrimination and identification of calls recorded from free-flying bats. This is particularly true for tropical and subtropical regions where bat species richness peaks (Willig and Bloch, 2006; Schoeman *et al.*, 2013). Two recent studies in southern Africa have developed localized echolocation call libraries using hand-released bats (Taylor *et al.*, 2013*a*; Schoeman, 2015). However, these call libraries may only be useful in the areas that they were developed, as substantial regional variation in call parameters has been observed (Thomas *et al.*, 1987; Barclay *et al.*, 1999; O'Farrell *et al.*, 2000).

There has been much debate over which type of detector should be used to record echolocation calls of bats (Fenton *et al.*, 2001; Adams *et al.*, 2012; Britzke *et al.*, 2013), and how the detector should be deployed (Broders, 2003; Gannon *et al.*, 2003; Milne *et al.*, 2005; Britzke *et al.*, 2013). Anabat detectors (Titley Australia) are a common type of acoustic detector that use frequency division to

record calls. Some previous limitations, such as potential damage from water or inclement weather (O'Farrell *et al.*, 1999; Britzke *et al.*, 2011, 2013), have been overcome with changes in design. The newest Anabat Express detectors (Titley, Australia) have a waterproof case and microphone. Although some studies have found Anabat detectors to be less sensitive than other types of detectors (Fenton *et al.*, 2001; Adams *et al.*, 2012), increased sensitivity alone may not improve the probability of detection (Britzke *et al.*, 2013). Another potential shortcoming of Anabat detectors is their use of zero-crossing that can miss some call details when compared with full spectrum recorders (Fenton *et al.*, 2001). Nonetheless, Anabat detectors have been widely and successfully used to monitor bat diversity and activity in a variety of locations and habitats (e.g., Murray *et al.*, 1999; Ochoa *et al.*, 2000; Broders, 2003; Milne *et al.*, 2005; Gorresen *et al.*, 2008; O'Keefe *et al.*, 2014), and are a recommended or preferred tool for conducting bat surveys in government protocols around the world (Battersby, 2010; Reardon, 2011; Sowler and Stoffberg, 2014; Rodrigues *et al.*, 2015). Further, Anabat detectors are able to store large numbers of calls and record in real-time (Britzke *et al.*, 2013).

Differences in detectability across bat species and families is an ongoing issue for studying bat assemblages and ecology, and requires further research attention (Murray *et al.*, 1999; Hayes, 2000; Adams *et al.*, 2012). Furthermore, the relationship between activity and abundance, and thus habitat suitability, is still not well understood, particularly in Africa (Taylor *et al.*, 2013a). While acoustic monitoring of bats has been used to estimate activity and abundance of bats (Broders, 2003), differences in detectability for different bat species, and even different types of calls (e.g. search phase versus feeding buzz), limits the ability to compare activity between different species (Adams *et al.*, 2012; Britzke *et al.*, 2013). One way to address this shortcoming is to calculate detection distances (the furthest distance that a bat can be from a microphone and still have its echolocation call detected) for different species could allow for more direct comparisons in activity levels between different species. Importantly, the detection distances of African bats are not known for any detector.

The goal of this study was to develop an echolocation call library and to estimate detection distances for bats in the savannas of Swaziland. Specifically, we developed an echolocation call library based on hand-released calls of bats captured.

Further, using the call parameters of each species, we developed a set of filters to automate identification of bat calls. We also determined detection distances for species in order to improve our ability to directly compare levels of bat activity between different species.

MATERIALS AND METHODS

Study Site

The study was conducted in low-lying savanna of north-eastern Swaziland covering an area of about 300 km² (Fig. 1). The area is mostly below 200 m above sea level, except for the Lubombo Mountains in the east which rise above 500 m. The climate is typically hot and wet in the summer months (November to March), and cooler and drier over the remaining months of the year. Mean monthly temperatures for January and July are 26°C and 18°C, respectively and mean annual rainfall ranges from 550–725 mm. The dominant vegetation on the study site was savanna with riparian forest along rivers and major drainage lines (for further detail on study area, see Roques *et al.*, 2001; Monadjem and Reside, 2008).

The bat community of this area has been relatively well surveyed (Monadjem, 1998; Monadjem and Reside, 2008) although new species continue to be added and at present 22 species are known from the region (Shapiro and Monadjem, 2016). Echolocation calls of most southern African bats have been described in broad terms (Monadjem *et al.*, 2010a), but few studies have compared calls between species within a geographical region (Monadjem *et al.*, 2007; Taylor *et al.*, 2013a). Since bat echolocation calls may vary geographically (Thomas *et al.*, 1987; Barclay *et al.*, 1999), call libraries should be developed *in situ* based on calls of bats captured within the study area. To develop a regional call library, we captured bats either in mist nets or harp traps between 2005 and 2016. We were unable to get useful hand-released calls from *Nycteris thebaica* and *Kerivoula lanosa*. The two species of Pteropodidae (*Epomophorus wahlbergi* and *E. crypturus*) known from the study area (Monadjem and Reside, 2008; Shapiro and Monadjem, 2016) do not echolocate and were therefore not part of the study.

Recording of Echolocation Calls

We used the program ANALOOK (Chris Corben, version 4.8, <http://www.hoarybat.com>) to examine the recorded echolocation calls following Monadjem *et al.* (2007, 2010b) and Taylor *et al.* (2013a). We examined the echolocation calls of hand-released bats and removed poorly recorded calls from the analysis. This included calls not showing the full bandwidth for the species or passes consisting of just one or two notes. Next we inspected the remaining passes (Anabat files) to find search-phase calls which we selected for analysis because of their consistency of structure (e.g. full-length pulses, no feeding buzzes), although there was variation between individuals of the same species (see Appendix: pp. 183–187) (Britzke *et al.*, 2011). Where possible, we selected a series of ≥ 10 consecutive search-phase notes and saved the measurements as a 'params.txt' file. ANALOOK typically measures 10 call parameters (Britzke *et al.*, 2011), but only four of these have been shown to be useful

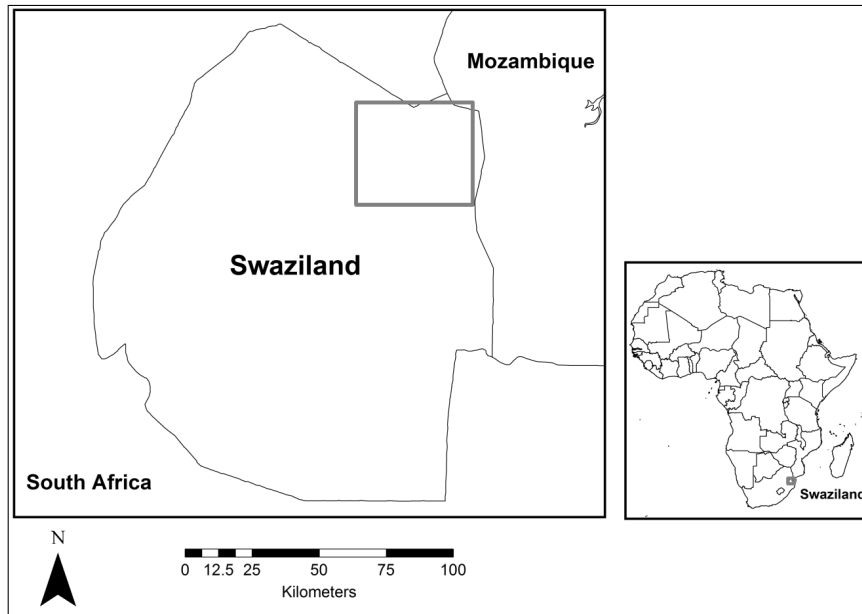


FIG. 1. Map of Swaziland with the north-eastern region that formed the study area outlined by the square. The inset shows the location of Swaziland on the African continent

in distinguishing between bats in other areas of southern Africa (Taylor *et al.*, 2013a). Since the bat species composition of our study site (as reported in Monadjem and Reside, 2008) was similar to that reported in Taylor *et al.* (2013a), we selected the same four call parameters for analysis: Dur (duration of the call), Fk (frequency of the knee), Fmin (minimum frequency of the call), Fc (frequency of the flattest part of the call).

Using these four parameters, we developed a filter for each bat species or species-group in Analook, which were used individually or together in a scan to automate the identification of bat species or species groups. We tested the scan by comparing the identifications made by the filters with a manual identification of 305 Anabat files recorded on the 23rd of November 2015 in our study area.

Detection Distance

In order to determine the detection distance of different species, we recorded hand-released bats at different distances. Recordings were made with Anabat Express detectors (Titley, Australia) on the default setting (sensitivity = level 8, 'high') using the standard omnidirectional microphone made for the Express detector, which can detect sounds within the range of 10–150 kHz (Broken-Brow and Corben, 2015). For low-duty cycle bats, one observer released the bat, while three observers stood at different distances from the bat, each holding an Anabat Express detector. When the bat commenced flying, all observers immediately turned off the detectors, in order to accurately assess the distance at which each bat was recorded. Initially, observers stood at 10 m, 20 m, and 30 m from the released bat; if no call was recorded at the closest observer distance, we reduced distances, initially by 5 m, then 2 m, and finally 1 m, for subsequent individuals of the same species.

For high-duty cycle bats, one person held the bat while another made recordings with the Anabat detector, beginning at 1 m from the bat and walking away at 1 m intervals between

calls. *Hipposideros caffer* could not be detected at 1 m and therefore detection distance began at 0.1 m and increased by 0.3 m for each subsequent recording attempt.

We used mean detection distance to calculate a correction factor for each species by calculating the volume of a half a sphere radiating out from the position of the bat detector in the direction of the bat. The Anabat Express detector has an omnidirectional microphone, however, we assumed that recordings from behind the detector would be significantly lower than in front based on the results of an earlier study of Anabat SD2 detectors which showed lower detection at 90 degrees compared with head on (Adams *et al.*, 2012). The volume of the half-sphere correctly defines the region of detectability of a bat for detection distances up to the height of the detector above the ground. When detection distances are longer than the height of the detector above the ground, the detection zone has to be reduced by the volume of the hypothetical sphere extending below ground. The volume of the sphere above the ground was calculated using the formula:

$$V = -\frac{\pi r^3 (\cos \vartheta - 1)}{3} + \frac{\pi (r^2 - (r - d)^2)(r - d)}{6}$$

where: $\vartheta = \pi - \cos^{-1} \frac{d}{r}$; r = detection distance of the bat; d = height of detector above the ground. The height of the detector above ground during this study was set at 1.5 m. We inserted mean detector distances into the formula to give a detection volume (the volume around the detector within which the bat is detectable) for the different species of bats. The inverse of this volume represents the correction factor for that species; this value needs to be multiplied by the activity or abundance of that species to allow comparisons between species.

We downloaded Anabat files and visually examined the calls. We classified the calls as 'clear calls' (clear, identifiable notes of a bat call), 'low quality calls' (notes resembling a bat call, but cut off or of very short duration), 'indistinct noise'

(notes that could not be readily identifiable as bat calls), or 'blank' (a file was made, but nothing recorded). We calculated mean detection distance and standard deviation for each species, based on clear and low quality calls; indistinct noise was not considered. We determined maximum detection distance as the maximum distance at which at least one note from at least one released individual could be detected.

We used Pearson's correlation coefficient to test whether mean detection distance was correlated with mean Fk (frequency of the knee) for different bat species. We conducted all statistical analyses using in the program R2.15.2 (R Core Team, 2014). All the necessary permits were obtained, and all handling and capture of animals were in accordance with guidelines of American Society of Mammalogy (Sikes *et al.*, 2011).

RESULTS

We obtained call parameters of the 178 calls from 145 individual hand-released bats (Table 1). We used sonograms to show typical and variable calls for each species (Appendix: pp. 183–187). Based on our four call parameters different families of bats could be distinguished, however, there was overlap between some species within families. Within the family Molossidae, *Chaerephon pumilus* and *Mops condylurus* showed overlap in all four call parameters (Table 1) but *C. pumilus* exhibited more variation in call structure (Appendix: p. 185). The lower frequency calls, with Fk below 28 kHz, were identified with some degree of certainty as *C. pumilus*, but at frequencies above this it was not possible to separate *M. condylurus* from *C. pumilus*.

Four small vespertilionid bats also showed considerable overlap in their call parameters (*Scotophilus viridis*, *Nycticeinops schlieffeni*, *Neoromicia zuluensis* and *Pipistrellus hesperidus* — Table 1 and Appendix: p. 186). While *S. viridis* had lower Fmin and Fc than *N. zuluensis* and *P. hesperidus*, it showed overlap with *N. schlieffeni*, which in turn overlapped with the other two species. The structure and shape of calls of *Myotis bocagii* and *M. tricolor* was easily distinguishable from that of other bats (Appendix: p. 186), however, these two *Myotis* species could not be acoustically distinguished from each other (Table 1).

There was little or no overlap between the echolocation calls of different bat families, with the exception of Molossidae and Emballonuridae (Table 1). The call parameters of *C. pumilus*-*M. condylurus* completely overlapped with that of *Taphozous mauritianus* (Table 1). Although the duration of calls of *T. mauritianus* were generally shorter than those of molossids, molossids showed a wider range in duration.

Comparing the efficacy of call identification by way of scanning in Anabat filters with manual identification, the filter was slightly more conservative. Manually, 98 passes were classified as bat calls (87%), while the scan classified 80 passes (75%). Both methods identified the same species as present, with the exception of one *T. mauritianus* identified by the scan. The scan considered 27 calls to be unidentifiable to species or species group. Manually, 15 calls were not assigned to a species or species group. In addition, manual identification resulted in slightly more calls being recognized as *C. pumilus*-*M. condylurus* (64 calls manual versus 52 calls by filter), *Miniopterus natalensis* (2 vs. 1 call), *Neoromicia nana* (3 vs. 1 call), *Scotophilus dinganii* (10 vs. 9 calls), and other vespers (19 vs. 16 calls).

However, the scan did not identify any *M. bocagii* or *M. tricolor* calls. Although the calls of *Myotis* species can easily be visually distinguished from other bats, due to their distinct vertical shape (Appendix, p.), the high variability in parameters, particular Fk and Fc (Table 1), made it impossible to characterize the calls of these two species using an Anabat filter. Anabat files had to be manually examined to identify *Myotis* calls.

Detection distance varied greatly between species (Table 2). *Mops condylurus* had the furthest detection distance, averaging 15 m, and a maximum of 30 m. *Scotophilus dinganii* and *C. pumilus* had maximum detection distances of 20 m. Most vespertilionid bats had maximum detection distances of 10–15 m. *Rhinolophus darlingi* could be detected at a distance of 2 m, while *Hipposideros caffer* was detectable at a maximum of 0.3 m. Two additional species, *Kerivoula lanosa* and *Nycteris thebaica*, were also tested, but yielded only indistinguishable noise. There was a significant negative correlation between detection distance and frequency of the knee (Fk) of the bats ($r = -0.77$, $d.f. = 9$, $P < 0.01$).

DISCUSSION

We present a relatively complete call library for the north-eastern savannas of Swaziland as recorded by Anabat detectors. This call library will facilitate acoustic research on the bats of the savannas of Swaziland and neighbouring South Africa and Mozambique. We were unable to differentiate between all species as call parameters of some species overlapped extensively, as was reported to be the case in savannas to the north of our region (Taylor

TABLE 1. Four call parameters (mean \pm SD) (min, max) of the 20 species of bats for which hand-released specimens were recorded; n = number of individual bats, Files = number of Anabat files, Dur = duration, Fk = frequency of the knee, Fmin = minimum frequency, Fc = frequency of the flattest part of the call (see text for further details)

| Family and species | n | Files | Dur | Fk | Fmin | Fc |
|---------------------------------|-----|-------|---------------------------------|------------------------------------|------------------------------------|------------------------------------|
| Hipposideridae | | | | | | |
| <i>Clootis percivali</i> | 3 | 3 | 2.3 \pm 0.04 (2.2, 2.3) | 103.1 \pm 0.65 (102.6, 103.8) | 99.2 \pm 1.02 (98.1, 100.1) | 102.6 \pm 0.51 (102.2, 103.2) |
| <i>Hipposideros caffer</i> | 8 | 8 | 4.8 \pm 1.08 (3.7, 6.7) | 141.4 \pm 1.97 (138.7, 144.3) | 121.2 \pm 5.88 (109.1, 127.3) | 141.7 \pm 1.69 (139.5, 144.0) |
| Rhinolophidae | | | | | | |
| <i>Rhinolophus blasii</i> | 1 | 3 | 20.8 \pm 0.72 (19.9, 21.3) | 86.3 \pm 0.24 (86.1, 86.6) | 79.4 \pm 1.86 (77.9, 81.5) | 86.2 \pm 0.21 (86.0, 86.4) |
| <i>R. clivosus</i> | 6 | 18 | 32.9 \pm 5.35 (23.3, 40.1) | 91.5 \pm 0.70 (90.0, 92.3) | 75.7 \pm 3.15 (70.4, 80.3) | 91.3 \pm 1.06 (88.9, 92.5) |
| <i>R. darlingi</i> | 3 | 3 | 26.5 \pm 3.74 (22.6, 30.0) | 85.7 \pm 0.46 (85.2, 86.1) | 74.3 \pm 4.28 (70.8, 79.1) | 85.6 \pm 0.38 (85.2, 85.8) |
| <i>R. simulator</i> | 3 | 8 | 16.8 \pm 4.70 (12.0, 25.9) | 83.8 \pm 0.18 (83.6, 84.1) | 72.1 \pm 2.97 (68.6, 76.0) | 83.4 \pm 0.20 (83.7, 84.2) |
| Emballonuridae | | | | | | |
| <i>Taphozous mauritianus</i> | 4 | 4 | 2.7 \pm 0.27 (2.4, 3.0) | 28.6 \pm 0.60 (28.1, 29.5) | 25.1 \pm 0.72 (24.3, 25.9) | 25.9 \pm 1.20 (24.3, 27.2) |
| Vespertilionidae | | | | | | |
| <i>Myotis bocagii</i> | 1 | 1 | 2.8 | 41.2 | 30.1 | 36.6 |
| <i>M. tricolor</i> | 9 | 10 | 2.4 \pm 0.33 (2.07, 2.72) | 55.4 \pm 10.8 (44.6, 66.2) | 38.0 \pm 3.78 (34.2, 41.7) | 49.4 \pm 11.4 (38.0, 60.8) |
| <i>Neoromicia nana</i> | 3 | 4 | 2.8 \pm 0.32 (2.6, 3.2) | 72.3 \pm 2.08 (70.6, 75.1) | 69.7 \pm 2.29 (66.8, 71.8) | 70.2 \pm 2.25 (67.5, 72.2) |
| <i>N. zuluensis</i> | 2 | 3 | 3.7 \pm 0.67 (3.0, 4.2) | 46.6 \pm 2.91 (43.3, 48.5) | 46.1 \pm 2.82 (39.9, 45.3) | 43.6 \pm 3.10 (40.1, 45.9) |
| <i>Nycticeinops schlieffeni</i> | 5 | 5 | 3.1 \pm 0.64 (2.4, 4.0) | 43.4 \pm 1.67 (41.7, 45.4) | 40.1 \pm 1.48 (38.7, 42.4) | 40.3 \pm 1.29 (39.2, 42.4) |
| <i>Pipistrellus hesperidus</i> | 14 | 15 | 3.1 \pm 0.63 (2.3, 4.5) | 49.6 \pm 2.42 (44.6, 54.3) | 45.3 \pm 1.87 (41.7, 49.1) | 46.0 \pm 1.83 (42.5, 50.0) |
| <i>Scotophilus dinganii</i> | 15 | 17 | 3.8 \pm 0.94 (2.6, 6.1) | 36.4 \pm 1.61 (32.1, 38.6) | 33.2 \pm 1.26 (30.3, 34.7) | 33.7 \pm 1.44 (30.3, 35.6) |
| <i>S. viridis</i> | 4 | 4 | 3.5 \pm 1.55 (2.0, 5.0) | 42.7 \pm 1.05 (41.6, 43.7) | 39.8 \pm 1.33 (38.5, 41.2) | 40.1 \pm 1.31 (38.8, 42.4) |
| Molossidae | | | | | | |
| <i>Chaerephon pumilus</i> | 35 | 35 | 9.0 \pm 2.10 (3.9, 12.6) | 26.1 \pm 2.09 (22.5, 29.6) | 23.3 \pm 1.41 (20.8, 26.5) | 24.0 \pm 1.53 (21.3, 27.2) |
| <i>Mops condylurus</i> | 16 | 17 | 4.3 \pm 2.08 (2.2, 6.4) | 30.1 \pm 2.03 (28.1, 32.1) | 25.1 \pm 1.68 (23.5, 26.1) | 27.3 \pm 1.56 (25.9, 28.8) |
| <i>M. midas</i> | 1 | 6 | 14.2 \pm 3.89 (9.0, 20.7) | 13.1 \pm 1.08 (11.9, 14.5) | 11.8 \pm 0.50 (11.3, 12.5) | 12.3 \pm 0.72 (11.6, 13.4) |
| Miniopteridae | | | | | | |
| <i>Miniopterus fraterculus</i> | 1 | 2 | 2.9 \pm 0.32 (2.7, 3.1) | 63.6 \pm 1.27 (62.7, 64.4) | 58.5 \pm 0.50 (58.1, 58.8) | 59.2 \pm 0.40 (58.9, 59.5) |
| <i>M. natalensis</i> | 11 | 12 | 2.8 \pm 0.37 (2.2, 3.7) | 57.0 \pm 0.96 (55.5, 58.5) | 53.2 \pm 0.87 (51.3, 54.8) | 53.6 \pm 0.83 (51.6, 55.0) |

et al., 2013a). In fact, such overlap in call parameters of sympatric species or species with similar foraging niches is not uncommon in bats (Barclay, 1999; Russo and Jones, 2002). In particular, we were not able to discriminate between the calls of several similar-sized vespers namely *P. hesperidus*, *N. zuluensis*, and *N. schlieffeni*; a problem encountered in similar study in South Africa (Taylor *et al.*,

2013a). Two species, *Neoromicia capensis* and *Hypsugo achietae*, were captured too infrequently (Monadjem and Reside, 2008) to allow for hand-released calls to be recorded and may also possibly overlap in call parameters (Monadjem *et al.*, 2010a). Except for *N. schlieffeni*, these species are also difficult to identify based on external features (Monadjem *et al.*, 2010a). Further work is required

to determine whether it is possible to tease apart these species within these pairs and groups that have such similar call parameters. Despite some difficulties in separating the calls of these species groups, this call library will allow easy comparison of relative bat activity at the family or functional group (Schnitzler and Kalko, 2001).

Detection distance is a fundamental component of the probability of species detection, but there is virtually no information available on the detection distances of bat species with Anabat or other bat detectors. Having a standardized factor for detection probability for a region will provide substantial improvement in the accuracy of relative activity levels estimated across a suite of different species (Hayes, 2000). Our correction factor, therefore, may be critical to acoustic surveys conducted in this region and may inform similar research in other regions. Detection distances differ markedly across species, from 0.3 m for *Hipposideros caffer* to a maximum of 30 m for *M. condylurus*. The negative correlation between detection distance and frequency of the call of bats has been reported before (Adams *et al.*, 2012) and makes sense on physical grounds since high frequency sounds attenuate more rapidly than low frequency sounds. The likelihood of detecting *H. caffer* is very low, and would only happen if an individual flew right past the detector. In contrast, because of the relatively large detection distance, the activity levels of molossids and *Scotophilus* species may have been over-estimated in previous studies. Obtaining accurate activity indices across species is critical for assessing relative

population sizes, which may have important consequences for monitoring and managing species or populations of conservation concern (Russo and Voigt, 2016).

We were not able to measure detection distances for all bat species in the study area, and this is an obvious area for future research. In the meantime, we suggest using the detection distances of congeners or closely related species within the same family for species lacking their own detection coefficient. It should be noted that the detection distances reported here will be sensitive to the detectors in use. We re-recommend that our correction factor be only applied to studies that using Anabat Express detectors. Having said this, we hypothesize that there will be a close correlation between detection distances reported here and those obtained with other detectors, and we suggest this as an area for future research.

While there are limits to Anabat Express detectors and the zero-crossing method, they are widely used, and substantial datasets have been collected using these methods. Monitoring protocols for South Africa (Sowler and Stoffberg, 2014), Australia (Reardon, 2011), Europe (Battersby, 2010), and the United States (Loeb *et al.*, 2015) suggest or recommend using Anabat detectors. Hence, developing correction factors using our method for other regions may improve the accuracy of activity level estimates and impacts of development, such as wind farms, on different species (Hayes, 2000).

Our results show that the use of complementary capture techniques, in addition to acoustic

TABLE 2. Mean (\pm SE) and maximum detection distances for 11 species of bats captured in Swaziland. The correction factor was calculated as detailed in the Materials and Methods

| Family and species | <i>n</i> | Mean distance (m) | Maximum distance (m) | Correction factor |
|---------------------------------|----------|-------------------|----------------------|-------------------|
| Hipposideridae | | | | |
| <i>Hipposideros caffer</i> | 3 | 0.2 \pm 0.07 | 0.3 | 59.68 |
| Rhinolophidae | | | | |
| <i>Rhinolophus darlingi</i> | 1 | 2 | 2 | 0.0639 |
| Vespertilionidae | | | | |
| <i>Myotis bocagii</i> | 1 | 5 | 5 | 0.005167 |
| <i>M. tricolor</i> | 9 | 4.6 \pm 0.73 | 10 | 0.006497 |
| <i>Neoromicia nana</i> | 6 | 5.8 \pm 1.07 | 10 | 0.003433 |
| <i>Nycticeinops schlieffeni</i> | 1 | 15.0 | 15 | 0.0002387 |
| <i>Scotophilus dinganii</i> | 2 | 17.5 | 20 | 0.0001535 |
| <i>S. viridis</i> | 2 | 12.5 | 15 | 0.0004009 |
| Molossidae | | | | |
| <i>Chaerephon pumilus</i> | 5 | 12.0 \pm 2.00 | 20 | 0.0004501 |
| <i>Mops condylurus</i> | 8 | 15.0 \pm 2.67 | 30 | 0.0002387 |
| Miniopteridae | | | | |
| <i>Miniopterus natalensis</i> | 1 | 5 | 5 | 0.005167 |

monitoring, are necessary to assess full bat species richness in the region. *Nycteris thebaica* is an abundant bat in the study area (Monadjem and Reside, 2008) but is difficult, if not impossible, to detect using the Anabat Express detector. *Nycteris thebaica* is a whispering bat that produces very soft (low db) echolocation calls that can be recorded with types of detector particularly time-expansion detectors (Monadjem *et al.*, 2010a). However, even at 0.1 m, we could not record clear acoustic calls on our Anabat Express detector. Similarly, clear calls could not be recorded with an Anabat Express for the rarely captured *Kerivoula lanosa*. Other species may be detected, but only at close distances. The echolocation calls of *H. caffer*, another common bat in the region (Monadjem and Reside, 2008) can be recorded by Anabat detectors (Monadjem *et al.*, 2007), but only within 0.3 m. Rhinolophids may be detected at a greater distance of up to about two metres away. Further, in order to correct for the bias towards larger, lower-frequency calling bats, the use of correction factors is necessary for any comparisons of activity or abundance between species, functional groups, or families.

In conclusion, this study presents a call library for north-eastern Swaziland together with detection distances of different bat species. Together, these may be used to identify bat species recorded during future acoustic surveys in the area. The detection distances and correction factors can be used within the region and our method for calculating detection distances and correction factor can be tested on and applied to other bat species across the globe. Calculating the detection distances for local bat fauna will greatly enhance the utility of acoustic surveys and for the first time, allow for accurate comparisons in activity and abundance between species and families.

ACKNOWLEDGEMENTS

Sincere thanks to Elena Oehmig, Katie Teets and Lauren Watine (University of Florida), Machawe Maphalala (University of Swaziland), Mduduzi Ngwenya and All Out Africa for field support. Mmqobi Mamba, Charles Gumbi, Muzi Sibiyi and Hervé Echecolonea assisted with the detection distance experimentation. Keyan Monadjem is thanked for assistance with the formula for calculating the detectability zone of the bat. This work was possible with the support and backing of the Savanna Research Center. The data for this manuscript was collected in part by work supported through the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1315138, a Student Research Grant from Bat Conservation International, and a National Geographic Young Explorer's Grant (J.T.S.).

LITERATURE CITED

- ADAMS, A. M., M. K. JANTZEN, R. M. HAMILTON, and M. B. FENTON. 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. *Methods in Ecology and Evolution*, 3: 992–998.
- BARCLAY, R. M. R. 1999. Bats are not birds: a cautionary note on using echolocation calls to identify bats. *Journal of Mammalogy*, 80: 290–296.
- BARCLAY, R. M. R., J. H. FULLARD, and D. S. JACOBS. 1999. Variation in the echolocation calls of the hoary bat (*Lasiurus cinereus*): influence of body size, habitat structure, and geographic variation. *Canadian Journal of Zoology*, 77: 530–534.
- BATTERSBY, J. (ed.). 2010. Guidelines for surveillance and monitoring of European bats. EUROBATs Publication Series No. 5. UNEP/EUROBATs Secretariat, Bonn, Germany. 95 pp.
- BOHMANN, K., A. MONADJEM, C. L. NOER, M. RASMUSSEN, M. R. K. ZEALE, E. CLARE, G. JONES, E. WILLERSLEV, and M. T. P. GILBERT. 2011. Molecular diet analysis of two African free-tailed bats (Molossidae) using high throughput sequencing. *PLoS ONE*, 6: e21441.
- BRITZKE, E. R., J. E. DUCHAMP, K. L. MURRAY, R. K. SWIHART, and L. W. ROBBINS. 2011. Acoustic identification of bats in the eastern United States: a comparison of parametric and nonparametric methods. *Journal of Wildlife Management*, 75: 660–667.
- BRITZKE, E. R., E. H. GILLAM, and K. L. MURRAY. 2013. Current state of understanding of ultrasonic detectors for the study of bat ecology. *Acta Theriologica*, 58: 109–117.
- BROEDERS, H. G. 2003. Another quantitative measure of bat species activity and sampling intensity considerations for the design of ultrasonic monitoring studies. *Acta Chiropterologica*, 5: 235–241.
- BROKEN-BROW, J., and C. CORBEN. 2015. Anabat Express bat detector user manual, version 1.5. Titley Scientific. Brendale Australia.
- CLEVELAND, C. J., J. D. FRANK, P. FEDERICO, and I. GOMEZ. 2006. Economic value of the pest control service provided by Brazilian free-tailed bat in south-central Texas. *Frontiers in Ecology and the Environment*, 4: 238–243.
- DJOSSA, B. A., J. FAHR, E. K. V. KALKO, and B. A. SINSIN. 2008. Fruit selection and effects of seed handling by flying foxes on germination rates of shea trees, a key resource in northern Benin, West Africa. *Ecotropica*, 14: 37–48.
- DUNCAN, R. S. and C. A. CHAPMAN. 1999. Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications*, 9: 998–1008.
- FENTON, M. B., S. BOUCHARD, M. J. VONHOF, and J. ZIGOURIS. 2001. Time-expansion and zero-crossing period meter systems present significantly different views of echolocation calls of bats. *Journal of Mammalogy*, 82: 721–727.
- FISCHER, J., J. STOTT, B. S. LAW, M. D. ADAMS, and R. I. FORRESTER. 2009. Designing effective habitat studies: quantifying multiple sources *Acta Chiropterologica*, 11: 127–137.
- GANNON, W. L., R. E. SHERWIN, and S. HAYMOND. 2003. On the importance of articulating assumptions when conducting acoustic studies of habitat use by bats. *Wildlife Society Bulletin*, 31: 45–61.
- GORRESEN, P. M., A. C. MILES, C. M. TODD, F. J. BONACCORSO, and T. J. WELLER. 2008. Assessing bat detectability and occupancy with multiple automated echolocation detectors. *Journal of Mammalogy*, 89: 11–17.

- HAYES, J. P. 2000. Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterologica*, 2: 225–236.
- JONES, G., D. S. JACOBS, T. H. KUNZ, M. R. WILLIG, and P. A. RACEY. 2009. Carpe noctem: the importance of bats as bio-indicators. *Endangered Species Research*, 8: 93–115.
- LOEB, S. C., T. J. RODHOUSE, L. E. ELLISON, C. L. LAUSEN, J. D. REICHARD, K. M. IRVINE, T. E. INGERSOLL, J. T. H. COLEMAN, W. E. THOGMARTIN, J. R. SAUER, *et al.* 2015. A plan for the North American Bat Monitoring Program (NABat). Gen. Tech. Rep. SRS-208. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, 100 pp.
- MAINE, J. J., and J. G. BOYLES. 2015. Bats initiate vital agroecological interactions in corn. *PNAS*, 112: 1238–1243.
- MILNE, D. J., M. ARMSTRONG, A. FISHER, T. FLORES, and C. R. PAVEY. 2005. Structure and environmental relationships of insectivorous bat assemblages in tropical Australian savannas. *Austral Ecology*, 30: 906–919.
- MONADJEM, A. 1998. Mammals of Swaziland. Conservation Trust of Swaziland and Big Game Parks, Mbabane, 154 pp.
- MONADJEM, A., and A. RESIDE. 2008. The influence of riparian vegetation on the distribution and abundance of bats in an African savanna. *Acta Chiropterologica*, 10: 339–348.
- MONADJEM, A., A. RESIDE, and L. LUMSDEN. 2007. Echolocation calls of rhinolophid and hipposiderid bats in Swaziland. *South African Journal of Wildlife Research*, 37: 9–15.
- MONADJEM, A., P. J. TAYLOR, F. P. D. COTTERILL, and M. C. SCHOEMAN. 2010a. Bats of southern and central Africa: a biogeographic and taxonomic synthesis. Wits University Press, Johannesburg, 589 pp.
- MONADJEM, A., M. ELLSTROM, C. MALDONALDO, and N. FASEL. 2010b. The activity of an insectivorous bat *Neoromicia nana* on tracks in logged and unlogged forest in tropical Africa. *African Journal of Ecology*, 48: 1083–1091.
- MONADJEM, A., L. RICHARDS, P. J. TAYLOR, and S. STOFFBERG. 2013. High diversity of pipistrelloid bats (Vespertilionidae: *Hypsugo*, *Neoromicia*, and *Pipistrellus*) in a West African rainforest with the description of a new species. *Zoological Journal of the Linnean Society*, 167: 191–207.
- MURRAY, K. L., E. R. BRITZKE, B. M. HADLEY, and L. W. ROBINS. 1999. Surveying bat communities: a comparison between mist nets and the Anabat II bat detector system. *Acta Chiropterologica*, 1: 105–112.
- OCHOA, J. G., M. J. O'FARRELL, and B. W. MILLER. 2000. Contribution of acoustic methods to the study of insectivorous bat diversity in protected areas from northern Venezuela. *Acta Chiropterologica*, 2: 171–183.
- O'FARRELL, M. J., B. W. MILLER, and W. L. GANNON. 1999. Qualitative identification of free-flying bats using the Anabat detector. *Journal of Mammalogy*, 80: 11–23.
- O'FARRELL, M. J., C. CORBEN, and W. L. GANNON. 2000. Geographic variation in the echolocation calls of the hoary bat (*Lasiurus cinereus*). *Acta Chiropterologica*, 2: 185–196.
- O'KEEFE, J. M., S. C. LOEB, S. C., H. S. HILL, JR., and J. D. LANHAM. 2014. Quantifying clutter: A comparison of our methods and their relationship to bat detection. *Forest Ecology and Management* 322: 1–9.
- R CORE TEAM. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at <http://www.R-project.org>. Accessed 15 January 2014.
- REARDON, T. 2011. Survey guidelines for Australia's threatened mammals: guidelines for detecting mammals listed as threatened under the Environment Protection and Biodiversity Conservation Act 1999. Australian Government, Canberra.
- RODRIGUES, L., L. BACH, M. J. DUBOURG-SAVAGE, B. KARAPANDZA, D. KOVAC, T. KERVYN, J. DEKKER, A. KEPEL, P. BACH, J. COLLINS, *et al.* 2015. Guidelines for consideration of bats in wind farm projects — Revision 2014. EURO-BATS Publication Series No. 6. UNEP/EUROBATS Secretariat, Bonn, 133 pp.
- ROQUES, K. G., T. G. O'CONNOR, and A. R. WATKINSON. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, 38: 268–280.
- RUSO, D., and G. JONES. 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *Journal of Zoology (London)*, 258: 91–103.
- RUSO, D., and C. C. VOIGT. 2016. The use of automated identification of bat echolocation calls in acoustic monitoring: a cautionary note for a sound analysis. *Ecological Indicators*, 66: 598–602.
- SCHNITZLER, H.-U., and E. K. V. KALKO. 2001. Echolocation by insect-eating bats. *Bioscience*, 51: 557–569.
- SCHOEMAN, M. C. 2015. Light pollution at stadiums favors urban exploiter bats. *Animal Conservation*, 19: 120–130.
- SCHOEMAN, M. C., F. P. D. COTTERILL, F. P. D., P. J. TAYLOR, and A. MONADJEM. 2013. Using potential distributions to explore environmental correlates of bat species richness in southern Africa: effects of model selection and taxonomy. *Current Zoology*, 59: 279–293.
- SHAPIRO, J. T., and A. MONADJEM. 2016. Two new bat species for Swaziland and a revised list for the country. *Mammalia* 80: 353–357.
- SIKES, R. S., W. L. GANNON, and THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American society of mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 92: 235–253.
- SOWLER, S., and S. STOFFBERG (eds.). 2014. South African good practice guidelines for surveying bats at wind energy facility developments — pre-construction, 3rd edition. Bat Conservation Trust, 43 pp.
- TAYLOR, P. J., A. MONADJEM, and J. N. STEYN. 2013a. Seasonal patterns of habitat use by insectivorous bats in a subtropical African agro-ecosystem dominated by macadamia orchards. *African Journal of Ecology*, 51: 552–561.
- TAYLOR, P. J., S. SOWLER, M. C. SCHOEMAN, and A. MONADJEM. 2013b. Diversity of bats in the Soutpansberg and Blouberg Mountains of northern South Africa: complementarity of acoustic and non-acoustic survey methods. *South African Journal of Wildlife Research*, 43: 12–26.
- THOMAS, D. W., G. P. BELL, and M. B. FENTON. 1987. Variation in the echolocation call frequencies recorded from North American vespertilionid bats: a cautionary note. *Journal of Mammalogy*, 68: 842–847.
- WILLIG, M. R., and C. P. BLOCH. 2006. Latitudinal gradients of species richness: a test of the geographic area hypothesis at two ecological scales. *Oikos*, 112: 163–173.

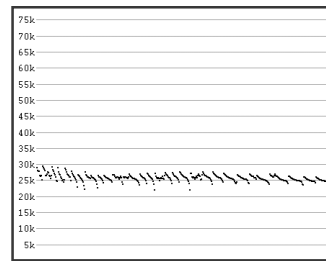
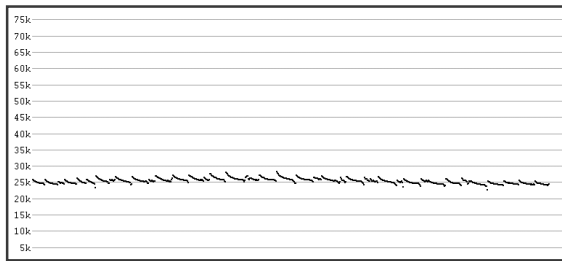
Received 30 June 2016, accepted 09 January 2017

Associate Editor: Wiesław Bogdanowicz

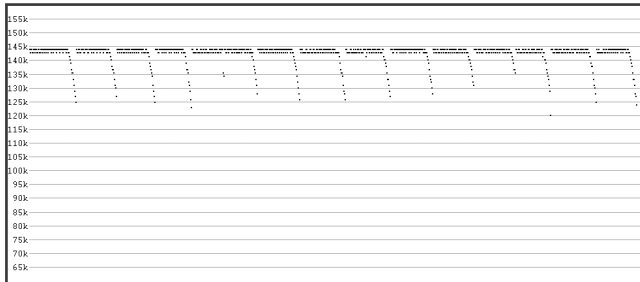
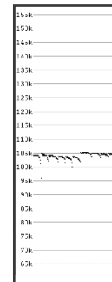
APPENDIX

Sonograms of emballonurids (*Taphozous mauritanus*), hipposiderids (*Clootis percivali*, *Hipposideros caffer*), rhinolophids (*Rhinolophus blasii*, *R. clivosus*, *R. darling*, *R. simulator*), molossids (*Chaerephon pumilus*, *Mops condylurus*, *M. midas*), vespertilionids (*Myotis bocagii*, *M. tricolor*, *Neoromicia nana*, *N. zuluensis*, *Nyctienops schlieffeni*, *Pipistrellus hesperidus*, *Scotophilus dinganii*, *S. viridis*), and miniopterids (*Miniopterus natalensis*, *M. fraterculus*) recorded in Swaziland

Emballonuridae

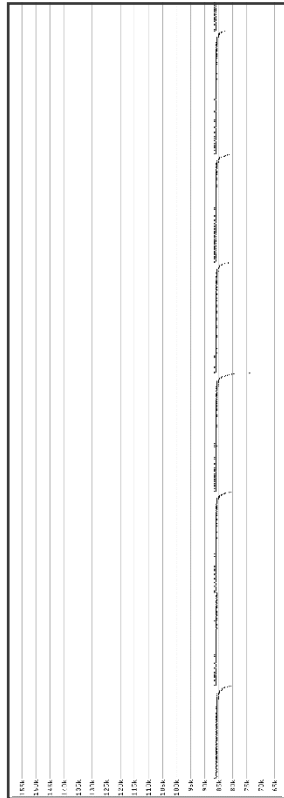
Taphozous mauritanus

Hipposideridae

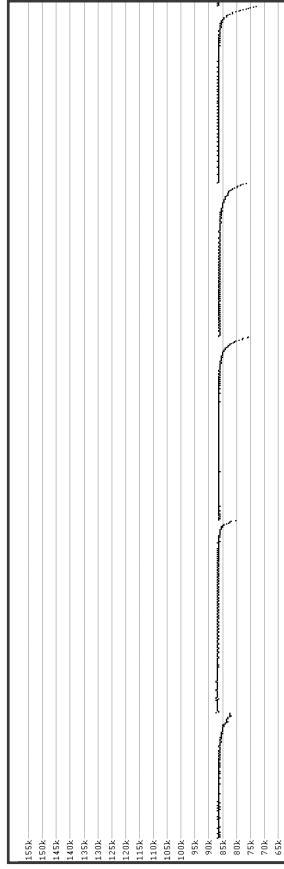
Hipposideros caffer*Clootis percivali*

Rhinolophidae

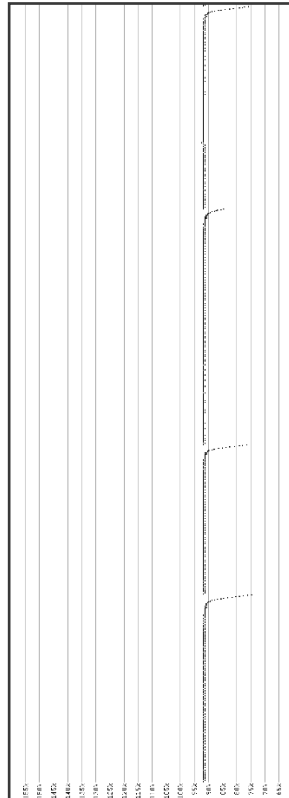
Rhinolophus blasii



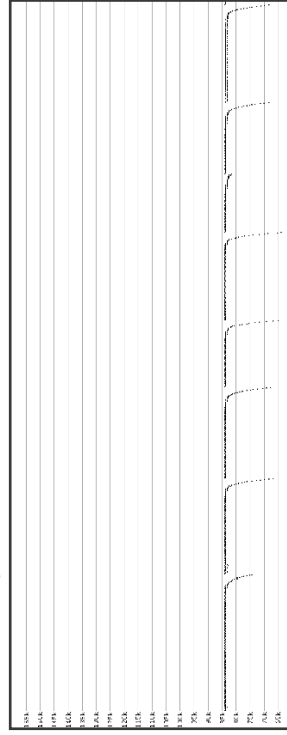
Rhinolophus darlingi



Rhinolophus clivosus

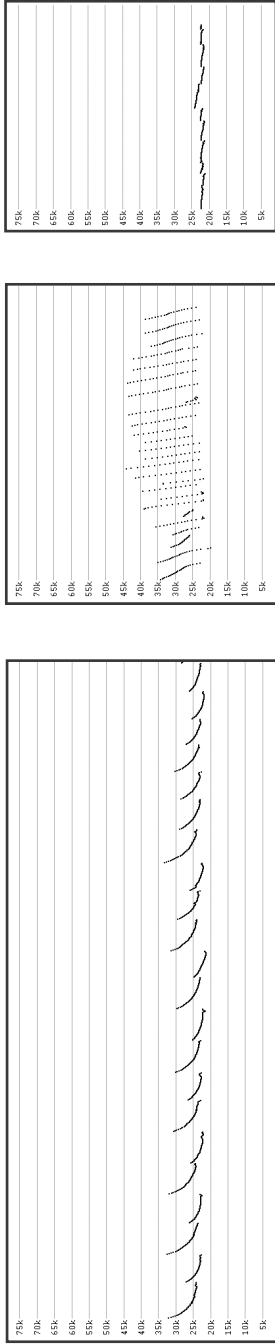


Rhinolophus simulator

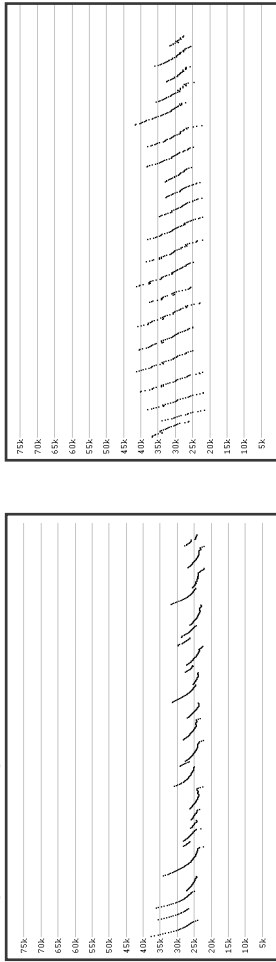


Molossidae

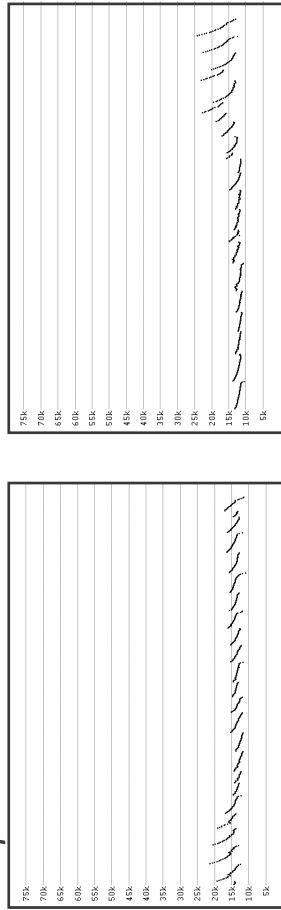
Chaerephon pumilus



Mops condylurus



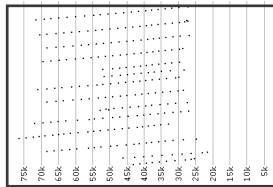
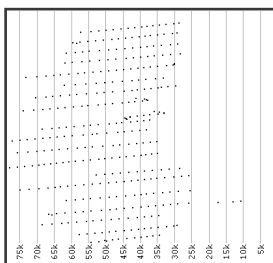
Mops midas



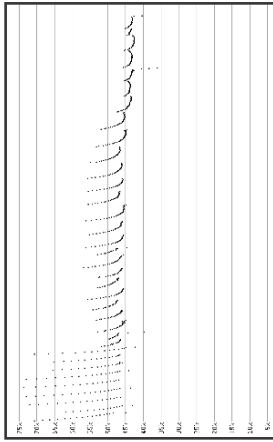
APPENDIX. Continued

Vespertilionidae

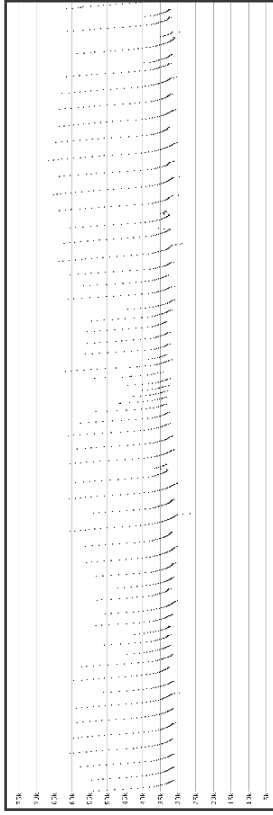
Myotis bocagii



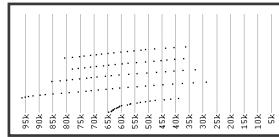
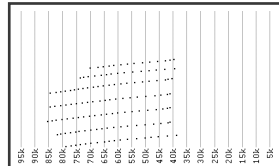
Neoromicia zuluensis



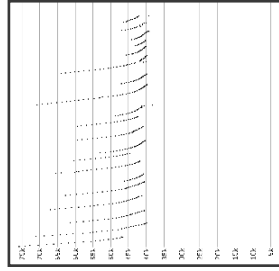
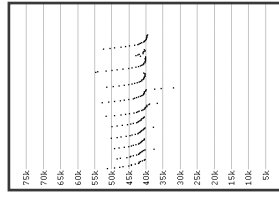
Scotophilus dinganii



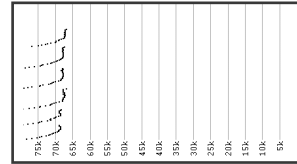
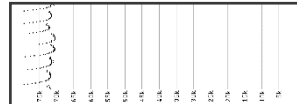
Myotis tricolor



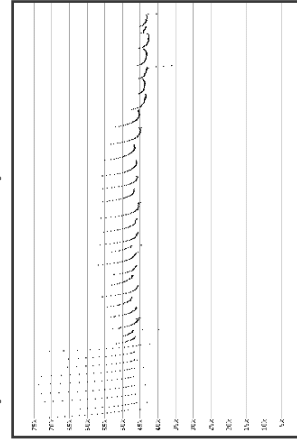
Nycticeinops schlieffeni



Neoromicia nana



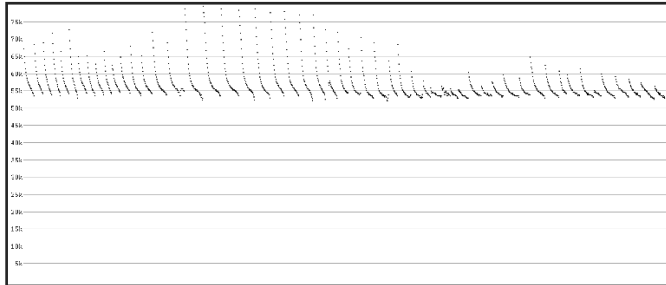
Pipistrellus hesperidus



APPENDIX. Continued

Miniopteridae

Miniopterus natalensis



Miniopterus fraterculus

