

Diversity of bats in the Soutpansberg and Blouberg Mountains of northern South Africa: complementarity of acoustic and non-acoustic survey methods

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We surveyed bats at 30 localities in the Soutpansberg and Blouberg Mountains within the newly proclaimed Vhembe Biosphere Reserve (VBR) of northern South Africa, based on ANABAT acoustic recordings (63 nights) conducted in parallel with captures of 260 individuals from harp traps (29 trap-nights) and mist nets (54 trap-nights), and searches of ten day-roosts and two night-roosts. Twenty-four species of bats were captured, or positively identified from roosts, out of 44 species previously recorded for the VBR. For those species captured during the study and one additional commonly recorded species, *Chaerephon ansorgei*, which was not captured, we compiled a library of ANABAT call parameters for reference calls, based on released bats or bats emerging from known-species roosts. Reference calls were obtained from the study area where possible, or from the closest possible site in the savanna region of southeastern Africa. Using principal component analysis and plots of frequency histograms of selected parameters, we investigated the extent to which reference calls of different species could be distinguished on call parameters. Complete separation was obtained for most species but certain species-pairs or trios showed overlap, particularly amongst molossid bats. Accurate identification of unknown calls was complicated by natural intraspecific variation in echolocation call structure due to habitat and behaviour in our species-rich study area. We advocate a conservative approach whereby species-pairs or groups with overlapping calls are treated as single 'species'. Such underestimation can be partly corrected using rarefaction approaches, as illustrated by data collected from Blouberg Nature Reserve. Particularly when surveying bats in species-rich areas such as the eastern savannas of southern Africa, both acoustic and capture-based surveys are necessary to accurately estimate true species richness. From our capture data and roost searches, we recorded nine to 14 species at four west-east, grouped localities defined by this study. Adding acoustic data using a conservative approach to classify overlapping species-pairs or trios, we obtained minimum richness estimates of 15 to 21 species, values which were close to those predicted by a recent macro-ecological model. We found no evidence for a west-east increase in richness with increasing precipitation as predicted by coarse-scale macroecological predictions.

Key words: ANABAT, Chiroptera, Limpopo Province, South Africa, bat species richness, species diversity.

INTRODUCTION

A number of hypotheses have been advanced to explain broad geographical (e.g. latitudinal or

elevational) patterns of variation in species richness, amongst which the productivity hypothesis is often agreed to be one of the most important (Field *et al.* 2009). However, different predictors may act at different spatial or taxonomic scales and in

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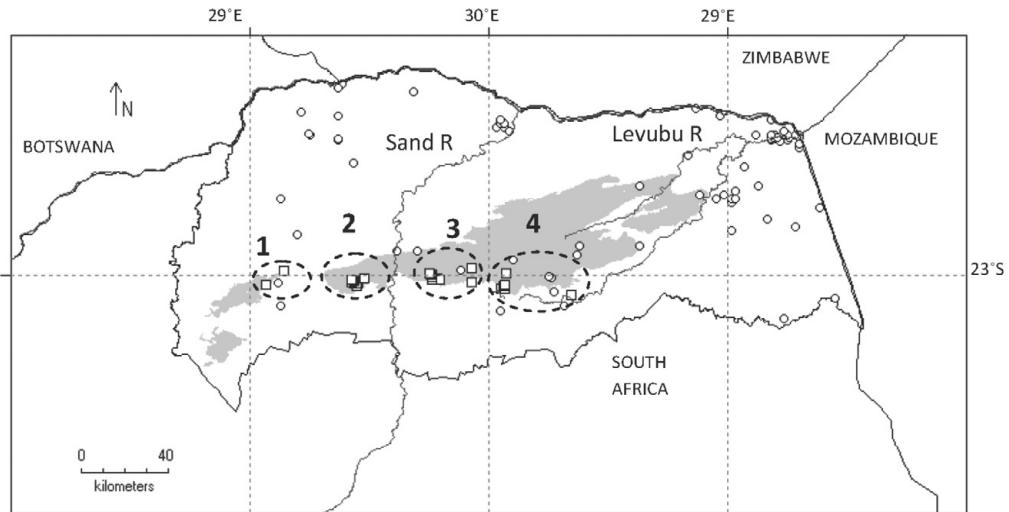


Fig. 1. Map of Vhembe Biosphere Reserve showing locations of sampling sites in the Blouberg and Soutpansberg Mountains (open squares) grouped into four geographical regions (see Table 1), in relation to historical museum collecting localities (open circles) obtained from Monadjem *et al.* (2010). Grey shading represents extent of the Soutpansberg and the Blouberg Mountains and Mahabeng Plateau.

narrow-ranging *versus* widespread species, and factors such as spatial autocorrelation and area effects can confound results (Jetz & Rahbek 2002; Ruggiero & Kitzberger 2004; Schoeman *et al.*, in press). Macroecological investigations of latitudinal variation in species richness in North American (Patten 2004) and European bats (Ulrich *et al.* 2007) identified significant latitudinal gradients which could best be explained by climate (temperature and precipitation) and topography. However, these studies identified distinct patterns and predictors in different families of bats. A general climate model was proposed to explain global patterns of elevational richness patterns in bats (McCain 2007), and this model was found to apply to an elevational transect of bats conducted at Mt Mulanje in Malawi (Curran *et al.* 2012).

In southern Africa, richness of woody plants was shown to be the best predictor of mammalian richness generally (Qian *et al.* 2009), but in bats of southern and central Africa, habitat heterogeneity (elevational variation) and productivity (climate) are important predictors of species richness (Schoeman *et al.*, in press). The hotspots of greatest species richness were located in the eastern savannas, often associated with mountainous areas such as the Soutpansberg in northern South Africa (Schoeman *et al.*, in press). This confirms the earlier study of Gelderblom *et al.* (1995) which found the Savanna Biome to be the hotspot of bat species richness in South Africa.

The Soutpansberg Range situated in the Savanna Biome of northern South Africa comprises a recognized Centre for Plant Endemism (Van Wyk & Smith 2001) with a very rich flora of 3000 plant species and 1066 genera (Hahn 2002). Animal diversity is concordantly high. The Soutpansberg harbours 33% of South Africa's reptiles, 60% of its mammals, 75% of its birds, 50% of the world's spider families and exceptionally diverse ant communities (Berger *et al.* 2003; Foord *et al.* 2008; Munyai & Foord 2012). Variation in aspect and topography within the Soutpansberg results in strong latitudinal, longitudinal and elevational gradients in climate. Precipitation varies from 367 mm in the north to >3000 mm in the south including mist precipitation (Hahn 2002), making this an ideal study area to corroborate at a local scale, predictions from global hypotheses about species richness (Munyai & Foord 2012).

The present study reports on a survey of bats in the Soutpansberg and Blouberg Ranges which form the core of the newly proclaimed UNESCO Vhembe Biosphere Reserve (UNESCO 2005). Whilst 44 species of bats have previously been recorded within the boundary of the Biosphere (Monadjem *et al.* 2010), most were collected from lower altitudes to the east (Kruger National Park) and north (vicinity of Musina) of the Soutpansberg, with almost no collections from the mountains themselves (Fig. 1). The present study included sites from a range of elevations from 600 to 1747 m,

Table 1. Summary of number of captures (from harp traps and mist nets) and roosts of 24 species of bats grouped into four geographical clusters from west to east in the Blouberg and Soutpansberg (see Fig. 1). # indicates identifications based on ANABAT calls using reference calls. ? indicates species which can be confused due to call overlap (see text).

Species	(1) Blouberg Nature Reserve: 845–941 m (4 localities)	(2) Luvhondo Nature Reserve: 956–1747 m (11 localities)	(3) Buzzard Mt/Eagles Nest: 988–1618 m (10 localities)	(4) Piesanghoek/Levubu 600–1400 m (6 localities)
Harp trap effort (no. of nights)	1	18	6	4
Mistnet effort (no. of nights)	3	39	10	2
ANABAT recordings (evenings – 2h/full nights)	0/5	0/18	7/5	16/12
<i>Rousettus aegyptiacus</i>			Roost (>100)	
<i>Epomophorus wahlbergi</i>	3	6	Roost (few)	
<i>Taphozous mauritanianus</i>	#	Roost (1)	Roost (1–2) #	#
<i>Nycteris thebaica</i>	Roost (>50)			2 night roosts #
<i>Hipposideros caffer</i>	#			2
<i>Rhinolophus simulator</i>	#	#	Roost (few) #	#
<i>R. darling</i>		3	1	
<i>R. clivovosus</i>		1 #	5; Roost (few) #	1 night roost #
<i>R. smithersi</i>	1 #		1; Roost (few) #	
<i>Miniopterus natalensis</i>	7 #?	#?	2 #?	#?
<i>Pipistrellus hesperidus</i>	1 #	90 #	67 #	9 #
<i>Neoromicia zuluensis</i>	#		2 #	#
<i>Neoromicia capensis</i>	3 #	1 #	#	#
<i>Pipistrellus rusticus</i>	3 #?	#?	#?	#?
<i>Neoromicia nana</i>	#		#	1 #
<i>Myotis tricolor</i>	#		#	2 #
<i>Myotis welwitschii</i>	#	1 #		#?
<i>Eptesicus hottentotus</i>	3 #	2 #	5 #	#
<i>Laephotis botswanae</i>	#			1 #
<i>Scotophilus dinganii</i>	2 #	5; Roost (<10) #	2; Roost (few) #	2; 1 roost #
<i>Chaerephon pumilus</i>	#?	#?	1; Roost (few) #?	1, 1 roost #?
<i>Mops condylurus</i>	#?	#?	#?	2;2 roosts (>10)#?
<i>Mops midas</i>	#	#	2 roosts (>10) #	2 roosts (>10) #
<i>Tadarida aegyptiaca</i>	#?	1 #?	#?	#?
Not captured; classified from reference calls				
<i>Chaerephon ansorgei</i>	#	#	#?	#?
Unclassified calls				
<i>Rhinolophus</i> Fc =100kHz	#	#		
Broad-band FM Fc 42 kHz			#?	#?
Broad-band FM Fc 65 kHz				#
Broad-band FM Fc 59 kHz			#	
Narrow-band Fc 21 kHz			#	
Narrow-band Fc 31 kHz				#
Narrow-band Fc 44 kHz				#
Narrow-band FM Fc 57 kHz				#
Total no. of captures	23	110	87	22
Total no. of species captured	9	10	14	11
Simpson <i>D</i>	0.88	0.35	0.48	0.85
ANABAT + captures	21	15	20	21
No. spp. predicted (model ¹)	18	18	27	27

¹Schoeman *et al.* (in press).

across a west–east rainfall gradient from Blouberg in the west (29°E) to the Levuvhu Valley in the east (30°E) along the southern aspect of the mountains. This west–east gradient of increasing rainfall corresponds to a gradient of increasing predicted

species richness (Schoeman *et al.*, in press; Table 1). Our data allowed us to sample species richness across this gradient at a local scale so as to make comparisons with predictions based on broad geographic scales.

Whether testing global hypotheses for species richness, planning core areas for protected areas or assessing environmental impacts of wind farms on bats, it is critical that survey methods adequately and completely sample representative local communities. Our survey concurrently employed multiple approaches using ANABAT bat detectors, a harp trap, mistnets and roost searches. Acoustic surveys have the advantage of being non-invasive and have recently been advocated as the standard method for conducting bat surveys for EIA studies for wind farm proposals in South Africa (Sowler & Stoffberg 2012). Acoustic surveys depend on the existence of good call reference libraries and may significantly underestimate true species richness, especially in species-rich areas such as savannas. We provide the first ANABAT library of call parameters for reference files for 24 bat species captured during our study in the Soutpansberg and one additional commonly acoustically-recorded species assumed to be *Chaerephon ansorgei*. We compared and combined data from invasive and non-invasive methods to: a) attempt to sample bat communities as completely as possible, and (b) to assess the performance of ANABAT recordings alone to estimate true species richness of bats in a hotspot of bat diversity. To address the second objective, we investigated the overlap in echolocation call parameters in reference calls of different bat species using multivariate and univariate statistical approaches. We recognize that our results may to some extent be biased by seasonal migration patterns which are known to occur in species such as *Myotis tricolor* (McDonald *et al.* 1990), *Miniopterus natalensis* (van der Merwe 1975) and *Eidolon helvum* (Richter & Cumming 2008).

METHODS

We surveyed 30 localities along the southern aspect of the Blouberg and Soutpansberg Ranges using 63 nights of ANABAT recordings (www.titley.com.au), a two-bank harp trap (Faunatech, Australia) set for 29 nights and 54 mistnet-nights (mistnets supplied by Ecotone, Poland) as well as *ad hoc* searches for day and night roosts (Table 1). We generally used two 9-m mistnets (of height c. 2.5 m set at ground level) per night of sampling and sampling was conducted for approximately two hours after sunset or until there was no further bat activity. In narrow flight paths an additional 6 m-long mistnet (of height c. 2.5 m) was very occasionally employed. Harp traps were

deployed from sunset till sunrise along presumed flightways.

ANABAT S.D.1 and S.D.2 detectors were used to make recordings of the ultrasonic vocalizations of bats which were stored automatically on an S.D. memory card and later analysed by the ANALOOK programme (Chris Corben, version 0.3.8.13, <http://www.hoarybat.com>). The ANABAT system is widely used for bat surveys worldwide and has the advantage of being able to record huge volumes of bat call data automatically and efficiently (O'Farrell *et al.* 1999; Milne *et al.* 2004; Monadjem *et al.* 2010; Williams-Guillen & Perfecto 2011; Skalak *et al.* 2012). In some cases, detectors were deployed continuously from sunset to sunrise whereas in other cases, recording was carried out only for the maximum foraging period of bats, approximately two hours after sunset (Table 1). We noted whether bat detectors were placed in 'open' or 'closed' habitats and where possible attempted to record both open and habitats at each locality surveyed.

All captured bats were sexed and adult status was determined by the completion of ossification of the wing bones. Mass (g) was recorded using a Pesola balance while forearm length (mm) was measured using either vernier or digital callipers. In order to reliably identify each species, voucher specimens (alcohol skins and skulls) were obtained for each species collected in addition to soft tissues (for possible DNA sequencing) and these were deposited in the collection of the Durban Natural Science Museum. Identification was based on matrices in Monadjem *et al.* (2010) based on external, cranial and dental characters. Collecting was conducted under a permit from the Limpopo Department of Economic Development, Environment and Tourism (Permit No. 001-CPM403-00010).

Where possible we obtained ANABAT reference calls of known species from released individuals collected during our study. We also incorporated data from existing libraries of reference calls from the Waterberg, Western Cape, KwaZulu-Natal and Namibia (data supplied by S.S.) as well as from Swaziland, Mozambique and KwaZulu-Natal (data supplied by A.M.).

RESULTS

A total of 260 individuals of 24 species was captured belonging to all eight southern African families of bats (Table 1). Based on captures, species totals for four grouped localities (Fig. 1)

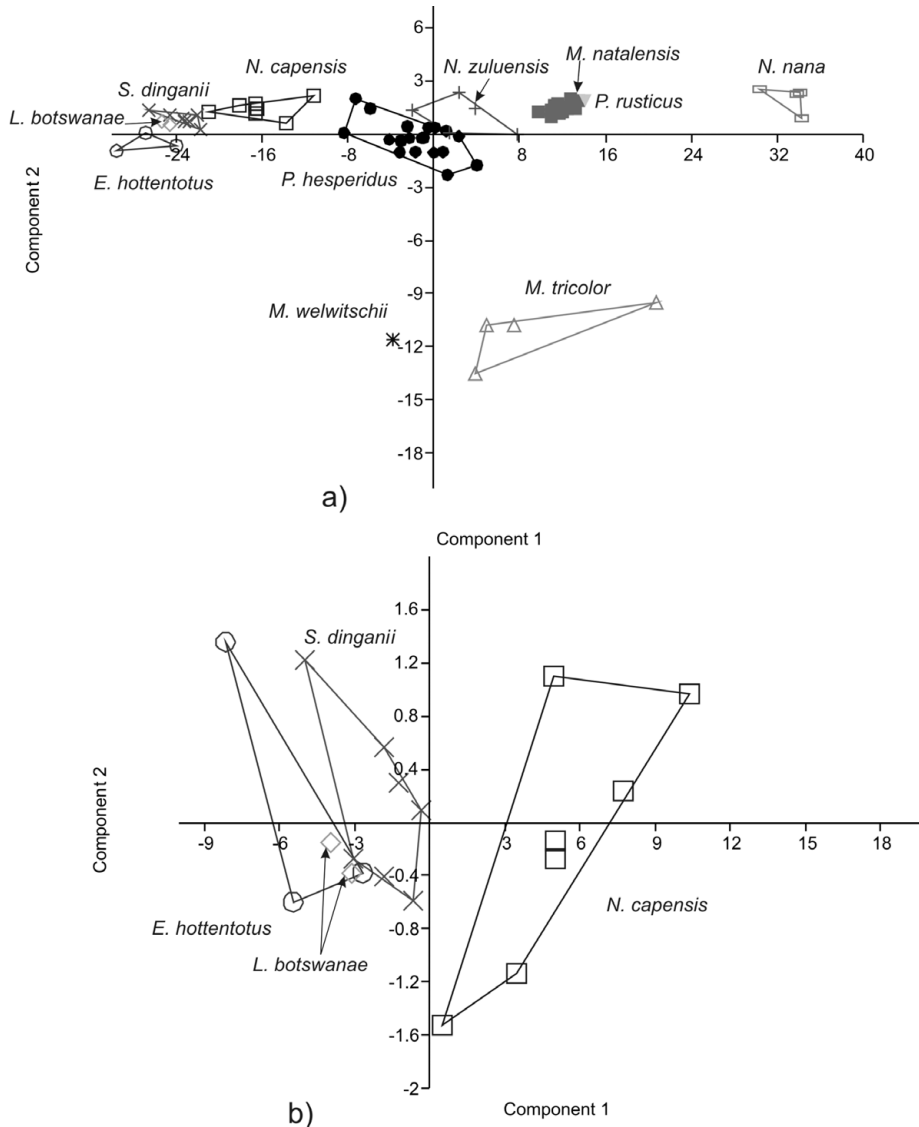


Fig. 2. Plots of first two components from principal components analysis for four parameters of reference calls (Fmin, Duration, Fc and Fk) for (a) all vespertilionid/miniopertid bat species, and (b) four species (*Neoromicia capensis*, *Scotophilus dinganii*, *Eptesicus hottentotus*, *Laephotis botswanae*).

varied from nine (Blouberg Nature Reserve) to 14 (Buzzard Mt/Eagle's Nest). When accounting for species occurrences based on acoustic identifications (as described later), species totals varied from 15 (Luvhondo Private Nature Reserve) to 21 (Blouberg Nature Reserve and Piesanghoek/Levubu).

Seven acoustic parameters are presented for 25 species based on reference calls obtained from released individuals or individuals recorded emerging from known-species roosts (Table 2). Based on

initial PCA's involving these seven parameters, we found four to be useful in separating calls into species within families (three variables were highly variable and obscured species patterns and hence were excluded: slope, Fmax and bandwidth). Variation in reference calls within and between species was summarised for vespertilionid and miniopertid calls using multivariate (Fig. 2) and univariate (Fig. 3) approaches, as was also the case for molossid and emballonurid bats (Figs 4 & 5). Since calls of rhinolophoid species

Table 2. Summary statistics for seven acoustic parameters obtained from ANABAT recordings of reference calls from released bats of known identification or emergences from known-species roosts. N1 and N2 refer to number of call sequences (bat passes) and total number of calls, respectively.

Species & localities		Fmax (kHz)	Duration (m)	Bandwidth (kHz)	Fmin (kHz)	Fk (kHz)	Fc (kHz)	Slope
FAMILY VESPERTILIONIDAE								
<i>Pipistrellus hesperidus</i> Soutpansberg (Luvhondo, Buzzard Mt)	Mean	66.9	2.6	22.0	44.9	50.3	45.8	586.0
	S.D.	8.91	0.85	8.24	1.53	2.50	1.78	219.59
	N1(N2)	19(309)	19(309)	19(309)	19(309)	19(309)	19(309)	19(309)
	Min	48.5	1.7	5.4	41.3	44.9	41.5	153.8
	Max	82.0	5.0	34.8	47.2	54.7	49.1	828.8
<i>P. rusticus</i> Waterberg (Lapalala)	Mean	62.1	3.1	6.8	55.3	57.6	55.4	294.4
	N1 (N2)	1(7)	1(7)	1(7)	1(7)	1(7)	1(7)	1(7)
<i>Neoromicia zuluensis</i> Waterberg (Lapalala)	Mean	73.8	2.4	25.7	48.1	51.3	49.0	666.1
	S.D.	14.93	0.52	14.64	1.94	2.85	1.81	164.55
	N1(N2)	5(88)	5(88)	5(88)	5(88)	5(88)	5(88)	5(88)
	Min	59.1	1.7	13.4	45.7	48.4	46.3	487.2
	Max	92.8	3.0	46.1	50.5	55.8	51.2	867.5
<i>N. capensis</i> Soutpansberg (Luvhondo), Waterberg (Lapalala), Greyton (W Cape)	Mean	48.9	3.6	11.4	37.6	40.0	38.2	341.8
	S.D.	6.15	1.05	5.55	1.86	1.92	1.68	88.18
	N1(N2)	7(215)	7(215)	7(215)	7(215)	7(215)	7(215)	7(215)
	Min	41.4	2.1	4.7	34.7	37.0	35.8	253.6
	Max	61.4	5.0	22.9	40.9	42.4	41.2	509.4
<i>N. nana</i> Swaziland (Mlawula), Gillitts (Durban)	Mean	77.9	3.2	11.7	66.2	68.2	66.9	529.9
	S.D.	3.34	0.59	2.52	0.92	1.60	0.96	220.48
	N1(N2)	4(74)	4(74)	4(74)	4(74)	4(74)	4(74)	4(74)
	Min	74.4	2.4	9.5	64.9	66.1	65.4	219.9
	Max	80.9	3.6	13.9	67.0	69.9	67.4	733.0
<i>Scotophilus dinganii</i> Soutpansberg (Buzzard Mt), Waterberg (Lapalala)	Mean	51.6	3.4	18.5	33.1	36.4	33.8	426.1
	S.D.	8.19	0.66	7.85	0.79	1.10	1.03	93.30
	N1(N2)	7(222)	7(222)	7(222)	7(222)	7(222)	7(222)	7(222)
	Min	42.1	2.7	9.7	31.6	34.4	31.9	287.1
	Max	65.2	4.6	32.0	34.1	37.4	35.3	587.6
<i>Eptesicus hottentotus</i> Soutpansberg (Luvhondo)	Mean	60.6	3.1	30.5	30.1	35.2	32.2	553.1
	S.D.	8.23	0.86	8.52	1.74	1.48	1.75	207.87
	N1(N2)	3(61)	3(61)	3(61)	3(61)	3(61)	3(61)	3(61)
	Min	54.0	2.6	22.3	28.2	34.2	30.4	359.7
	Max	69.8	4.1	39.3	31.6	36.9	33.8	772.9
<i>Laephotis botswanae</i> Waterberg (Lapalala)	Mean	51.6	3.0	19.6	32.0	35.6	33.0	472.5
	N1(N2)	2(46)	2(46)	2(46)	2(46)	2(46)	2(46)	2(46)
	Min	50.3	2.9	18.1	31.8	35.3	32.8	433.8
	Max	53.0	3.1	21.1	32.2	35.8	33.3	511.2
	<i>Myotis welwitschii</i> Soutpansberg (Luvhondo)	Mean	73.8	2.1	40.0	33.8	52.9	50.3
N1(N2)		1(5)	1(5)	1(5)	1(5)	1(5)	1(5)	1(5)
<i>M. tricolor</i> Waterberg (Lapalala), Swaziland	Mean	86.1	2.0	43.3	42.7	57.6	52.4	671.8
	S.D.	5.92	0.40	7.75	4.43	7.25	6.13	359.67
	N1(N2)	6(120)	6(120)	6(120)	6(120)	6(120)	6(120)	6(120)
	Min	76.6	1.6	33.6	37.1	48.5	45.3	287.1
	Max	91.9	2.6	53.2	50.0	67.5	62.2	1128.9
FAMILY MINIOPTERIDAE								
<i>Miniopterus natalensis</i> Swaziland, Namibia	Mean	65.9	2.6	12.2	53.7	56.5	54.1	379.4
	S.D.	5.76	0.48	6.00	0.58	0.31	0.78	95.78
	N1(N2)	21(392)	21(392)	21(392)	21(392)	21(392)	21(392)	21(392)
	Min	59.0	1.9	5.4	52.5	55.7	52.7	235.3
	Max	80.9	3.8	27.4	54.9	57.0	55.5	622.8

Continued on p. 18

Table 2 (continued)

Species & localities		Fmax (kHz)	Duration (m)	Bandwidth (kHz)	Fmin (kHz)	Fk (kHz)	Fc (kHz)	Slope
FAMILY MOLOSSIDAE								
<i>Chaerephon ansorgei</i> Mozambique	Mean	23.1	10.6	4.5	18.6	21.5	19.8	57.2
	S.D.	3.5	1.2	2.8	1.5	1.4	1.1	47.7
	N1(N2)	3(26)	3(26)	3(26)	3(26)	3(26)	3(26)	3(26)
	Min	20.1	9.4	2.6	16.9	19.9	18.5	24.0
	Max	27.0	11.9	7.8	19.8	22.6	20.5	111.9
Waterberg (Lapalala)	Mean	22.1	6.4	3.6	18.5	20.1	19.0	106.6
	S.D.	1.53	1.51	1.08	0.92	1.05	0.94	43.80
	N1(N2)	12(298)	12(298)	12(298)	12(298)	12(298)	12(298)	12(298)
	Min	19.5	4.5	1.4	17.5	18.9	17.8	46.7
	Max	24.3	9.3	5.4	20.0	21.8	20.5	212.4
<i>Chaerephon pumilus</i> Swaziland	Mean	27.7	8.3	4.4	23.3	26.2	24.3	56.7
	S.D.	4.40	2.10	2.46	2.38	3.34	2.91	39.30
	N1(N2)	8(194)	8(194)	8(194)	8(194)	8(194)	8(194)	8(194)
	Min	23.0	5.3	1.6	20.9	22.6	21.5	13.2
	Max	32.8	11.9	8.6	27.4	30.8	28.1	124.1
Tembe Elephant Park, KwaZulu-Natal, South Africa	Mean	31.6	8.4	7.224.5	28.9	25.6	59.1	
	S.D.	4.05	1.71	2.88	1.55	2.51	1.57	20.93
	N1(N2)	6(95)	6(95)	6(95)	6(95)	6(95)	6(95)	6(95)
	Min	24.6	6.6	2.9	21.7	24.4	22.7	19.9
	Max	36.7	11.0	11.9	26.5	31.3	27.3	82.6
<i>Mops midas</i> Waterberg (Lapalala)	Mean	14.5	10.3	1.7	12.8	13.8	13.1	51.5
	S.D.	1.45	2.89	0.71	0.82	1.02	0.88	12.67
	N1(N2)	6(109)	6(109)	6(109)	6(109)	6(109)	6(109)	6(109)
	Min	12.7	7.8	1.0	11.7	12.5	12.0	32.2
	Max	16.2	15.8	2.8	13.7	15.0	14.0	65.8
<i>Mops condylurus</i> Swaziland (Mlawula)	Mean	34.8	5.5	9.0	25.8	30.2	27.3	101.1
	S.D.	2.78	1.40	2.23	1.79	2.16	1.98	46.18
	N1(N2)	6(147)	6(147)	6	6(147)	6(147)	6(147)	6(147)
	Min	31.5	3.4	6.4	23.9	27.4	24.9	39.5
	Max	38.6	7.2	12.9	28.2	32.4	29.3	160.8
<i>Tadarida aegyptiaca</i> Waterberg (Lapalala)	Mean	28.3	7.2	6.8	21.6	24.2	22.8	167.8
	S.D.	3.36	3.10	3.58	2.73	1.47	1.39	57.30
	N1(N2)	8(222)	8(222)	8(222)	8(222)	8(222)	8(222)	8(222)
	Min	24.8	3.3	2.2	17.2	21.9	20.5	65.5
	Max	34.1	10.9	10.4	24.0	26.1	24.5	221.3
FAMILY EMBALLANURIDAE								
<i>Taphozous mauritianus</i> Soutpansberg (Buzzard Mt), Waterberg (Lapalala)	Mean	29.0	2.9	3.7	25.3	28.3	26.2	135.8
	S.D.	1.17	0.64	1.63	1.49	1.29	0.94	59.80
	N1(N2)	10(98)	10(98)	10(98)	10(98)	10(98)	10(98)	10(98)
	Min	27.8	2.0	1.7	22.1	27.0	24.9	55.8
	Max	31.1	3.6	6.4	27.9	30.2	27.9	279.5
RHINOLOPHIDAE								
<i>Rhinolophus smithersi</i> Blouberg	Mean	45.2	34.9	4.6	40.6	44.7	44.6	-35.0
	S.D.	0.17	6.69	1.19	1.28	0.13	0.13	55.68
	N1(N2)	7(192)	7(192)	7(192)	7(192)	7(192)	7(192)	7(192)
	Min	44.9	26.0	3.4	38.1	44.5	44.3	-112.3
	Max	45.4	46.9	6.8	41.7	44.8	44.7	27.1
Waterberg (Lapalala)	Mean	47.8	18.2	2.1	45.7	47.2	47.3	-13.3
	S.D.	0.31	4.52	0.71	0.91	0.31	0.29	49.20
	N1(N2)	13(524)	13(524)	13(524)	13(524)	13(524)	13(524)	13(524)
	Min	47.0	10.9	1.2	44.1	46.3	46.4	-73.0
	Max	48.4	24.8	3.5	47.1	47.7	47.7	101.5
Soutpansberg (Buzzard Mt)	Mean	46.0	12.0	1.2	44.8	45.2	45.5	162.4
	S.D.	0.12	2.22	0.27	0.20	0.07	0.05	36.15
	N1(N2)	10(207)	10(207)	10(207)	10(207)	10(207)	10(207)	10(207)
	Min	45.9	9.6	0.9	44.4	45.2	45.5	103.0
	Max	46.2	16.5	1.9	45.0	45.4	45.6	223.0

Continued on p. 19

Table 2 (continued)

Species & localities		Fmax (kHz)	Duration (m)	Bandwidth (kHz)	Fmin (kHz)	Fk (kHz)	Fc (kHz)	Slope
<i>R. clivosus</i> Soutpansberg (Buzzard Mt)	Mean	92.1	14.3	5.4	86.7	90.3	90.7	442.8
	S.D.	0.51	3.63	3.46	3.21	0.42	0.40	96.80
	N1(N2)	10(13)	10(130)	10(130)	10(130)	10(130)	10(130)	10(130)
	Min	91.5	8.6	2.2	79.3	89.6	90.1	280.1
	Max	92.8	19.4	13.6	89.6	90.9	91.4	605.6
<i>R. darlingi</i> Waterberg (Lapalala)	Mean	87.4	28.0	3.2	84.2	85.6	85.1	219.8
	N1(N2)	1(2)	1(2)	1(2)	1(2)	1(2)	1(2)	1(2)
Swaziland	Mean	85.8	17.8	11.2	74.5	84.8	85.2	147.3
	S.D.	0.25	3.39	1.77	4.54	0.52	0.54	76.28
	N1(N2)	4(192)	4(192)	4(192)	4(192)	4(192)	4(192)	4(192)
	Min	85.5	13.3	9.5	72.3	84.1	84.5	96.8
	Max	86.0	21.5	13.7	76.1	85.2	85.6	259.2
<i>R. simulator</i> Waterberg (Lapalala)	Mean	82.0	12.4	2.7	79.3	80.5	81.5	299.3
	S.D.	0.58	1.71	1.35	1.42	0.46	0.47	34.63
	N1(N2)	9(99)	9(99)	9(99)	9(99)	9(99)	9(99)	9(99)
	Min	81.1	9.6	1.8	75.9	79.8	80.9	257.3
	Max	82.9	14.4	6.0	80.6	81.2	82.1	367.6
Swaziland	Mean	84.0	13.1	5.5	78.6	83.1	83.4	83.9
	S.D.	0.34	3.66	3.63	3.77	0.83	1.20	10.28
	N1(N2)	16.(750)	16(750)	16(750)	16(750)	16(750)	16(750)	16(750)
	Min	83.2	7.0	1.9	71.5	80.3	79.2	69.7
	Max	84.4	18.9	12.5	82.3	83.7	84.1	101.3
FAMILY HIPPOSIDERIDAE								
<i>Hipposideros caffer</i> Swaziland	Mean	142.9	4.2	19.7	123.2	141.5	142.0	181.8
	S.D.	0.96	0.28	6.60	6.40	0.95	1.00	131.75
	N1(N2)	13(176)	13 (176)	13(176)	13(176)	13(176)	13(176)	13(176)
	Min	140.4	3.7	12.6	108.9	139.3	139.8	-133.7
	Max	144.1	4.7	34.1	130.3	142.9	143.5	434.8

showed complete non-overlap in frequency parameters (Table 2), no further analysis was necessary. With notable exceptions, based on four acoustic parameters (duration, Fmin, Fk, Fc), PCA grouped 76 recorded reference call sequences into their respective 11 distinct species of vespertilionid and miniopterid bats. Two *Laephotis botswanae* call sequences grouped either with *Scotophilus dinganii* or *Eptesicus hottentotus*. One *Pipistrellus rusticus* sequence grouped close to sequences of *Miniopterus natalensis*. Certain species-pairs had calls which, whilst not overlapping, bordered each other closely in multivariate space: *Pipistrellus hesperidus*/*Neoromicia zuluensis*; *Neoromicia capensis*/*S. dinganii*; and *E. hottentotus*/*S. dinganii*). Based on character loadings (Table 3), separation on the first component (PC1) was explained equally by the three frequency parameters. Variation on PC2, which resulted in separation of the two *Myotis* species from all others, was due to a negative relationship between Fk and Fmin whereby calls of *Myotis* species had Fk values much higher than Fmin values

compared to other species. This was because in most vespertilionid species, these parameters (Fk and Fmin) were closer in value due to the presence of a 'knee' in their calls. This 'knee' is largely absent in the characteristically broad-band and short-duration calls of *Myotis* bats. In spite of the general separation of species' reference calls in multivariate space, overlap was detected in reference calls in Fmin (Fig. 3). Thus, minimal overlap was shown between *P. hesperidus* and *N. zuluensis* (Fig. 3a) and between *E. hottentotus*, *L. botswanae* and *S. dinganii* (Fig. 3d). Problems of call identification of unknown calls can be further compounded by natural variation, e.g. due to habitat, as shown by frequency histograms of Fmin from recordings of *P. hesperidus* from open and closed habitats (Fig. 3b, c). Despite these problems, analysis of frequency histograms of Fmin from recordings obtained over 63 nights during our survey demonstrated that frequency distributions are often distinctly multi-modal with modes indicative of different species (Fig. 3e–g). Furthermore, careful examination of ANABAT sequences

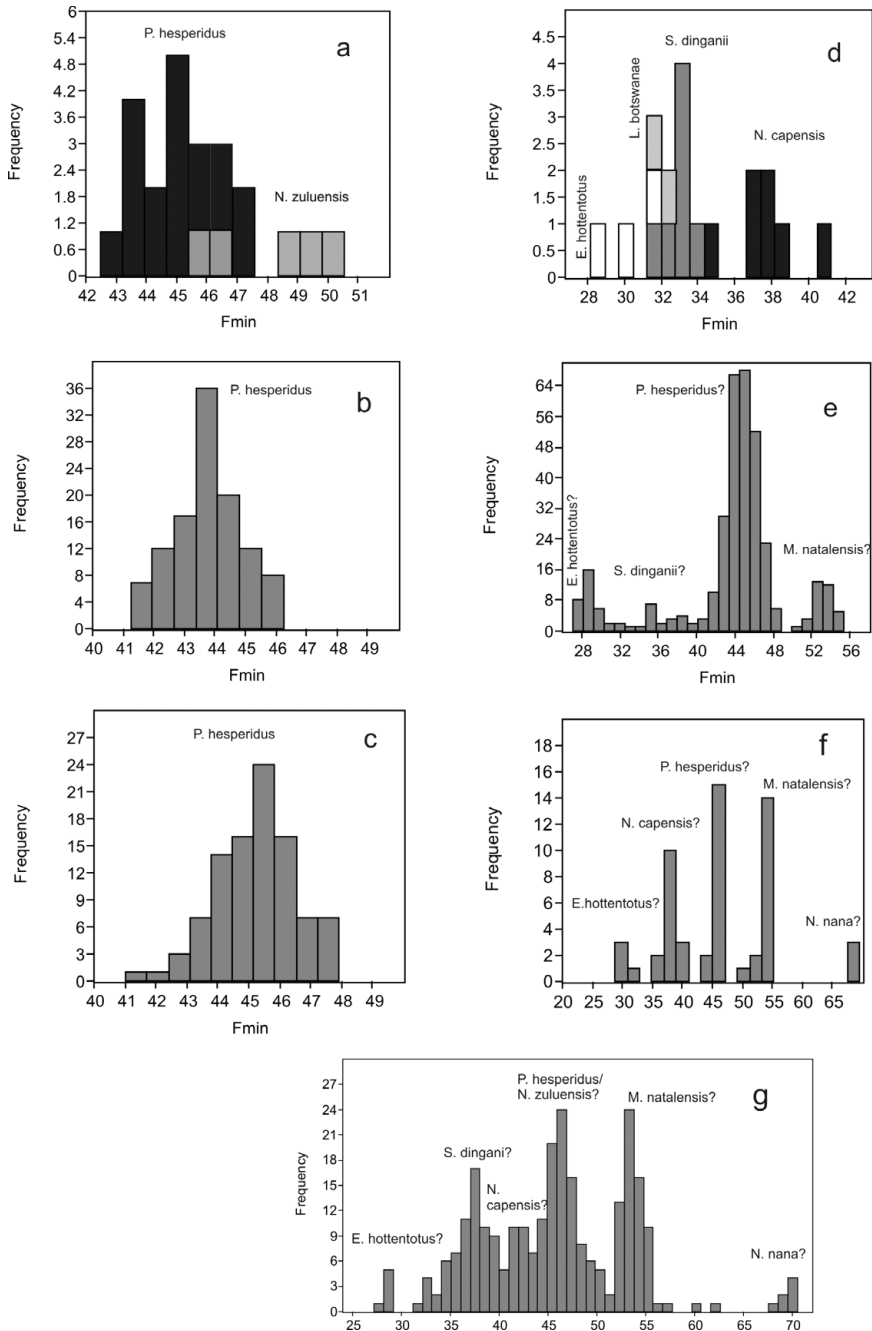


Fig. 3. Frequency histograms for mean Fmin from vespertilionid and miniopterid reference call sequences (**a, d**) and 'unknown' recordings (**b, c, e, f, g**). In (**a**), overlap of Fmin is shown between reference calls of *Pipistrellus hesperidus* (black shading) and *Neoromicia zuluensis* (grey shading); (**b**) and (**c**) represent mean Fmin for sequences (presumed to be *P. hesperidus*) recorded at the same locality (Lajuma farm house) on consecutive nights in open (forest clearing) and closed (road through forest) habitats; (**d**) represents reference calls of *Neoromicia capensis* (black), *Scotophilus dinganii* (dark grey), *Laephotis botswanae* (light grey) and *Eptesicus hottentotus* (white); (**e**) represents calls recorded from one night at Bergplaats Farm in the far western Soutpansberg; (**f**) represents calls recorded from one night at Blouberg Nature Reserve (Mashatu Camp) and (**g**) represents calls recorded from one night at Blouberg Nature Reserve (Office Reservoir).

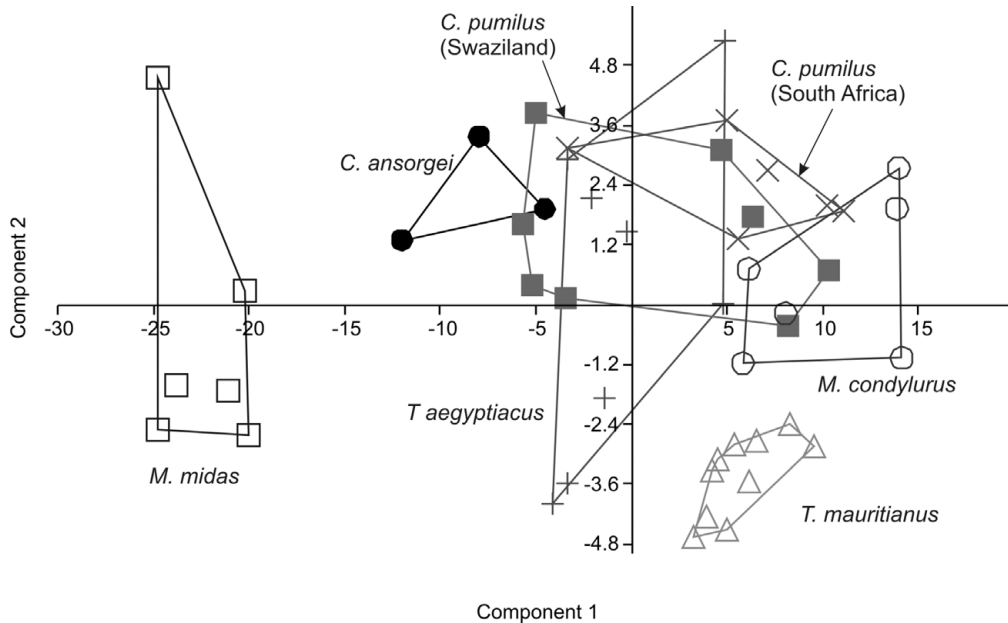


Fig. 4. Plot of first two components from principal components analysis for four parameters of reference calls (Fmin, Duration, Fc and Fk) for molossid and emballanurid bats.

from the same habitat where bats of different species having similar calls were recorded together assisted in reliable identifications of calls as shown by examples of ANALOOK displays from recordings taken at Blouberg Nature Reserve (Fig. 6).

Of five molossid bats recorded in the study area, reference call sequences of *M. midas* and *C. ansorgei* appear to be distinct whilst those of *C. pumilus*, *T. aegyptiaca* and *M. condylurus* show varying degrees of overlap (Figs 4, 5). As with vespertilionids and miniopterids, frequency parameters are the most important variables responsible for species differences (Table 4). In spite of this overlap, recordings of unknown molossids often involved just one or two species and inspection of frequency histograms of Fmin often resulted in clearly multimodal distributions with minimal or no

overlap between modes (Fig. 4e); however in some cases, the range of values associated with modes suggested the presence of at least two species (Fig. 4b, c, d, f). Such cases usually involved a combination of *T. aegyptiaca*, *C. pumilus* and *M. condylurus*.

Using the call reference library (Table 2) and ranges and frequency distributions of key acoustic parameters (e.g. Figs 2, 4), we classified unknown calls obtained during this study (Table 1) and used these to update species totals. More detailed analyses of call data are presented elsewhere (Linden *et al.* 2012; Taylor *et al.* 2013). We adopted a conservative approach whereby certain species pairs or trios having indistinguishable calls were grouped together. Species richness estimators showed that sampling was, with one exception, incomplete (Table 5; 60–92%).

Table 3. Component loadings for principal components analysis (PCA) of means of four acoustic variables (Duration, Fmin, Fc and Fk), obtained by ANALOOK from ANABAT sequences from reference calls of 10 species of Vespertilionidae and one of Miniopteridae (see Fig. 2).

Variable	PC1	PC2	PC3	PC4
Duration (ms)	-0.0165	0.0739	0.4032	0.9120
Fmin (kHz)	0.5705	0.7992	-0.1869	0.0282
Fk (kHz)	0.5789	-0.5475	-0.5305	0.2894
Fc (kHz)	0.5824	-0.2367	0.7218	-0.2894

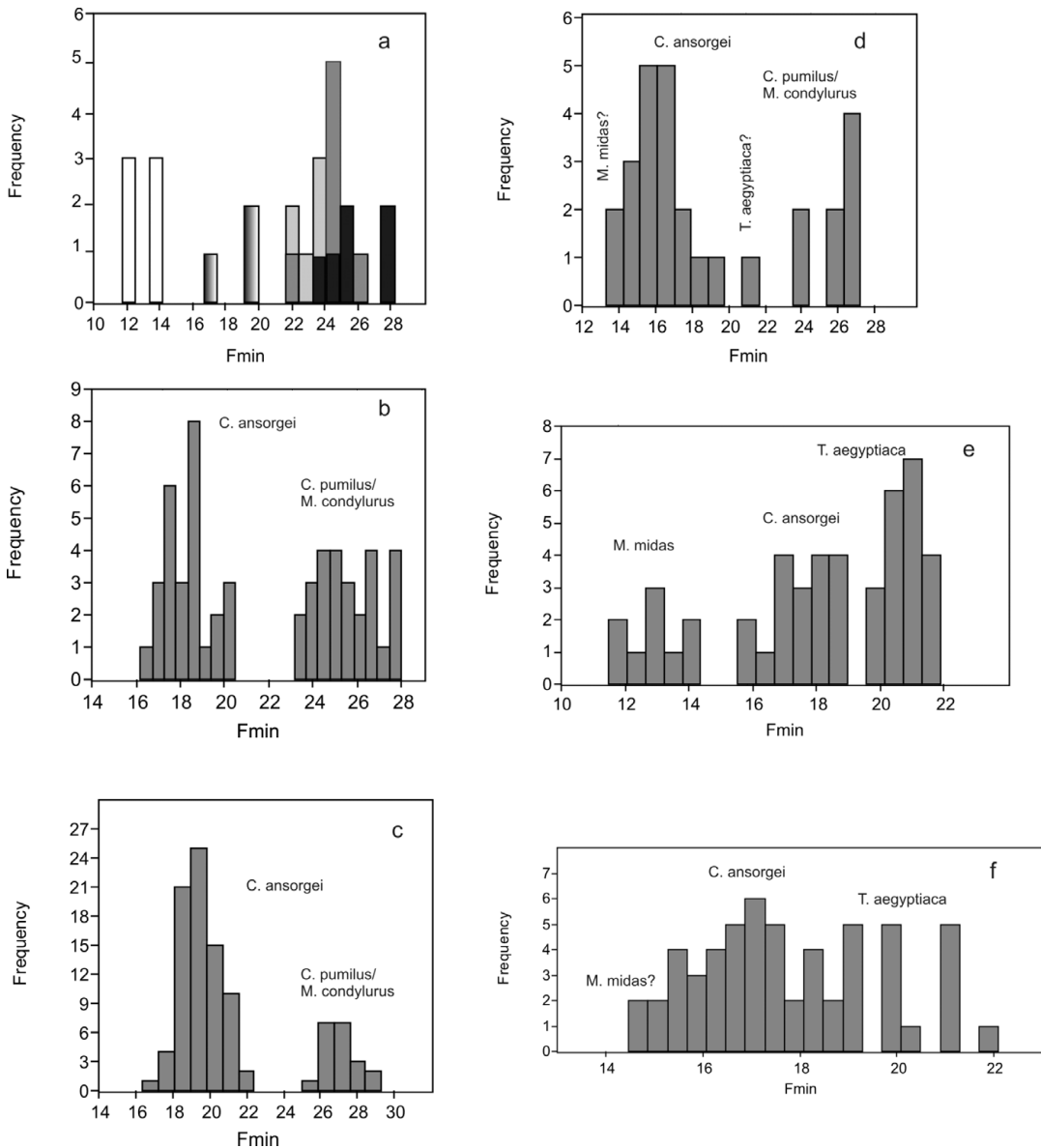


Fig. 5. Frequency histograms for mean Fmin from molossid reference call sequences (a) and 'unknown' recordings (b-f). In (a) distribution of Fmin is shown for reference calls of *Mops condylurus* (black shading), *Chaerephon pumilus* (dark grey shading), *Tadarida aegyptiaca* (pale grey shading), *Chaerephon ansorgei* (fountain fill shading) and *Mops midas* (white); distribution of Fmin from recordings of unknown molossid calls shown for selected nights: (b) Blouberg Nature Reserve (Office Reservoir), 18 May 2012; (c) Bergplaats Farm, 25 October 2011; (d) Eagle's Nest Farm, 25 March 2012; (e) Vlakfontein Farm, 21 September 2012.; (f) Buzzard Mt, 7 February 2011.

Richness indicators showed that expected species richness could be as high as 23 species at one site located at the office reservoir. When pooling data for 18 species from four nights from two sites (1290 individual call sequences) located within 500 m of each other (Mashatu Camp and the office

reservoir), richness estimates were between 20 (Chao2) to 24 (Jackknife2) species, suggesting that our sampling was 75% to 90% complete. Since we conservatively grouped species with overlapping calls (*T. aegyptiaca*/*C. pumilus*/*M. condylurus*; *M. natalensis*/*P. rusticus*; and

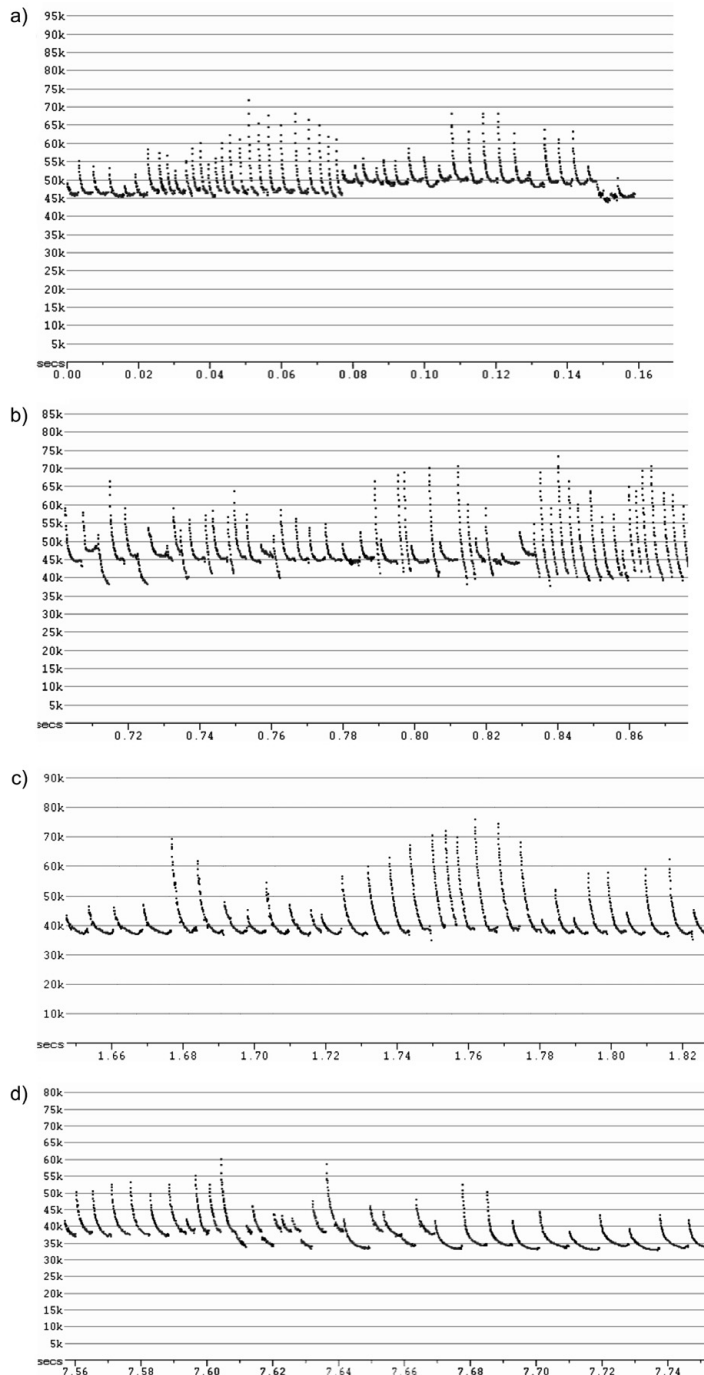


Fig. 6. Selected ANALOOK sonographs recorded on 19 May 2012 from Blouberg Nature Reserve. **a**, Call sequence showing *Pipistrellus hesperidus* calls on left and *Neoromicia zuluensis* on right (spaces between calls removed); **b**, call sequence showing *Myotis tricolor* calls overlapping those of *P. hesperidus* (distribution not indicative of feeding buzz); **c**, call sequence showing feeding buzz within a sequence of *Neoromicia capensis* calls (distribution of calls indicative of feeding buzz with call duration decreasing and then increasing); although having call parameters similar to *M. tricolor*, the calls in the middle clearly belong to *N. capensis*; **d**, call sequence showing overlap of calls of *N. capensis* and *Scotophilus dinganii*.

Table 4. Component loadings for principal components analysis (PCA) of means of four acoustic variables (Duration, Fmin, Fc and Fk), obtained by ANALOOK from ANABAT sequences from reference calls of five species of Molossididae and one of Emballanuridae (see Fig. 4).

Variable (unit)	Axis 1	Axis 2	Axis 3	Axis 4
Duration (ms)	-0.1950	0.9772	-0.0803	0.0235
Fmin (kHz)	0.5166	0.1744	0.8259	-0.1437
Fk (kHz)	0.6245	0.0965	-0.5122	-0.5816
Fc (kHz)	0.5524	0.0727	-0.2216	0.8003

N. capensis/unidentified vespertilionid with Fc of 42 kHz), species richness estimators to some extent compensated for the underestimation caused by our failure to detect at least four 'hidden' acoustic species.

DISCUSSION

A recent coarse-scale (one-degree square resolution) macroecological model for bat species richness in southern and central Africa predicted local species richness values which were generally close to values obtained independently from local surveys (Schoeman *et al.*, in press). This was corroborated by the current study. The above-mentioned model predicts 18 species for the degree-square representing the two westerly localities surveyed in the present study (Blouberg and Luvhondo Nature Reserves) and 27 for the degree-square representing the easterly two (Buzzard Mt/Eagles Nest and Piesanghoek/Levubu) (Table 1). Given the expected underestimation of species richness using our conservative approach for species identification from acoustic data, our estimated species richness values of 15–21 species were reasonably close to the predicted values. However, we found no evidence for an increase in species richness with precipitation from west to east and the westernmost and easternmost localities had the same richness (21 species). In spite of its much greater sample effort, Luvhondo Private Nature Reserve had the lowest species richness of 15 species as well as the lowest species diversity ($D = 0.35$). The latter is due to domination of the bat community by *P. hesperidus* at higher altitudes (1300 m and above); thus based on captures, *P. hesperidus* constituted 82% of captures at Luvhondo (altitude 956–1745 m), compared to only 4.3% at Blouberg ($D = 0.88$) which mostly sampled lower altitudes (845–941 m).

Based only on captures for comparison, we obtained species totals of 9–14 species which

matched or exceeded values previously recorded for two protected areas in Limpopo Province, Musina Nature Reserve (eight species) in the Limpopo Valley and Lapalala Wilderness Area (nine species) in the Waterberg Range (Kearney *et al.* 2008), thus confirming the predictions of the macroecological model of Schoeman *et al.* (in press) that the Soutpansberg and Blouberg constitute a South African bat richness hotspot.

Our results indicate that neither acoustic (non-invasive) nor capture-based (invasive) methods provide complete estimates of species richness in a bat richness hotspot. A combined approach is essential. Moreover, the extent of overlap in acoustic parameters of certain species reference calls coupled with the extreme intra-specific variability observed due to habitat alone, renders surveys based only on acoustic data as being prone to significant identification error, especially when such surveys (*e.g.* for wind farm Environmental Impact Assessment studies) are undertaken by consultants who are not bat specialists and in the absence of local reference calls libraries based on captured and released individuals. By providing data on acoustic parameters for 25 savanna bat species, we hope to provide a baseline reference library which can be expanded on by future research. Whilst an automated bat acoustic identification tool has recently been developed for Europe (Walters *et al.* 2012), this remains a challenging goal in southern Africa, although novel statistical approaches such as that advocated by Agranat (2012) are promising, assuming that a representative selection of reference calls can be compiled.

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Table 5. Summary of acoustic data for five nights of ANABAT recordings at three sites in Blouberg Nature Reserve during March and May 2012.

Species	Fountain 19 May	Mashatu 21 March	Mashatu 18 May	Reservoir 18 May	Reservoir 19 May
Family Molossidae					
<i>Chaerephon ansorgei</i>	0	8	11	28	40
<i>C. pumilus/Tadarida aegyptiaca/Mops condylurus</i>	0	0	0	1419	
<i>Mops midas</i>	0	0	1	0	0
Family Hipposideridae					
<i>Hipposideros caffer</i>	0	0	0	1	1
Family Rhinolophidae					
<i>Rhinolophus smithersi</i>	80	0	2	0	1
' <i>Rhinolophus 100 khz</i> '	0	0	0	0	5
<i>R. simulator</i>	17	0	0	0	3
Family Miniopteridae					
<i>Minioterus natalensis/Pipistrellus rusticus</i>	18	17	7	76	88
Family Vespertilionidae					
<i>Eptesicus hottentotus</i>	6	3	1	13	10
<i>Laephotis botswanae</i>	0	0	0	0	6
<i>Myotis tricolor</i>	0	0	0	0	18
<i>Myotis welwitschii</i>	0	0	0	1	0
<i>Neoromicia capensis</i> 'Pip42'	9	15	4	84	209
<i>Neoromicia nana</i>	1	3	0	15	51
<i>Neoromicia zuluensis</i>	0	0	0	19	103
<i>Pipistrellus hesperidus</i>	45	19	7	107	224
<i>Scotophilus dinganii</i>	0	1	0	24	26
Family Emballonuridae					
<i>Taphozous mauritanus</i>	0	0	1	2	2
No. calls	176	66	34	384	806
No. species	7	7	8	10	16
Estimated richness					
Chao2	7.54	7	12	12.55	19.03
% sampling (Chao2)	92.8	100.0	66.7	79.7	84.1
Jack2	9.72	8.75	13.21	14.22	23.16
% sampling (Jack2)	72.0	80	60.56	70.32	69.08
Species diversity					
Shannon <i>S</i>	1.46	1.64	1.75	1.94	1.99
Simpson <i>D</i>	3.43	4.81	5.39	5.61	5.44
<i>D</i> (Classic formula)	0.78	0.81	0.81	0.82	0.82

and Kim Labuscagne, Jabu and Birthe Linden, Johnson Madzhuta, Delver Mkhari, Vusani Mphethe, Rhuliani Mthombeni, Tovho Mukwevho, Peter Nemudivhiso, Philip Potgieter, Koos Steyn, Paul, Pierre Thomas and Sina M. Weier,

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