Echolocation calls of twenty southern African bat species

P.J. Taylor
Durban Natural Science Museum & Durban Bat Interest Group, P.O. Box 4085, Durban, 4000 South Africa
petert@prcsu.durban.gov.za

Received 20 October 1998, accepted after revision 26 May 1999

Echolocation data and sonograms are reported for twenty southern African bat species from 13 localities, recorded with the Pettersson D980 time-expansion bat detector. Data for eight species have not previously been reported. For seven species, two or more individuals were analysed in a range of situations, including hand-held, tethered and free-flying (in a room and in different natural habitats). Sonograms, and seven echolocation call parameters agreed, with a few exceptions, with published data for individual species. Although intraspecific variation in echolocation call structure was documented, species tended to have recognisable 'vocal signatures', particularly when dominant frequency and harmonic structure were considered. The latter variables are readily retrieved by time expansion detectors, but not by frequency division or heterodyne detectors. Although generally they should be interpreted with caution, recordings from room-flown (five species) and hand-held (six species) bats obtained during this study matched, reasonably closely, additional recordings and observations of naturally flying individuals of the same species, using time expansion and heterodyne bat detectors. In four species, recordings obtained from a known species flying in a room or hand-held enabled the accurate, *a posteriori* species identification of unknown call sequences obtained during subsequent general recordings from bat feeding areas.

Ultrasonic bat detectors are being used increasingly by bat researchers, conservationists and amateurs worldwide to census and identify bats in flight (Fenton & Bell 1981; Kuenzi & Morrison 1998; O'Farrell & Miller 1997; O'Farrell, Miller & Gannon 1999a; Vaughan, Jones, & Harris 1997a), as well as to investigate the relationship between echolocation, flight morphology and foraging ecology (Fenton, Gaudet & Leonard 1983; Fenton 1985; 1986; Aldridge & Rautenbach 1987; Norberg & Rayner 1987; Barclay & Brigham 1991; Bowie, Jacobs & Taylor 1999). Their use in southern Africa has been limited, and data on echolocation calls of local species are largely lacking (but see Fenton & Bell 1981; Fenton *et al.* 1983; Fenton 1986; Aldridge & Rautenbach 1987; Rydell & Yalden 1997). Fenton & Bell (1981) obtained sonograms of 23 species of bats at Sengwa (Zimbabawe) using a bat detector, period meter, recorder and dedicated oscillogram. They examined the usefulness of bat detectors for the identification of individual species in the Zimbabwe assemblage, compared to less species-rich bat communities in Arizona, New York and northeastern Ontario, and concluded that at Sengwa positive identification from calls was only possible during the dry season when bat activity was much reduced. Aldridge & Rautenbach (1987) obtained sonograms for 16 species from Pafuri in the Kruger National Park in South Africa.

Recent studies reinforce the notion that bat detectors can often provide accurate identification of bats in flight. O'Farrell *et al.* (1999a) concluded that, while 20–40% of ANABAT-recorded calls of bats belonging to the family Vespertilionidae are non-identifiable, this is usually <10% for other families. Vaughan *et al.* (1997a) found that multivariate analysis of echolocation parameters from time-expanded recordings from 15 British species resulted in correct classification of 67% of unknown FM calls, and 89% of FM/CF calls. On the other hand, intraspecific variability in sonar signal design has long been recognised (Griffin 1958; Obrist 1995). Sources of intraspecific variability in echolocation call structure, which can confound species identification, include geographic location (Thomas, Bell & Fenton 1987; Barclay 1999), habitat differences (Barclay 1999; Obrist 1995; Rhodes & Schnitzler 1998), sexual dimorphism (Whybird, Coles & Clague 1998), individual variation (Obrist 1995), atmospheric attenuation (Griffin 1971), and presence of conspecifics, or clutter (Obrist 1995). Barclay (1999) has further pointed out that bat echolocation calls are not as complex or species-specific as bird songs, although O'Farrell, Corben, Gannon & Miller (1999b) have countered that, once intraspecific variation has been corrected for, species-specific 'vocal signatures' can usually be retrieved from sonograms obtained from the ANABAT system using a qualitative approach. O'Farrell *et al.* (1999a, b) argued that qualitative parameters such as call shape and temporal patterns of pulse production are more useful in species identification than adopting a purely quantitative approach. Schwenk (1998) cautioned that frequency, duration and call shape data obtained from ANABAT recordings during a Pennsylvania survey were insufficient to accurately identify all species, and added that intensity and harmonic information (not available through ANABAT recordings) would have proved useful for identification.

The aim of this study is to present new echolocation data for 20 southern African species using a time-expansion Pettersson D980 bat detector, particularly with the view to corroborating published echolocation data, assessing the extent of intraspecific variation in call structure under deliberately varied conditions, and assessing the potential usefulness of bat detectors for routine identification of species in flight. Although the use of recordings from hand-held bats, or from room-flown low-duty cycle bats is not generally advocated (Barclay 1999), they were included in this study for two reasons: (1) as a first estimation for hitherto unrecorded species (see also O'Farrell *et al.* 1999a); and (2) in order to quantify the nature of differences between hand-held, room-flown and 'natural' recordings of the same species. The relative

usefulness of inexpensive (heterodyne or frequency division) *versus* expensive (time-expansion) detectors is examined, in terms of the ability of different call variables to resolve species differences. Should intensity or harmonic information prove crucial to species recognition, this would indicate the need for more expensive time-expansion detectors, at least for obtaining accurate species vocal signatures for building up a basic call library. The echolocation calls summarised in this article should provide a foundation for a proposed southern African call library, whose goal should ultimately be to provide accurate vocal signatures for as many local species as possible for future species-based surveys.

Material and methods

Recordings were made with a Pettersson D980 bat detector and Sony digital tape recorder. Using a multimedia Pentium personal computer with Windows 95, and the Batsound programme (supplied by Pettersson Elektronik AB, Uppsala, Sweden), calls were analysed, and sonograms produced. To measure intraspecific variation, multiple sequences from different individuals were recorded in a range of circumstances wherever possible; for example hand-held, flying in a room, on release after capture and identification, tethered, and on emergence from known-species roosts. In seven out of the 20 species, two or more individuals were recorded; the remainder were described from only single individuals. A total of 34 call sequences, containing 283 individual calls, was analysed. In 27 of these 34 recordings, individuals were positively identified after capture, or at emergence from known-species roosts, taking care to stand at least 15 m from the roost exit so as to avoid social or other calls not associated with echolocation. Seven unknown call sequences (from general recordings from bat feeding areas) were identified to species by, *a posteriori*, matching their sonograms and call parameters with previously obtained sonograms and call parameters of known species (such individuals are indicated in Table 1). Independent factors, such as knowledge of species occurring in the general area, proximity of known roosts, foraging behaviour, flight pattern and overall body size, were also taken into consideration in the identification of unknown call sequences.

Recordings were taken at the following 13 localities between March 1997 and September 1998: Umbilo Park, Durban North and Newstead Park in the Durban area (KwaZulu-Natal province of South Africa), Biggarsberg Conservancy, Shongweni Resource Reserve, St Lucia Game Reserve, Mkuzi Game Reserve, Dundee and Jozini Dam in KwaZulu-Natal province of South Africa, Vrolijkheid Nature Reserve and Farm Kersefontein in the Western Cape province of South Africa, and Mlawula Game Reserve in Swaziland (Table 1). One captive individual of *Pipistrellus rusticus* collected at Messina Nature Reserve in the Northern Province of South Africa was later recorded flying in a room at Durban (Table 1).

Time-expanded recordings were analysed via Batsound to produce sonograms, from which seven call parameters were obtained: minimum, maximum and dominant frequency, bandwidth (difference between maximum and minimum frequency), harmonic structure (i.e. whether the measured component represented the fundamental component or the second or third harmonic), shape of call (CF-dominated, shallow-FM, steep-FM, steep-FM followed by shallow-FM, or 'quasi-CF', i.e. very shallow FM) and search call duration. Within a sequence of calls (excluding calls associated with feeding buzzes, or obviously 'fragmented' calls, as defined by O'Farrell *et al.* 1999a), means and standard deviations were calculated for the following: minimum, maximum and dominant frequency; bandwidth, and call duration. The above parameters were recorded only for the component having the most energy, for example the fundamental component for vespertilionid, molossid, nycterid and emballonurid species, and the second harmonic of rhinolophid and hipposiderid bats.

Results and discussion

Qualitative approach (sonograms)

Figure 1 presents sonograms of representative calls of each species. Families or groups of families are plotted separately.

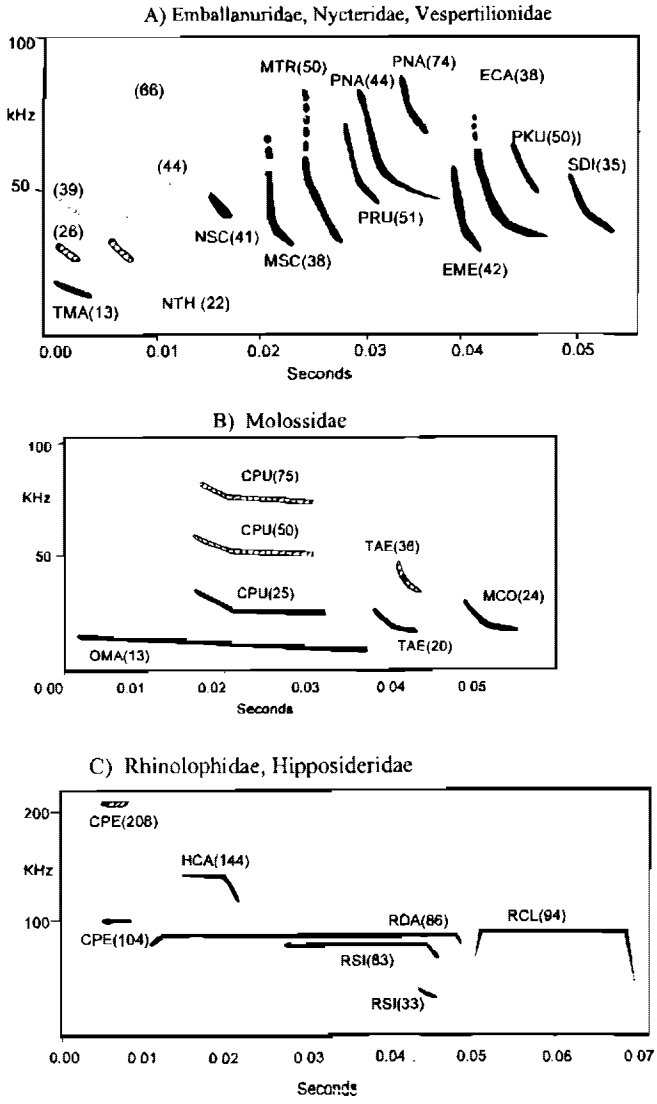

Figure 1 Representative sonograms of 20 southern African bats, according to family: A) Emballonuridae (TMA), Nycteridae (NTH) and Vespertilionidae (rest); B) Molossidae; C) Hipposideridae (CPE, HCA), and Rhinolophidae (RCL, RDA, RSI). Dominant frequencies indicated in parentheses. Hatched components indicate harmonics. Absence of shading for *Nycteris thebaica* (NTH) indicates low intensity calls. Broken lines indicate variable loss of higher frequencies due to attenuation. Explanation of species codes given in Table 1.

Table 1 Echolocation parameters and mean forearm lengths (FA) for 36 species of southern African bats. Families are listed in the same order as Fig. 1; species are listed alphabetically under families. Published data were obtained from Fenton & Bell (1981) (F&B), from Sengwa, Zimbabwe, Fenton *et al.* 1983 (FGL), from Sengwa and Mana Pools National Park, Zimbabwe; Fenton (1986) (FEN) from Sengwa and from Luvuvhu, South Africa, and Aldridge & Rautenbach (1987) (A&R) from Pafuri, Kruger National Park, South Africa. Parameters of calls of *Miniopterus schreibersii* recorded at De Hoop were used with the permission of D. S. Jacobs. Calls of individual bats recorded during the present study are given codes (e.g. TMA) corresponding to those used in Fig. 1. The following mean (± standard deviation) call parameters are shown: minimum (FMIN), maximum (FMAX) and dominant frequency (DOMF), frequency bandwidth (BAND), and maximum call duration (DUR). HARM indicates whether the recorded parameters refer to the fundamental component (F), or to the second or third harmonic (2, 3). Call parameters are shown only for the component having the most energy, usually the fundamental component of FM (frequency modulated) bats, and the second harmonic of CF-FM bats. Call type (TYPE) was expressed as steep-FM (stFM), shallow-FM (shFM), steep-shallow-FM (stshFM), very shallow FM, or 'quasi-constant frequency' (QCF), or constant frequency, usually with preceding or following short FM sweeps (CF-FM). 'N' refers to the number of individual calls analysed. Abbreviations of countries are as follows: SA = South Africa, SW = Swaziland, Z = Zimbabwe.

Family and species	Locality (Country)	Code/ source	FA (mm)	Context	N	FMIN (kHz)	FMAX (kHz)	BAND (kHz)	HARM	DOMF (kHz)	DUR (ms)	TYPE
Emballonuridae:												
Taphozous mauritianus	Pafuri (SA)	A&R	62	Flying (room)	–	15	59	44			20	shFM
	Sengwa (Z)	F&B	62	Flying (open)		12	55	43	F–3	25	15	shFM
	Durban (SA)	TMA1	62	Hand-held	8	22.6 (1.1)	29.4 (1.1)	6.8 (1.4)	2	24.9 (2.0)	2.5 (0.5)	stFM
	Mlawula (SW)[1]	TMA2	62	Flying (open)	5	11.1 (0.7)	15.1 (1.1)	4.0 (1.3)	F	13.0 (1.0)	4.2 (0.8)	stFM
	Mlawula (SW)[1]	TMA3	62	Flying (open)	12	23.1 (1.3)	30.1 (0.8)	6.9 (0.9)	2	25.0 (1.5)	2.4 (0.5)	stFM
	Umbilo (SA)[1,3]	TMA4	62	Flying (open)	1	9.9	15.6	5.7	F	12.8	18	shFM
	Umbilo (SA)[1,3]	TMA5	62	Flying (open)	5	23.2 (2.9)	26.8 (2.3)	3.7 (1.5)	2	24.3 (2.5)	14.0 (1.9)	shFM
Nycteridae:												
Nycteris grandis	Sengwa (Z)	FGL	64	Flying (room)	32	17	110	93	F–4	20 (1)	0.6–2.8	StFM
N. thebaica	Sengwa (Z)	F&B	46	Flying (room)	–	61	97	36	3?	94	2	stFM
	Mlawula (SW)	NTH	46	Flying (open)	9	20.4 (0.6)	26.8 (1.0)	6.1 (1.2)	F	21.8 (0.4)	1.5 (0.5)	stFM
N. woodi	Sengwa (Z)	F&B	38	Flying (room)	–	35	55	20	F	43	2	
Vespertilionidae:												
Eptesicus capensis	Sengwa (Z)	F&B	33	Flying (open)	–	35	65	30	2	40	5	–
	Pafuri (SA)	A&R	33	Flying (open)		35	65	30			5	stFM
	Durban (SA)	ECA1	33	Flying (room)	7	36.7 (0.7)	67.5 (6.5)	30.8 (6.1)	F	39.8 (0.8)	3.3 (1.0)	stFM
	Vrolykheid (SA)	ECA2	33	Flying (open)	11	36.0 (0.7)	74.8 (4.6)	38.8 (4.2)	F	38.1 (0.8)	6.3 (1.3)	stFM
E. 'melckorum'	Kersefontein (SA)	EME	33	Flying (open)	8	38.3 (1.0)	56.2 (7.3)	18.0 (7.3)	F	41.0 (1.3)	2.8 (0.7)	stFM
Kerivoula argentata	Sengwa (Z)	F&B	37	Flying (room)	–	85	120	35	F	90–118	2	–
Laephotis botswanae	Sengwa (Z)	F&B	36	Flying (open)	–	32	55	23	?	33	5	
Miniopterus schreibersii	Kersefontein (SA)	MSC1	45	Flying (open)	6	34.4 (4.5)	51.6 (0.8)	17.2 (4.0)	F	39.6 (2.5)	4.2 (0.8)	stFM
	Shongweni (SA)	MSC2	45	Hand-held	6	36.2 (5.6)	58.2 (3.9)	22.1 (5.3)	F	38.9 (4.2)	3.0 (0.0)	stFM
	De Hoop (SA) – open vlei habitat	MSC3[6]	45	Flying (open)	195	37.5	51.6	–	F		4.4	–
Myotis tricolor	Shongweni (SA)	MTR	51	Tethered	11	36.2 (2.0)	83.7 (1.9)[4]	47.5 (3.2)[4]	F	50.0 (3.2)[4]	3.5 (0.5)	stFM
Nycticeinops schlieffenii	Pafuri (SA)	A&R	30	Flying (open)	–	33	78	45	F	42	5	stFM
	Sengwa (Z)	F&B	30	Flying (open)	–	33	78	45		–	5	–
	Mlawula (SW)	NSC	30	Flying (open)	3	39.5 (0.2)	45.5 (0.7)	6.0 (0.9)	F	41.0 (1.0)	3.7 (0.6)	stFM
P. kuhlii	St Lucia (SA)	PKUI	30	Flying (open)	6	48.7 (0.4)	65.7 (5.3)	17.0 (5.7)	F	50.3 (0.4)	3.5 (0.5)	stFM
Pipistrellus nanus	Pafuri (SA)	A&R	31	Flying (open)	–	62	90	28	F	–	5	stFM
	Sengwa (Z)	F&B	31	Flying (open)	–	62	90	28	F	70	4	stFM
	Jozini (SA)	PNA1	31	Flying (open)	2	42.4 (-)	82.1 (-)	39.7 (-)	F?	43.4 (-)	2.5 (-)	st-shFM
	Jozini (SA)	PNA2	31	Flying (open)	4	67.4 (1.4)	86.3 (1.7)	18.9 (1.5)	F	71.1 (2.7)	1.8 (0.5)	stFM
P. rueppelli	Pafuri (SA)	A&R	34	Flying (room)	–	40	70	30			4	stFM
	Sengwa (Z)	F&B	34	Flying (open)	–	40	70	30	F	45	8	stFM
P. rusticus	Messina (SA)	PRU	28	Flying (room)	15	46.8 (2.4)	77.8 (5.2)	31.0 (5.4)	F	53.1 (1.8)	2.8 (0.6)	stFM
Scotophilus dinganii	Pafuri (SA)	A&R	55	Flying (open)	–	35	58	23	–		5	st-shFM
	Sengwa (Z)	F&B	55	Flying (open)	–	28	55	27	F	30	15	
	Durban (SA)	SDI1	55	Flying (room)	5	32.3 (1.1)	48.5 (0.5)	16.4 (1.5)	F	37.0 (1.4)	4.8 (0.8)[5]	stFM
	Biggarsberg (SA) closed habitat	SDI2[3]	55	Flying (open)	9	36.8 (1.7)	65.4 (5.0)	28.5 (5.2)	1	40.6 (0.6)	5.7 (1.2)	st-shFM
	Biggarsberg (SA), open habitat	SDI3[3]	55	Flying (open)	6	34.3 (0.4)	46.6 (3.1)	12.2 (3.3)	1	36.3 (0.2)	7.5 (0.5)	st-shFM
	Durban North (SA)	SDI4[3]	55	Flying (open)	7	30.8 (1.0)	51.8 (3.8)	21.0 (3.2)	F	33.8 (1.7)	8.0 (3.2)	st-shFM
S. viridis	Pafuri (SA)	A&R	48	Flying (open)		40	70	30	–	–	5	st-shFM
	Sengwa (Z)	F&B	49	Flying (open)		34	59	45	F	10	10	–

Table 1 Echolocation parameters and mean forearm lengths (FA) for 36 species of southern African bats. Families are listed in the same order as Fig. 1, species are listed alphabetically under families. Published data were obtained from Fenton & Bell (1981) (F&B), from Sengwa, Zimbabwe, Fenton *et al.* 1983 (FGL), from Sengwa and Mana Pools National Park, Zimbabwe; Fenton (1986) (FEN) from Sengwa and from Luvuvhu, South Africa, and Aldridge & Rautenbach (1987) (A&R) from Pafuri, Kruger National Park, South Africa. Parameters of calls of *Miniopterus schreibersii* recorded at De Hoop were used with the permission of D.S. Jacobs. Calls of individual bats recorded during the present study are given codes (e.g. TMA) corresponding to those used in Fig. 1. The following mean (± standard deviation) call parameters are shown: minimum (FMIN), maximum (FMAX) and dominant frequency (DOMF), frequency bandwidth (BAND), and maximum call duration (DUR). HARM indicates whether the recorded parameters refer to the fundamental component (F), or to the second or third harmonic (2, 3). Call parameters are shown only for the component having the most energy, usually the fundamental component of FM (frequency modulated) bats, and the second harmonic of CF-FM bats. Call type (TYPE) was expressed as steep-FM (stFM), shallow-FM (shFM), steep-shallow-FM (stshFM), very shallow FM, or 'quasi-constant frequency' (QCF), or constant frequency, usually with preceding or following short FM sweeps (CF-FM). 'N' refers to the number of individual calls analysed. Abbreviations of countries are as follows: SA = South Africa, SW = Swaziland, Z = Zimbabwe.

Family and species	Locality (Country)	Code/ source	FA (mm)	Context	N	FMIN (kHz)	FMAX (kHz)	BAND (kHz)	HARM	DOMF (kHz)	DUR (ms)	TYPE
Molossidae:												
Chaerephon ansorgei	Sengwa (Z)	F&B	43	Flying (open)	–	16	28	12	F	18	15	
C. chapini	Sengwa (Z)	F&B	–	Flying (open)	–	19	27	8	F	20	10	
C. pumila	Durban (SA)	CPU1	38	Flying (room)	7	22.8 (1.4)	43.0 (1.0)	20.2 (2.2)	F	29.2 (2.9)	5.7 (1.0)[5]	stFM
	Mlawula (SW)	CPU2	38	Flying (open)	5	25.9 (1.0)	32.9 (4.5)	5.2 (1.3)	F	27.7 (2.0)	9.0 (1.4)	shFM
	Newstead (SA)	CPU3[3]	38	Flying (open)	5	22.0 (0.6)	28.7 (1.8)	6.7 (1.3)	F	23.7 (0.8)	13.2 (1.3)	shFM
	Umbilo (SA)	CPU4[3]	38	Flying (open)	11	24.4 (1.1)	28.7 (2.5)	4.3 (1.5)	1	25.6 (1.5)	12.4 (0.9)	shFM
C. ingeniae	Sengwa (Z)	F&B	–	Flying (open)	–	16	26	10	F	17	10	-
Mops condylurus	St Lucia (SA)	MCO	47	Landing	6	22.7 (0.7)	38.8 (0.8)	16.0 (1.2)	F	24.7 (0.8)	6.8 (0.8)	stFM
Otomops martiensseni	Sengwa (Z)	F&B	64	Flying (open)	–	10	17	7	F	13	5–30	-
	Durban North (SA)	OMA1	64	Flying (open)	3	24.9 (0.7)	29.5 (2.4)	4.6 (1.7)	F	26.0 (0.9)	57.3 (12.9)	QCF
	Umbilo (SA)	OMA2	64	Emergence	6	9.4 (0.3)	14.7 (1.5)	5.4 (1.6)	F	10.4 (0.2)	24.3 (4.7)	QCF
Tadarida aegyptiaca	Sengwa (Z)	F&B	48	Flying (open)	–	15	26	11	F	18	15	-
	Durban (SA)	TAE1	48	Crawling	2	18.6 (-)	28.7 (-)	10.1 (-)	F	25.3 (-)	5.5 (-)[5]	stFM
	Durban (SA)	TAE2	48	Tethered	21	18.7 (0.7)	31.1 (2.5)	12.4 (2.3)	F	24.7 (2.8)	4.1 (2.7)	shFM
	Biggarsberg (SA)	TAE3[3]	48	Flying (open)	3	18.7 (1.3)	23.2 (1.9)	4.5 (0.8)	F	20.0 (2.0)	7.0 (2.6)	shFM
T. fulminans	Sengwa (Z)	F&B	60	Flying (open)	–	14	27	13	F	17	20	-
	Pafuri (SA)	A&R	60	Flying (room)	–	14	27	13			20	shFM
T. midas	Pafuri (SA)	A&R	60	Flying (open)	–	30					12	shFM
Hipposideridae:												
Cloeotis percivali	Sengwa (Z)	F&B	34	Flying (room)	–	183	212	29	2	212	3	CF-FM
	Jozini (SA)	CPE[2]	34	Hand-held	13	101.3 (1.1)	104.2 (0.4)	3.0 (1.0)	F	103.5 (0.2)	3.4 (0.6)	CF-FM
Hipposideros caffer	Sengwa (Z)	F&B	48	Flying (room)	–	105	138	33	2?	138	7	CF-FM
	Sengwa (Z)	FEN	48	Flying (room)	–	–	141.5 (2.7)	20.7	2?		8	CF-FM
	Luvuvhu (SA)	FEN	48	Flying (room)	–	–	145.4 (2.5)	27.7	2?		8	CF-FM
	Jozini Dam (SA)	HCA	48	Flying (open)	14	131 (7.3)	145 (0.2)	13.9 (7.4)	2?	143.5 (0.6)	6.2 (0.8)	CF-FM
H. commersoni	Sengwa (Z)	F&B	95	Flying (open)	–	55	62	7	2?	61	12	CF-FM
	Pafuri (SA)	A&R	95	Flying (open)	–	55	62	7	2?	61	12	CF-FM
Rhinolophidae:												
Rhinolophus clivosus	Dundee (SA)	RCL	52	Hand-held	21	73.9 (2.4)	94.3 (0.2)	20.4 (2.4)	2?	93.6 (0.1)	19.7 (2.6)	CF-FM
R. darlingi	Mlawula (SW)	RDA	46	Hand-held	10	80.4 (3.5)	86.2 (0.1)	5.8 (3.5)	2?	85.8 (0.2)	35.2 (3.9)	CF-FM
R. denti	Sengwa (Z)	F&B	42	Flying (room)	–	82	110	28	2?	110	15	CF-FM
R. hildebrandti	Sengwa (Z)	F&B	64	Flying (open)	-	24-29	37-46	17	2?	37-46	15	CF-FM
	Pafuri (SA)	A&R	64	Flying (open)	-	c 24	c 40	16	-	–	15	CF-FM
R. landeri	Pafuri (SA)	A&R	42	Flying (room)	–	105	110	5	2?	–	15	CF-FM
R. simulator	Sengwa (Z)	F&B	46	Flying (room)	-	64	78	14	2?	78	20	CF-FM
	Shongweni (SA)	RSI	46	Hand-held	10	69.1 (5.6)	82.7 (0.4)	13.6 (5.8)	2	81.8 (0.6)	17.5 (3.9)	CF-FM
R. swinnyi	Pafuri (SA)	A&R	43	Flying (room)	–	100	115	5	2?		15	CF-FM

1. Within the same sequence calls were recorded which emphasized either the fundamental or the first harmonic.
2. The first harmonic (200-208 kHz) in *Cloeotis percivali* exceeded the detection range of the Petterrson D980 bat detector but was demonstrated from recordings obtained simultaneously using an ANABAT detector (recordings made by D.S. Jacobs).
3. Species identification based on matching of unknown call sequences with sonograms from positively identified individuals.
4. Measurement of maximum and dominant frequencies (and therefore bandwidth) for *Myotis tricolor* was ambiguous, because of the effects of atmospheric attenuation of higher frequencies, and the difficulty of distinguishing fundamental from harmonic frequencies.
5. Duration taken for first discernible pulse in a 'train' of pulses (including possible echoes?); duration of composite call was much longer, *ca* 40–50 kHz.
6. Mean values of call parameters are presented; data obtained with permission of D. Jacobs.

Calls shown in Figure 1a and b represent low duty cycle bats (Fenton, Audet, Obrist & Rydell 1995); for example species which separate pulse and echo in time, to avoid deafening or jamming themselves by not broadcasting and receiving at the same time. Search call sequences of low duty cycle bats are characterised by inter-pulse intervals which greatly exceed the duration of individual calls. By comparison, high duty cycle bats (Figure 1c) separate pulse and echo in frequency so that they can broadcast and receive simultaneously. As a result, these bats can produce echolocation signals almost continuously, with inter-pulse intervals being shorter than call durations. High duty cycle bats typically use doppler shift compensation and an acoustic fovea to avoid deafening themselves, and also to enhance their sensitivity to the fluttering of insect wings (Fenton *et al.* 1995).

Figure 1a represents the families Emballonuridae, Nycteridae & Vespertilionidae. Calls are characteristically steeply frequency-modulated (FM). The shape of FM calls is highly distinctive and useful for identification (Fenton & Bell 1981; O'Farrell & Miller 1997; O'Farrell *et al.* 1999a). This was borne out in the present study. For example, the presence or absence of a 'heel', or 'bi-linear' call shape (present in *Scotophilus dinganii*, *Miniopterus schreibersii*, *Myotis tricolor*, *Pipistrellus rusticus*, *Pipistrellus nanus*, *Eptesicus melckorum* and *Eptesicus capensis*) and its shape and position, was found to be reasonably species-specific and constant within a species. The angle of the heel predicts accurately the dominant frequency (shown in parentheses in Figure 1) of FM bats. This was tested in two species where a distinct 'heel' was invariably present. In *E. capensis* and *S. dinganii* the dominant frequency was found to lie precisely on the angle, or the point of maximum curvature, of the heel in 91% (n = 11), and 86% (n = 21) of calls respectively, with mismatches occurring only in fragmented calls which tended to have no heel or a poorly defined heel. The length of the heel, and correspondingly, dominant wavelength, can show intraspecific variation, for example, due to habitat differences, as documented in *S. dinganii* (Figure 2: Table 1), but, where multiple calls have been measured for the same species under different conditions (e.g. *S. dinganii* and *M. schreibersii*) this variation does not appear to detract from the distinctiveness of a species call, particularly when the frequency range, call duration, and patterns of pulse production, are also simultaneously considered. Patterns of pulse production can be useful in certain instances; for example, calls of *Taphozous mauritianus* were emitted in two's or three's separated by longer intervals, while in *M. schreibersii*, minimum frequency followed a rising and falling pattern (contrary to most other species where it was remarkably constant), at least for recordings of one released individual

Certain broad-band FM species show a tendency for atmospheric attenuation of the higher frequencies, as indicated for *Miniopterus schreibersii*, *Myotis tricolor* and *Eptesicus capensis* in Figure 1a (shown by dotted lines), and as recognised by high variability in measurements of maximum frequency (see Table 1, and discussion below under *Quantitative approach*). This problem, which confounds species identification, has long been recognised (Griffin 1971). The sonogram

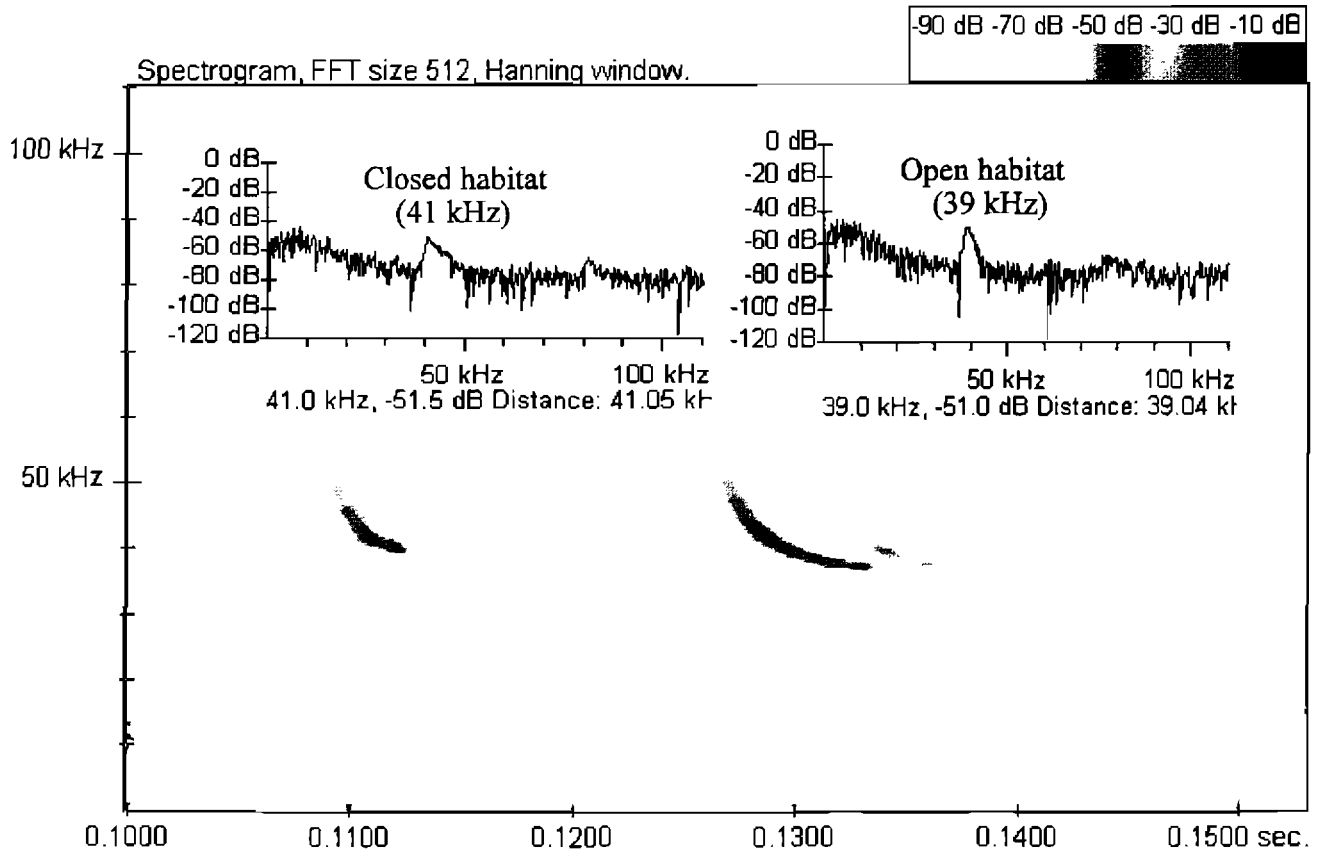

Figure 2 Sonograms of representative calls taken from different sequences of *Scotophilus dinganii* recorded in closed (left sonogram) and open (right sonogram) habitats at Biggarsberg, KwaZulu-Natal. Insets represent frequency-intensity graphs of the corresponding sonograms, depicting dominant frequency peaks. Note the longer 'heel' (and therefore longer call duration) and lower dominant frequency in the open habitat. Each interval on the horizontal time axis represents 10 ms

(Figure 1a) and data (Table 1) for *Eptesicus melckorum*, collected from individuals collected and released at the type locality of the species (Farm Kersefontein, Berg River, in the Western Cape), differs slightly in dominant and maximum frequency from calls of *E. capensis* recorded during this study, but this may be at least partly due to problems of high frequency attenuation in calls recorded at varying distances from the bat detector microphone. Kearney (personal communication) considers *E. melckorum* to be conspecific with *E. capensis* based on morphological and karyological data.

Figure 1b shows sonograms of free-tailed bats, family Molossidae. Calls tend to be longer in duration with shallower FM calls at a lower frequency than for the previous bats. Both *Chaerephon pumila* (CPU) and *Tadarida aegyptiaca* (TAE) showed the variable presence of either one or more harmonics (indicated in Figure 1b by a hatched fill).

Recordings of *Otomops martiensseni* were made as individuals emerged from a known roost in the roof of an apartment in Umbilo, Durban. A loud, audible (9–15 kHz), long-duration (28 ms) call, having up to three harmonics, and a very narrow bandwidth ('quasi constant frequency', or QCF) was emitted in pairs at emergence (Figure 1b). Published data for *O. martiensseni* indicate a very similar echolocation structure, although wide variation in call duration (5–30 ms) was reported (Fenton & Bell 1981; Table 1). Based on only three calls analysed, a distinct call structure was recorded from individuals released outside their roost in a residential house in Durban North (Table 1; not shown in Figure 1b); these QCF calls were of very long duration (57 ms), and ranged in mean frequency from 25–30 kHz (dominant frequency was 26 kHz). These calls did not appear to represent the second harmonic of the previous call type, since they produced second and third harmonics at around 50 kHz and 75 kHz. Based on its low echolocation frequency and the long, narrow wings, Rydell & Yalden (1997) predicted that the species should be a high-flying moth specialist, a prediction born out from dietary analysis.

Finally, sonograms of the high duty cycle bats belonging to the families Rhinolophidae and Hipposideridae (superfamily Rhinolophoidea) typically have high frequency, CF-dominated calls (Figure 1c). The highest known frequency for a CF bat is the hipposiderid, *Cloeotis percivali* (CPE) (212 kHz: Fenton & Bell 1981), which, in the present study, had a fundamental frequency of 104 kHz and a (predicted) second harmonic of 208 kHz. The frequency of the second harmonic exceeded the frequency threshold of the Pettersson bat detector, and only the fundamental component was visible, but the presence of a second harmonic was confirmed by means of the simultaneous recording of individuals of the same colony at Jozini Dam, using the ANABAT system (D.S. Jacobs, personal communication, 30th November 1997). A second hipposiderid included in this study, *Hipposideros caffer* (HCA), had a CF component of 144 kHz of relatively short duration, followed by a FM sweep.

Horseshoe bats (Family Rhinolophidae) tended to have longer duration calls than hipposiderids (Figure 1c), especially *Rhinolophus darlingi* (RDA) (40 ms), which had a CF portion at 86 kHz, and FM portions before and after; *R. simulator* (RSI) had a CF portion of 83 kHz followed by a FM sweep, while *R. clivosus* had a CF component of 94 kHz. In *R. simulator*, the FM component is probably a first harmonic as part of the FM sweep, is represented at half the frequency. It is well known that European *Rhinolophus* emphasize the second harmonic, with the fundamental component being much softer or even absent (Vaughan *et al.* 1997a).

Quantitative approach

Table 1 includes summary statistics for call parameters from a total of 283 individual calls contained in 34 sequences obtained from the 20 species included in the present study. Because of the small sample sizes of calls available for most sequences (mean of 7.9 calls per sequence), as well as the fact that data for 13 species were based on only a single individual, further quantitative analysis, such as discriminant analysis, principal component analysis, or analysis of variance (ANOVA), was not attempted. However, coefficients of variation (CV) of call parameters provide an index of the constancy of these variables within analysed sequences, and hence their usefulness for species identification. CVs for call duration were considerably higher (0% to 65.8%) than for minimum frequency (1.1–15.4%), maximum frequency (1.0–13.6%), dominant frequency (0.1–10.8%), and somewhat higher than for bandwidth (7.5–53.2%). Greater variability in temporal variables (call duration and inter-pulse interval) compared to spectral variables has also been noted by other workers (Obrist 1995; O'Farrell *et al.* 1999a). O'Farrell *et al.* (1999a) noted extremely low CVs for the genus *Pteronotus* for both minimum frequency (0–0.25%) and maximum frequency (0–0.34%), suggesting that these characters were highly reliable indicators of species identity. Similar values have been obtained in the present study for maximum frequency (0.1–0.5%) and dominant frequency (0.1–0.7%) for high duty cycle bats of the families Rhinolophidae and Hipposideridae, indicating their usefulness for species identification in these families. With the exception of *Miniopterus schreibersii*, in which minimum and dominant frequency appear relatively variable (CV 13.1–15.4% and 6.3–10.8% respectively), minimum frequency and dominant frequency appear to be less variable (and hence more useful) than maximum frequency in Nycteridae (2.9% and 1.8%, compared to 3.7%), Vespertilionidae (0.5–5.5% and 0.8–5.0%, compared to 1.0–13.0%), and Molossidae (2.8–7.0% and 1.9–9.9%, compared to 2.1–13.6%), probably owing to the effects of atmospheric attenuation on higher frequencies. The high CV for minimum frequency in *M. schreibersii* correlates with the observation of a 'rising and falling' pattern of pulses noted earlier for this species. D.S. Jacobs (personal communication) has also found high CVs for minimum frequency in recordings of *M. schreibersii* in two open habitats at De Hoop Nature Reserve in the Western Cape province of South Africa (8.8–14.1%), but not in a cluttered habitat (2.2%). In the Emballonuridae, minimum, maximum and dominant frequency have similar CVs (4.9–12.5%; 2.6–11.7% and 6.0–10.3% respectively).

Comparison with published data

Table 1 summarises data for 36 southern African species, based on the present study as well as the literature. Of the 36 species, eight have not previously been recorded, 12 are common to the present and previous studies, and 16 are based

entirely on previous studies. As such, comparison of data from species common to the present and previous studies provides a measure, either of measurement bias, or of intraspecific variation due to geographical, habitat or other factors. Strong concordance between the present and past studies, using very different techniques, would imply a measure of the robustness and usefulness of echolocation data for species identification. From Table 1, data from the present study show a high degree of concordance for the 12 species measured previously by Fenton & Bell (1981); Fenton *et al.* (1983); Fenton (1986); Aldridge & Rautenbach (1987) and D.S. Jacobs (personal communication), using very different equipment to the present study, in that close matches in frequency (< 5 kHz for at least two of the three frequency parameters) and call duration (<5 ms) were obtained for the following eight species: *Rhinolophus simulator*, *Cloeotis percivali* (although only the fundamental component was measured in this study, its multiple closely matches previous data for the second harmonic), *Miniopterus schreibersii*, *Pipistrellus nanus* (for type PNA2 but not PNA1; Table 1), *Eptesicus capensis*, *Scotophilus dinganii*, *Otomops martiensseni* (for OMA2 but not OMA1; Table 1) and *Tadarida aegyptiaca* (with the exception of call duration which was one half or less of that reported previously, but was also highly variable in this study: note high standard deviations reported in Table 1). The definition of a 'match' was somewhat arbitrary, and it is acknowledged that, for high duty cycle species where maximum and dominant frequencies are remarkably constant within a sequence of calls (Table 1), even small differences, such as reported for *R. simulator* between the present study (dominant frequency = 82 kHz) and Fenton & Bell (1981: dominant frequency = 78 kHz) may be significant.

Maximum and dominant frequencies (i.e. CF frequency) of *Hipposideros caffer* calls from individuals flying in inspection tunnels at Jozini Dam exceeded values reported by Fenton & Bell (1981) at Sengwa, by 6–7 kHz, but matched closely the mean CF frequencies recorded by Fenton (1986) at Sengwa and Luvuvhu (Table 1). Fenton (1986) reported a high degree of individual variation in the CF component of *H. caffer* recorded at Sengwa (137–144 kHz) and Luvuvhu (143–147 kHz). Pye (1972) further noted a bimodal distribution of CF frequency in hipposiderid bats, including *H. caffer*, from 130 kHz (Nigeria) to 160 kHz (Kenya).

Calls of *Nycticeinops schlieffeni* recorded from a free-flying individual in Swaziland matched published data from Sengwa and Pafuri very closely in dominant frequency and call duration, but exhibited a much narrower bandwidth and lower maximum frequency; but this apparent discrepancy is explained by the fact that previous authors cited the maximum frequency of the third harmonic (Fenton & Bell 1981: in their Table 1), whereas data for the fundamental component only was reported in the present study. Similarly, harmonic structure can explain the apparent discrepancies in present and previous data for *Taphozous mauritianus*. The presence

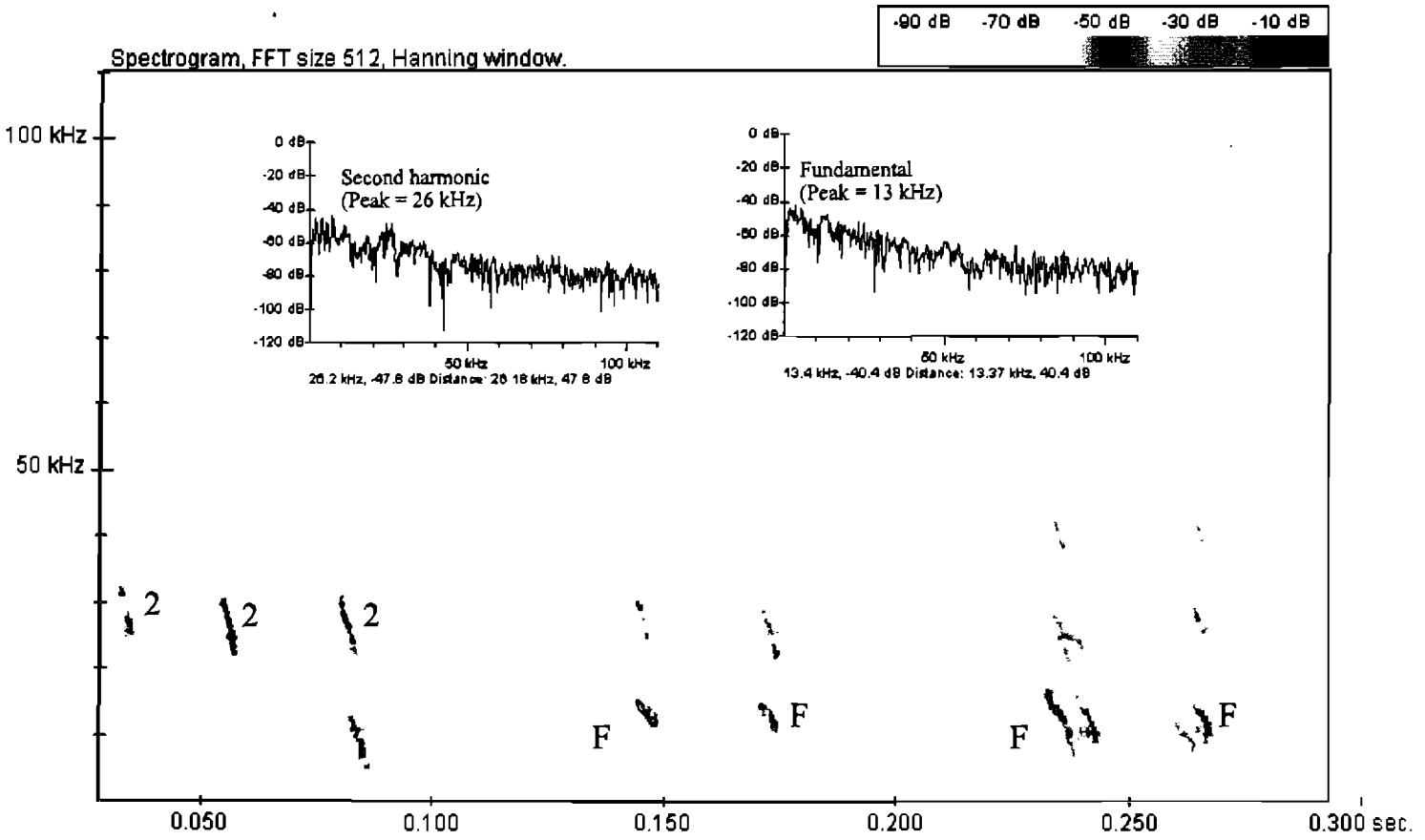

Figure 3 Sonogram showing portion of typical sequence of calls for *Taphozous mauritianus* recorded from an individual released and recorded at Mlawula, Swaziland. Each call is marked to indicate whether most energy is concentrated in the fundamental (F) or second harmonic (2) component. Insets represent frequency-intensity graphs of the third (left graph) and fourth (right graph) calls from the left, in which the second harmonic (dominant frequency = 26 kHz) and fundamental (dominant frequency = 13 kHz) components, respectively, are emphasized. Intervals on the horizontal time axis represent 50 ms

of a fundamental and two harmonics in the call of *T. mauritianus* recorded in the present study is shown in Figure 1a. The range of frequencies quoted for previous studies at Sengwa and Pafuri (12–59 kHz: Table 1) actually encompasses the fundamental as well as three additional harmonics (Fenton, Bell & Thomas 1980; Fenton & Bell 1981). The dominant frequency of 25 kHz cited by Fenton & Bell (1981: in their Table 1) closely matches the second harmonic in the present study. While the second harmonic was found to be emphasized in a hand-held captive individual in the present study, an individual recorded on release at Mlawula, Swaziland, alternated maximum energy between the fundamental and second harmonic; out of a sequence of 17 calls, five had most energy allocated to the fundamental component at 13–14 kHz, while the remaining 12 calls emphasized the second harmonic (Figure 3). In this study, calls were emitted typically in groups of three (second harmonic) or two (first harmonic) separated by longer inter-pulse intervals (Figure 3). This may indicate behavioural flexibility in this species, which would allow it to effectively decrease its echolocation frequency below 20 kHz in order to escape detection by tympanate (hearing) insects which are optimally sensitive to bat echolocation frequencies between 20 and 60 kHz (Fullard 1987). At the same time, using the alternative, higher frequency harmonic (25 kHz) confers the advantage of foraging in less open habitats, since lower frequencies are associated with fast-flying bats which require longer range detection of their prey, hence more open spaces. The long, narrow wings of *T. mauritianus* (and *T. perforatus*) suggest that the species is predominantly a high-flying, long-range aerial feeder (Rydell & Yalden 1997).

Another difference in the call of *T. mauritianus* between the present and earlier studies concerns the much shorter duration recorded in known-species recordings in the present study (2.5–4.0 ms, compared with 15–20 ms). However, an individual recorded fortuitously over water at Umbilo Park, Durban (in the general vicinity of known roosts of this species), was identified as *T. mauritianus* based on spectral call characteristics, harmonic structure (with calls alternating the fundamental and second harmonic) and the distinctive 'cadence' of calls (groups of two or three), and this individual demonstrated a call duration of 14–18 ms, much closer to the values recorded previously (Table 1).

Nycteris thebaica is known to use sounds emanating from its prey while hunting, although echolocation also seems to be important (Fenton *et al.* 1983). Calls of *N. thebaica* recorded in the present study are not immediately reconciled with published data (Table 1). Fenton & Bell (1981) recorded a range of frequencies from 61 to 97 kHz, and noted the apparent absence of any harmonics. However, the present study revealed a fundamental plus two harmonics in individuals foraging naturally in Swaziland (Figure 4). Because of the low intensity of calls of this species, recordings were made at very close distances (<1 m) as individuals emerged from a night roost. Both the fundamental (22 kHz), and to a slightly less degree, the second harmonic (44 kHz), were emphasized in the same calls; the third harmonic was usually very faint (Figure 4). Interestingly, the range of frequencies of the third

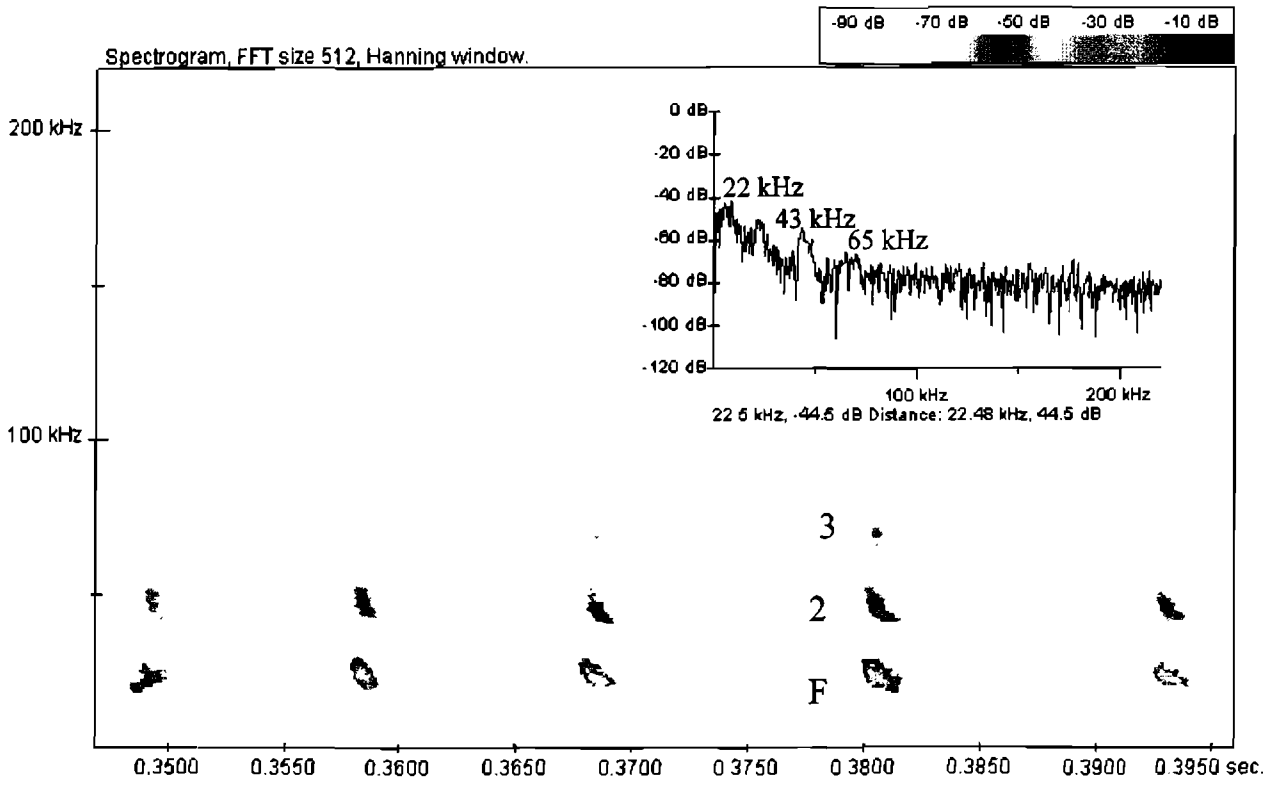

Figure 4 Sonogram showing portion of typical sequence of calls for *Nycteris thebaica* recorded from individuals foraging near a night roost at Mlawula, Swaziland. Fundamental (F), second (2) and third (3) harmonics indicated. Inset shows frequency-intensity graph for the fourth call from the left; three peaks (22, 43, and 65 kHz), coinciding with the fundamental, second and third harmonic, are indicated. Intervals on the horizontal time axis represent 5 ms

harmonic (62–72 kHz: see Figure 4) falls within the range given by Fenton & Bell (1981). The call of a related species, *N. grandis*, recorded by Fenton *et al.* (1983), on the other hand, comprises a fundamental component with a peak of 20 kHz, and up to three additional harmonics, that is very similar in structure to *N. thebaica* from Swaziland reported here (Figure 4). Fenton *et al.* (1983) found that the lower frequency components of the call are lost as the bat approaches its feeding target, leaving a band of 60–95 kHz, similar to their recorded range for *N. thebaica*. It is not clear why the lower frequency components of *N. thebaica* were recorded in the present, but not in previous studies (which nevertheless recorded them in a related species, *N. grandis*). Possibly, the individuals recorded leaving their night roost into the open in the present study were in non-foraging mode, and had no need for high frequencies to improve background perception; room-flown individuals used in previous studies may have perceived their immediate environment to be cluttered, requiring high frequencies.

Another feature of the sequence of *N. thebaica* calls shown in Figure 4 is the relatively short inter-pulse interval for an FM bat (five calls within 50 ms in Figure 4, compared to six calls in 600 ms for a typical sequence of *Scotophilus dinganii*, and seven calls in 250 ms for a typical sequence for *T. mauritianus*). Vaughan *et al.* (1987a) recorded similar calls (very short duration, steeply FM, with short inter-pulse intervals, and the presence of two harmonics) in another low-intensity, large-eared, gleaning species, *Plecotus auritus*. They further noted that this species sometimes diverted most of its energy into the second harmonic, as was reported for *N. thebaica* in the present study.

Room-flown and hand-held recordings

Although recordings from room-flown and hand-held bats are often assumed to contain little information of value (Barclay 1999; M.B. Fenton, personal communication), few published data seem to be available directly comparing these with more 'natural' calls. Recordings of four species of bats were obtained from individuals flying inside a room: *Pipistrellus rusticus*, *Eptesicus capensis*, *Scotophilus dinganii*, and *Chaerephon pumila*. Recordings of *Tadarida aegyptiaca* were obtained from an individual allowed to crawl freely along a ledge whilst 'echolocating'. Of the above five species, recordings of the latter four were additionally obtained from bats flying in their natural habitats, either after release (*E. capensis*), or in 'unknown' individuals recorded fortuitously whilst surveying feeding areas in the vicinity of known roosts of these species (*S. dinganii*, *C. pumila*, *T. aegyptiaca*), and identified from *a posteriori* analysis of sonograms and close matching with previously recorded room-flown bats, or with published data and sonograms (Table 1). From Table 1, the above-mentioned room-flown bats showed very similar spectral properties (usually varying by no more than 2–3 kHz), but much shorter call durations, compared with their naturally flying counterparts. In the larger-sized bats (*S. dinganii*, *C. pumila*, *T. aegyptiaca*), but not in the smaller species

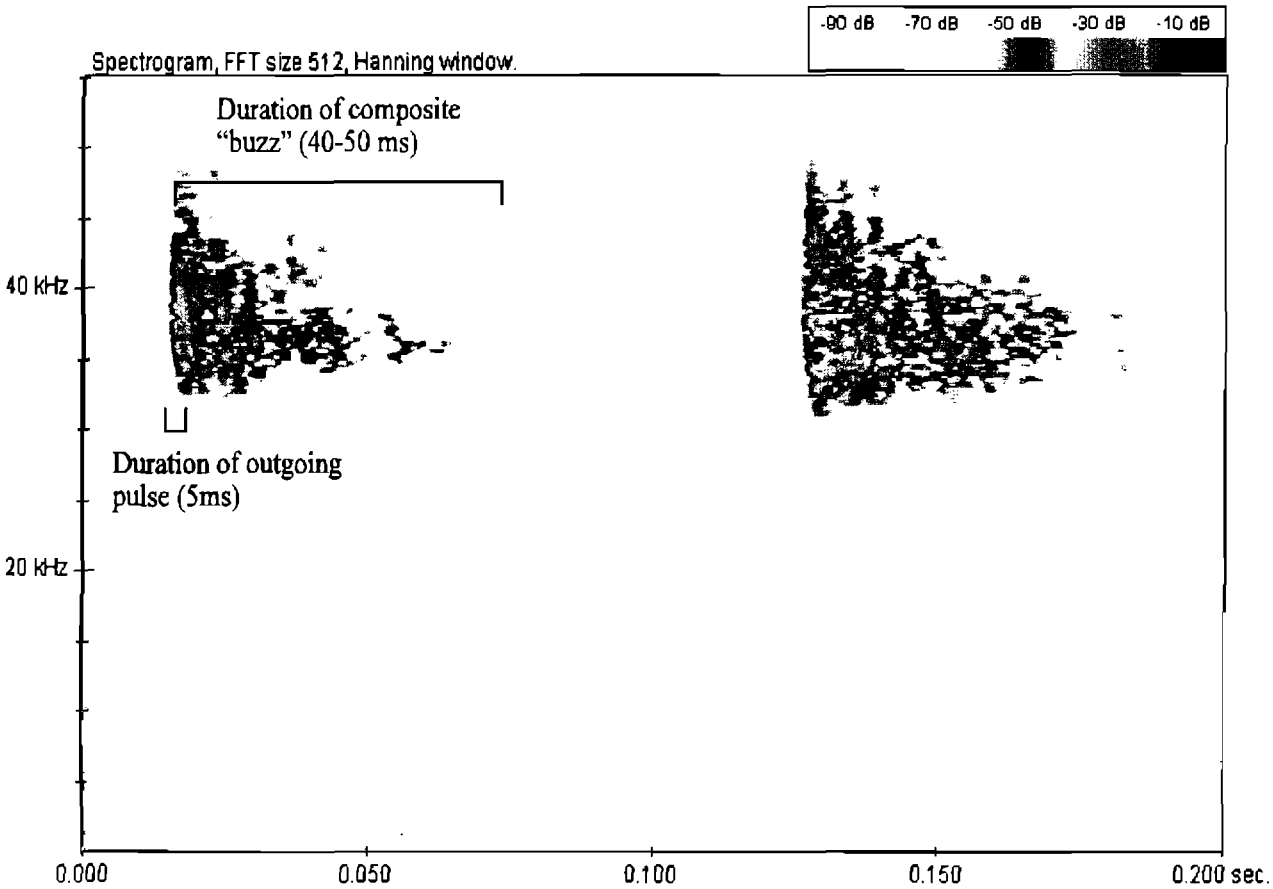

Figure 5 Sonogram showing portion of typical sequence of calls for *Scotophilus dinganii* recorded in a room. Note the extremely long (40–50 ms) 'buzz' which follows each short (5 ms) outgoing pulse. Intervals on the horizontal time axis represent 50 ms.

(*E. capensis* and *P. rusticus*), recordings made in a room tended to display long-duration composite 'buzzes' (possibly incorporating echoes), of some 40–50 ms (see footnote 5 in Table 1), of which only the initial short-duration pulse was assumed to represent the outgoing signal (see Figure 5).

Hand-held recordings were made from the following five species: *Taphozous mauritianus*, *Miniopterus schreibersii*, *Rhinolophus clivosus*, *R. darlingi* and *R. simulator*. In the case of the latter three CF species, which have constant maximum and dominant frequencies, heterodyne bat detectors were used in conjunction with the time expansion bat detector to verify the maximum and dominant frequencies of each species based on the audible output from individuals flying freely in their tunnel roosts. In the case of both *T. mauritianus* and *M. schreibersii*, call parameters agreed very closely with data obtained from bats of the same species recorded flying on release (usually within 1–2 kHz for frequency variables, or 1–2 ms for call duration: Table 1), indicating that calls emitted by hand-held bats may closely approximate genuine search phase echolocation calls emitted by foraging bats.

The above observations suggest that, at least for the few species studied here, representative echolocation calls may be produced from both room-flown and hand-held individuals, and this seems to apply to both low duty cycle and high duty cycle bats. However, such recordings should be checked against data from naturally foraging bats, and it should never be assumed that hand-held and room-flown recordings will represent natural echolocation calls for all species.

Intraspecific variation

Examples have been mentioned in passing in the above discussion. The effect of atmospheric attenuation of higher frequencies in broadband species is illustrated in Figure 1a (by broken lines), and reflected in high standard deviations for maximum frequency compared with minimum or dominant frequency for non-rhinolophoid species (Table 1, and above discussion). At least two sonic types have been found in both *Pipistrellus nanus* and *Otomops martiensseni*. Unfortunately, the small number of sequences available precludes a full explanation for these differences, but the presented data merely serve as a starting point for further investigation based on larger samples. Variation in harmonic expression within a single sequence has been demonstrated in *Taphozous mauritianus* (Figure 3).

Minor differences in call structure due to habitat were noted in *Scotophilus dinganii* from open (treeless) and closed (between tall gum trees and farm buildings) habitats, separated by less than 50 m, at the same locality (Figures 1, 2). D.S. Jacobs (personal communication) has demonstrated quite profound differences in calls of *Miniopterus schreibersii* foraging in open vlei (frequency range of 38–79 kHz; mean duration = 4.4 ms) and cluttered (54–95 kHz; duration = 2.2 ms) habitats. Yet, significantly, calls recorded by Jacobs in open vlei, using the ANABAT system (data included in Table 1), agree very closely with data obtained from bats released into a reasonably open habitat (open clearing surrounded by low farm buildings) at Kersefontein in the present study (Table 1), suggesting that variability in call structure may be largely related to gross habitat differences. Using nested multivariate analysis of variance (MANOVA) to analyse variation in six call parameters in four European species, Obrist (1995) found that, for most species, individual differences explained most of the observed variability in the data, followed by observation (repeated recordings of the same marked individuals), behavioural situation and, lastly, site effects. Sites comprised different-sized clearings within the same vegetation matrix, and significant differences in calls were noted in two species foraging within small and large clearings. However, gross habitat differences were not examined by this study. Although the effects identified by Obrist (1995) were statistically significant sources of intraspecific variability within each species, they did not prevent the clear-cut separation of the four species on their echolocation parameters using multidimensional scaling.

As noted above, call duration appears to be far more susceptible to intraspecific variation than do spectral parameters. This was most clearly indicated in the case of *Taphozous mauritianus*, where recordings of a hand-held, and a released individual exhibited much shorter calls (2–4 ms) than reported by published studies (15–20 ms; Table 1).

Conclusions

The echolocation data presented here for 20 southern African bat species show a high degree of concordance generally with previous studies. Eight species have not previously been reported for southern Africa, or elsewhere to my knowledge. Intraspecific differences were demonstrated in some of the species, but this was usually a result of widely differing recording methods (e.g. hand-held, flying in the open and in a room). Nevertheless, species generally possessed distinctive vocal signatures, especially when dominant frequency and harmonic information was considered.

Information on dominant frequency and the number of harmonics is considered to have been useful for species diagnosis in the present study. In the case of *Taphozous mauritianus*, *Nycteris thebaica*, *Nycticeinops schlieffenii* and *Otomops martiensseni*, having complete harmonic information clarified observed differences between published and current data, and between different sequences within a species obtained under different conditions during the present study. Where frequency bandwidths overlapped considerably, the dominant wavelength was sufficiently divergent to allow accurate species identification (e.g. between *Miniopterus schreibersii* and *Myotis tricolor*).

The findings of this study suggest that a time-expansion detector capable of retrieving harmonic and intensity information is optimal for the procedure of establishing a basic call library for each species. Thereafter, cheaper detectors such as the ANABAT II system, and heterodyne ('tunable') detectors relying only on audio output, should prove useful for routine identification of species in flight, as well as supplementing the call library. A trained observer is able to determine dominant frequency from audio output of a tunable detector. Furthermore, the shape of FM calls is often highly distinctive and can be used to predict dominant frequency, for example in many vespertilionid bats, the dominant frequency appears to coincide with the point at which the steep part of the slope flattens out at the lower frequencies.

It seems likely that, once a substantial and representative call library is established, preferably containing at least ten

individuals per species, and ideally employing calls from naturally-flying bats, routine accurate identification of most species from their vocal signatures using a variety of bat detectors will be possible. This is already proving feasible for the commoner species encountered in KwaZulu-Natal. Field identification using bat detectors will prove to be much simpler in species-poor communities, and more difficult in the more species-rich bat communities occupying savanna regions in the northern regions of southern Africa (Gelderblom, Bronner, Lombard & Taylor 1995).

Acknowledgements

Martyn Boonman and David Jacobs provided a great deal of technical assistance and fruitful discussions, and David Jacobs is thanked for the use of echolocation data on *Cloeotis percivali* and *Miniopterus schreibersii*. David Jacobs, Cassandra Miller, Mario and Michelle Di Maggio, Ara Monadjem, Teresa Kearney and members of the Durban Bat Interest Group assisted with the collection of some of the bats. The National Research Foundation (NRF) provided financial assistance for the purchase of the Pettersson D980 bat detector, and with field expenses, through a grant to the author.

References

ALDRIDGE, H.D.J.N. & RAUTENBACH, I.L. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *J. Anim. Ecol.* 56: 763–778.

BARCLAY, R.M.R. 1999. Bats are not birds – a cautionary note on using echolocation calls to identify bats: a comment. *J. Mamm.* 80(1): 290–296.

BARCLAY, R.M.R. & BRIGHAM, R.M. 1991. Prey detection, dietary niche breadth and body size in bats: why are aerial insectivores so small? *Am. Nat.* 137: 699–703.

BOWIE, R.C.K., JACOBS, D.S. & TAYLOR, P.J. 1999. Resource utilization by two morphologically similar insectivorous bats (*Nycteris thebaica* and *Hipposideros caffer*). *S. Afr. J. Zool.* 34(1): 27–33.

FENTON, M.B. 1985. The feeding behaviour of insectivorous bats: echolocation, foraging strategies, and resource partitioning. *Bull. Tvl. Mus.* 21: 5–19.

FENTON, M.B. 1986. *Hipposideros caffer* (Chiroptera: Hipposideridae) in Zimbabwe: morphology and echolocation calls. *J. Zool., Lond.* 210: 347–353.

FENTON, M.B., AUDET, D., OBRIST, M.K. & RYDELL, J. 1995. Signal strength, timing, and self-deafening: the evolution of echolocation in bats. *Paleobiology* 21(2): 229–242.

FENTON, M.B. & BELL, G.P. 1981. Recognition of species of insectivorous bats by their echolocation calls. *J. Mamm.* 62 (2): 233–243.

FENTON, M.B., BELL, G.P. & THOMAS, D.W. 1980. Echolocation and feeding behaviour of *Taphozous mauritianus* (Chiroptera: Emballonuridae). *Can. J. Zool.* 58: 1774–1777.

FENTON, M.B., GAUDET, C.L. & LEONARD, M.L. 1983. Feeding behaviour of the bats *Nycteris grandis* and *Nycteris thebaica* (Nycteridae) in captivity. *J. Zool., Lond.* 200: 347–354.

FULLARD, J.H. 1987. Sensory ecology and neuroethology of moths and bats: interactions in a global perspective. In: Recent advances in the study of bats (eds.) M.B. Fenton, P.A. Racey & J.M.V. Rayner. Cambridge University Press, United Kingdom.

GELDERBLOM, C.M., BRONNER, G.N., LOMBARD, A.T. & TAYLOR, P.J. 1995. Patterns of distribution and current protection status of the Carnivora, Chiroptera and Insectivora in South Africa. *S. Afr. J. Zool.* 30(3): 103–114.

GRIFFIN, D.R. 1958. Listening in the dark. Yale University Press, New Haven.

GRIFFIN, D.R. 1971. The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). *Anim. Behav.* 19: 55–61.

KUENZI, A.J. & MORRISON, M.L. 1998. Detection of bats by mist-nets and ultrasonic sensors. *Wildl. Soc. Bull.* 26(2): 307–311.

NORBERG, U.M. & RAYNER, J.M.V. 1987. Ecological morphology and flight in bats (Mammalia, Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Lond.* B316: 335–427.

OBRIST, M.K. 1995. Flexible bat echolocation: the influence of individual, habitat and conspecifics on sonar signal design. *Behav. Ecol. Sociobiol.* 36: 207–219.

O'FARRELL, M.J. & MILLER, B.W. 1997. A new examination of echolocation calls of some Neotropical bats (Emballonuridae and Mormoopidae). *J. Mamm.* 78(3): 954–963.

O'FARRELL, M.J., MILLER, B.W. & GANNON, W.L. 1999a. Qualitative identification of free-flying bats using the ANABAT detector. *J. Mamm.* 80(1): 11–23.

O'FARRELL, M.J., CORBEN, C., GANNON, W.L. & MILLER, B.W. 1999b. Confronting the dogma: a reply. *J. Mamm.* 80(1): 297–302.

PYE, J.D. 1972. Bimodal distribution of constant frequencies in some hipposiderid bats (Mammalia: Hipposideridae). *J. Zool., Lond.* 166: 323–335.

RHODES, M. & SCHNITZLER, H. 1998. Variation in echolocation call structure with changing clutter conditions: problems for identification. Abstract, 8th Australasian Bat Conference. *Bat Research News* 39 (1): 18.

RYDELL, J. & YALDEN, D.W. 1997. The diets of two high-flying bats from Africa. *J. Zool., Lond.* 242: 69–76.

SCHWENK, J. 1997. Application of ANABAT II to Pennsylvanian bat surveys. Abstract, 27th Annual North American Symposium on Bat Research, October 8–11, 1997, Tucson, Arizona. *Bat Research News* 38(4): 127–128.

THOMAS, D.W., BELL, G.P. & FENTON, M.B. 1987. Variation in echolocation call frequencies recorded from North American vespertilionid bats: a cautionary note. *J. Mamm.* 68: 842–847.

VAUGHAN, N., JONES, G. & HARRIS, S. 1997a. Identification of British bat species by multivariate analysis of echolocation call parameters. *Bioacoustics* 7: 189–207.

VAUGHAN, N., JONES, G. & HARRIS, S. 1997b. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *J. App. Ecol.* 34: 716–730.

WHYBIRD, O.J., COLES, R.B. & CLAGUE, C.I. 1998. Sexual dimorphism and the echolocation calls of *Hipposideros semoni*. Abstract, 8th Australasian Bat Conference. *Bat Research News* 39 (1): 21.