

ORIGINAL ARTICLE

Echolocation calls of high duty-cycle bats (Hipposideridae and Rhinonycteridae) from Kenya

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ABSTRACT

We describe the echolocation calls of six species of Hipposideridae: *Doryrhina camerunensis*, *Hipposideros beatus*, *H. caffer*, *H. ruber*, *Macronycteris gigas*, and *M. vittata* and two species of Rhinonycteridae: *Cloeotis percivali* and *Triaenops afer*. The recordings were made in Kenya during 2013-2018, using Pettersson D500X and D1000X real time, full spectrum bat detectors. All species used high-intensity constant-frequency echolocation of high duty-cycle. Most of them separate clearly in the constant-frequency component of the echolocation calls and can be recognized based on that feature alone. This study provides the first description of the echolocation calls of *D. camerunensis*, whereas those of *H. beatus*, *H. ruber*, and *C. percivali* from Kenya are also described for the first time. Additionally, call frequencies for some of these species differ from those of other parts of their range, demonstrating the need for collection and publication of more local call libraries from tropical regions.

INTRODUCTION

Bats (Mammalia: Chiroptera) are usually difficult to study in the field by direct methods such as visual observation or capture; in addition, available methods are usually severely biased with respect to species and habitat (Murray et al. 1999, Larsen et al. 2007, Meyer et al. 2011). In contrast, modern acoustic techniques involving ultrasound detectors allow eavesdropping on the ultrasonic signals generated by bats for navigation and prey detection, permitting assessment of species presence and behaviour. Acoustic methods are now used routinely in bat surveys and research throughout much of the world, sometimes in combination with other methods (O'Farrell & Gannon 1999, MacSwiney et al. 2008, Apoznanski et al. 2018, Musila et al. 2019a).

Bat detectors, instruments sensitive to the ultrasonic frequencies of bat calls, allow echolocating bats to be surveyed and recorded non-invasively (e.g. Webala et al. 2010) and results from such efforts often guide important wildlife management decisions and planning (e.g. Rydell et al. 2017). The use of bat detectors can provide more extensive data sets on bat occurrence and activity patterns than surveys based on other methods, although acoustic methods also have drawbacks. For instance, some species

are easier to detect and recognize than others, which can lead to biased samples (Meyer et al. 2011, Barataud 2015). Despite its great potential, acoustic sampling has been rarely used in bat surveys and monitoring studies in tropical Africa (but see Musila et al. 2019a). This is partly because acoustic identification of species requires reference call libraries that provide detailed descriptions of the echolocation calls of local species (Parsons & Szewczak 2009, Russ 2012).

Like most of tropical Africa, Kenya has a very rich bat fauna with well over 100 species (Patterson & Webala 2012, Musila et al. 2019b). However, bats are generally overlooked and their importance in ecosystems is unrecognized in Kenya, where they also remain without legal protection. Indeed, many caves and other important bat habitats are under severe threat from a growing human population and from rapidly expanding "development" for agriculture, human settlement, tourism and urbanization (Mwale 2000, Okello & Kiringe 2004).

There is no comprehensive guide to the echolocation calls of Kenyan or East African bats. Although relevant information exists for some species, this was collected over many years with the use of very different equipment, and hence is of variable quality (e.g. Novick 1958, Pye 1972, McWilliam 1982). Also, the information is often hard to

find, because it appears in many publications and recent summaries refer either to the entire African continent (Happold & Happold 2013) or to other regions in Africa (Monadjem et al. 2010). Our compilation is also motivated because there has been confusion about the identity and the corresponding echolocation calls in some previously recognized “species”. Observed bimodality in the frequency distribution of calls (Pye 1972) has been referred either to the presence of cryptic species or sexual differences (Jones et al. 1993, Taylor et al. 2005, 2012), and the situation is not yet clarified for many taxa.

The bats presented here all use a sophisticated form of high-intensity echolocation (Jones & Teeling 2006), employing long pulses with relatively short intervening intervals. It is called “high duty-cycle” echolocation, because the signal is “on” for a high proportion of the time (Lazure & Fenton 2011). Their hearing is characterized by the presence of “auditory foveae”, which correspond to the frequency of the echolocation calls. Both their hearing and the calls are dominated by a narrow frequency band (“constant frequency”; CF), and the echoes are Doppler-shifted when reflected by moving targets (Neuweiler 1989, Jones 1999). These characteristics provide a movement- or “flutter-detection” system and permit automatic rejection of the clutter (non-interesting echoes) arising from stationary targets such as the surrounding vegetation. This type of echolocation is particularly suitable for acoustically complex environments such as in dense vegetation or in narrow spaces (Bell & Fenton 1984, Lazure & Fenton 2011, Fenton et al. 2012). The echolocation calls of the high duty-cycle bats are loud and easily recorded in most cases, and once documented, the species identification is usually straightforward. These bats are therefore particularly suitable for acoustic monitoring by the use of automatic or manual bat detectors.

The high duty-cycle bats normally emphasize the second harmonic of the echolocation calls rather than the first, and thereby achieve higher frequencies (shorter wavelengths) and more detailed information. However, the first harmonic is sometimes apparent as well as the second and sometimes also the third and the fourth. True harmonics are multiples of the frequency of the fundamental (first) harmonic. The first harmonic probably facilitates the ranging performance and the third may have a similar function (Suga 2018).

Most features of bat echolocation calls are typically subject to considerable variation, depending not only on the species but also on the situation, habitat and what the bat is doing, and are therefore of limited diagnostic value (Schnitzler & Kalko 2001, Denzinger & Schnitzler 2013). On the other hand, the frequency of the CF-component in high duty-cycle bats is strongly species-specific and therefore suitable for species recognition. Hence, we concentrate most of the species accounts and the discussion on this feature.

In an effort to stimulate interest in bats and their conservation in Kenya and tropical Africa in general, we provide an acoustic identification guide to the Hipposideridae and Rhinonycteridae, two families of “high-duty-cycle” bats. The main purpose is to facilitate research and conservation

of bats in East Africa. The immediate aims are to a) provide a comprehensive guide to the identification of the Hipposideridae and Rhinonycteridae of Kenya for acoustic surveys and monitoring, and b) add new information about the frequency distribution for several poorly known species.

MATERIALS AND METHODS

The recordings for this compilation were made during many expeditions throughout most of the accessible parts of Kenya (Fig. 1, Table 1) over several years (2013–2018), and opportunistically cover all parts of the year. Bats were captured at roosts using standard hand nets, or in natural flyways using harp traps or mist nets set at ground level or triple high nets, as they dispersed, foraged, and drank at night. Identification to species followed keys in Patterson & Webala (2012), sometimes consulting other sources directly in the field (e.g. Monadjem et al. 2010). In some cases, where bats were recorded while flying freely inside a cave or along a trail in the forest, we attempted to capture and identify at least one individual at the same site for identification of species and sex. Some of them were also recorded in the hand or in the flight cage (see below) and photographed close up, using a Canon 5D with a 100 mm Canon macro lens and a ring flash. The identifications were documented by voucher specimens deposited at the National Museums of Kenya (Nairobi).

Echolocation calls were recorded from bats held in the hand ca. 30 cm away from the microphone of either Pettersson D500X or D1000X bat detectors (Pettersson Elektronik AB, Uppsala, Sweden - www.batsound.se) at sampling frequencies of either 384 kHz or 500 kHz, and with variable gain settings. We recorded mostly hand-held bats because the “resting frequency” of such non-moving individuals shows very little variation within a sequence (because there is no Doppler-shift compensation; see below) and therefore is most suitable for frequency comparisons between individuals or populations. A few bats were also recorded while flying in a 32 m³ portable cloth flight chamber. However, because we aimed to provide a practical field guide to the echolocation calls, we also recorded free-flying individuals, as such calls better represent what is obtained during a field survey. Recordings from bats in flight show higher variation in frequency because of Doppler shift compensation, which involves a slight lowering of the frequency by the bat to control for the frequency-shift caused by its own movement (Schnitzler 1973, Neuweiler 1989).

The recorded sequences were usually three seconds long but sometimes much longer (up to ca. 30s), depending on the recording situation. They were stored as .wav files and later analysed using the software BatSound 4.3 (Pettersson Elektronik, Uppsala, Sweden). For each recording we usually analysed a sequence of ten consecutive “search-phase” pulses with good signal-to-noise ratio. The pulse duration was defined as including both the CF- and FM-components. The duty cycle was measured as the mean duration of the pulse divided by the mean duration of the pulse plus the pulse interval (Lazure & Fenton 2011). This was done for ten pulses per sequence. The peak frequency of the CF-component (F_{max}) was measured using the power spectrum

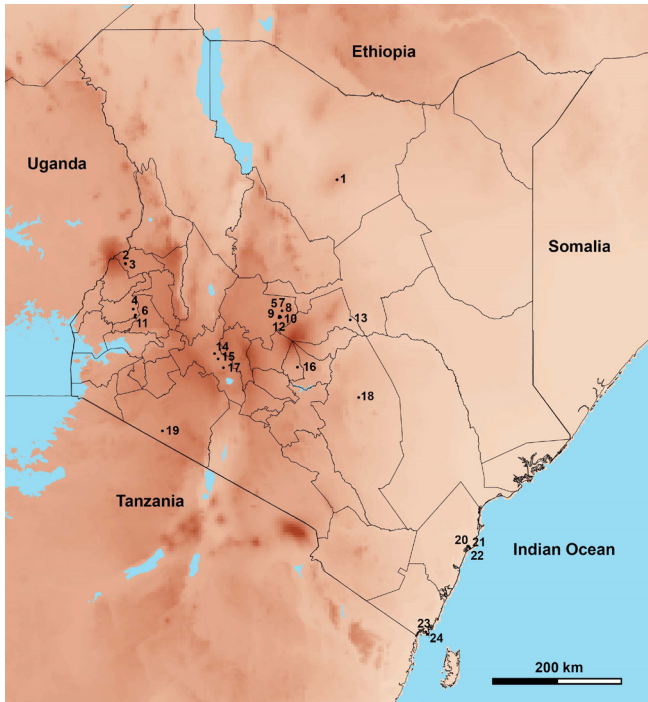


Fig. 1 - Map of Kenya indicating localities where bats were captured for echolocation call recordings. The projected borders within Kenya are counties and the background correspond to a digital elevation model.

analysis function of BatSound. The data are given as means for each recorded sequence or range of means when several recordings were included. We employed simple non-parametric statistics (Sokal & Rohlf 1981) when necessary.

SPECIES ACCOUNTS

Family Hipposideridae

Hipposideros beatus K. Andersen, 1906

Like the other small *Hipposideros*, this rainforest species uses short (7-9 ms) echolocation calls of high frequency (114-124 kHz) and high repetition rate, each pulse ending in a steep FM-component (Fig. 2A). The frequency of the CF-component was very consistent within each individual (variation 0.0-0.2 kHz) but varied between them by as much as 10 kHz (Table 2). It seems unlikely that the observed difference is related to sex (in contrast to *H. ruber*, see below and Jones et al. 1993), but our sample size is too small to exclude this possibility. The CF band employed by *H. beatus* is distinctly lower than in the other small *Hipposideros* in Kenya (*H. caffer* and *H. ruber*), so *H. beatus* can be recognized easily based on this character alone.

Table 1 - Localities in Kenya where bats were captured for echolocation call recordings. The localities are numbered sequentially from north to south. Co-ordinates are given in decimal degrees, and elevation above sea level is recorded in meters.

N°	Locality	Site	County	Latitude	Longitude	Elevation
1	Marsabit Forest Reserve	Marsabit Camp	Marsabit	2.3203	37.9941	1346
2	Mt. Elgon National Park	Makingeny Cave	Trans-Nzoia	1.0355	34.7530	2374
3	Mt. Elgon National Park	Kitum Cave	Trans-Nzoia	1.0294	34.7558	2362
4	Kakamega Forest Reserve	Salazar Trail	Kakamega	0.3351	34.8740	1558
5	Lolldaiga Hills Conservancy	Kibirutu Camp	Laikipia	0.3082	37.1525	1816
6	Kakamega Forest Reserve	Mahiakalo Mine	Kakamega	0.2445	34.9069	1641
7	Lolldaiga Hills Conservancy	Shaita Valley	Laikipia	0.2283	37.1130	2027
8	Lolldaiga Hills Conservancy	Munanda Dam	Laikipia	0.2268	37.1174	2030
9	Lolldaiga Hills Conservancy	Farm house	Laikipia	0.2131	37.1299	2099
10	Lolldaiga Hills Conservancy	Main house	Laikipia	0.2121	37.1218	2139
11	Kakamega Forest Reserve	Lirhanda Mine	Kakamega	0.2118	34.8986	1391
12	Lolldaiga Hills Conservancy	Simba Camp Dam	Laikipia	0.2038	37.1047	2223
13	Meru National Park	Kinna Hq	Meru	0.1715	38.1964	189
14	Nakuru National Park	Lion Hill Cave	Nakuru	-0.3459	36.1192	1816
15	Gilgil	Diatomite Mine	Nakuru	-0.4301	36.1737	1900
16	Mururi	Nyamindi River Cave	Kirinyaga	-0.5552	37.3881	1374
17	Thome	Jaika Cave	Nakuru	-0.5637	36.2542	1945
18	Mwingi	Nuu Mwola Dam	Kitui	-1.0190	38.3260	723
19	Maasai Mara National Reserve	Sarova Mara	Narok	-1.5311	35.3205	1764
20	Arabuko-Sokoke National Park	Campsite	Malindi	-3.3001	39.9951	70
21	Gede-Watamu	Gede Village	Malindi	-3.3022	40.0108	29
22	Watamu	Kaboga Cave	Malindi	-3.3345	40.0307	19
23	Fikirini	Three Sisters Caves	Kwale	-4.6149	39.3538	9
24	Shimoni	"Slave Cave"	Kwale	-4.6472	39.3804	-2

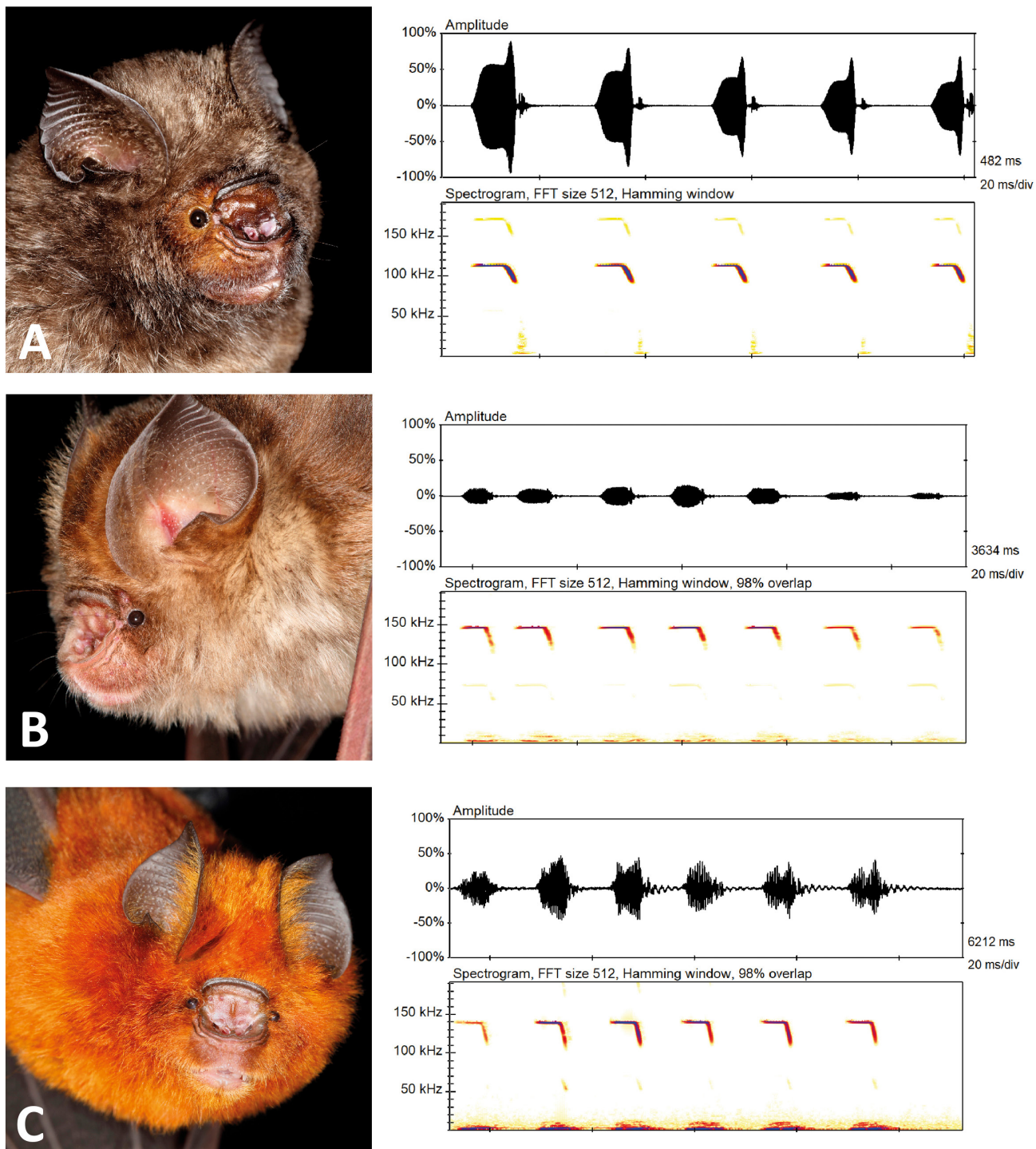


Fig. 2 - Portrait, oscillogram and spectrogram of three free-flying small *Hipposideros* spp. from Kenya; *Hipposideros beatus* from Kakamega forest (A), *Hipposideros caffer* from Gilgil (B) and *Hipposideros ruber* from Kakamega forest (C). The sound panels are 100 ms.

This seems to be the first report of *H. beatus* occurrence in Kenya. The species has been found in Uganda (Happold & Happold 2013) although, as far as we know, there are no previous recordings of *H. beatus* from East Africa. Calls from the Ivory Coast have CF-components at 139-147 kHz, about 20 kHz higher than in Kenya, but this population is recognized as a different subspecies (Happold & Happold 2013).

***Hipposideros caffer* (Sundevall, 1846)**

This is a small bat that occurs throughout much of Kenya's savannas but also in some forested areas, including

Mt Elgon and Marsabit. It uses short pulses (5-10 ms) with CF-components that are generally higher in frequency (145-156 kHz) than in *H. beatus* and *H. ruber*. The calls are emitted at high repetition rate and typically include a terminal FM-component (Fig. 2B, Table 2). The CF-component of *H. caffer* in our study was relatively consistent in frequency between localities and individuals, varying by ca 10 kHz.

For comparison, Pye (1972) recorded CF-components of 146.5-159.7 kHz in a single cave (Shimoni Cave) and 136.7-152.5 kHz in Uganda. As in *H. beatus*, but in contrast to *H. ruber*, there is no indication of variation in frequency related to sex ($P > 0.05$, Mann-Whitney U-test). From Gambia

to Malawi, the CF of *H. caffer* varies by as much as 24 kHz (Happold & Happold 2013). However, it should be kept in mind that *H. caffer* may be a complex of several cryptic species, replacing themselves across Africa (Vallo et al. 2008).

***Hipposideros ruber* (Noack, 1893)**

Like other small *Hipposideros* species, *H. ruber* uses short echolocation calls of high frequency (132-145 kHz) and fast repetition rate, ending in a steep FM-component (Fig. 2C Table 2). The frequency of the CF-component is intermediate between *H. beatus* and *H. caffer*, but there is a slight frequency overlap with *H. caffer* at ca 145 kHz. The frequency distribution is bimodal, with females using higher frequencies than males (Jones et al. 1993). In our sample, the CF-components were at 132-135 kHz in males and 140-145 kHz in females (Table 2). However, our sample size was too small for a meaningful statistical test.

There was no previous information about the echolocation calls of this species from East Africa. The CF varies between 132 and 144 kHz across Africa, i.e. from Gambia (Jones et al. 1993) to Malawi (Happold & Happold 2013). This variation is almost the same as within our single study locality (Kakamega) and is probably attributable to sexual dimorphism.

***Hipposideros megalotis* (Heuglin, 1862)**

This enigmatic species occurs in Kenya, Somalia, Eritrea and Ethiopia (Happold & Happold 2013, Lanza et al. 2015). We did not encounter it during our survey and its echolocation calls remain undescribed. It is a small bat (forearm 34-38 mm) with very large ears (50% of forearm length), linked at the base by a low fold across the crown. The small upper premolar is absent (Patterson & Webala 2012; illustration in Lanza et al. 2015).

***Doryrhina camerunensis* (Eisentraut, 1956)**

We found this unusual rainforest species only at Kakamega forest in western Kenya. It is considerably larger than the previous species and uses much longer (23-28 ms) echolocation calls of lower frequencies (ca 51 kHz) and slower repetition rate (Fig. 3, Table 2). Like other *Hipposideridae*, its calls typically feature a terminal FM-component of various amplitude and frequency content. This is the first description of the echolocation calls of this species. Its taxonomy was recently revised (Foley et al. 2017).

***Doryrhina cyclops* (Temminck, 1853)**

We did not encounter this species, so this account relies entirely on other published sources. This is a medium-sized species (forearm 59-71 mm) with a rather characteristic appearance. The antorbital foramen is relatively large (Patterson & Webala 2012). The echolocation calls of *D. cyclops* have not been recorded in Kenya, but it is reported to use CF-components at 51.4±0.5 kHz (n=6) in Uganda (Monadjem et al. 2011) and 59.7 kHz (range 58.4-60.8 kHz) in West Africa (Decher & Fahr 2005).

Genus *Macronycteris*

Pye (1972) recorded two “phonotypes” of big *Hipposideros* in two caves in coastal Kenya and this observation together with those of McWilliam (1982) in Shimoni and Similani caves suggested that two “species” (“*H. commersoni*” and “*H. gigas*”) occurred together in these caves. The two were clearly separated by distinct and non-overlapping frequencies of the CF-components (Table 3). Both are strongly sexually dimorphic but in each species, the sexes use similar frequencies. The two forms recorded by Pye (1972) were subsequently referred to *Hipposideros gigas* and *H. vittatus*, respectively, with the former being larger and using lower frequencies (Guillen-Servent 1996). These bats were recently transferred to the genus *Macronycteris* (Foley et al. 2017).

***Macronycteris gigas* (Wagner, 1845)**

We captured and recorded two females and three males of *H. gigas*, and we observed and recorded them inside Shimoni Slave Cave. In this cave, two colonies of “large *Hipposideros*” indeed occur adjacent to each other, one of *M. gigas* and one of *M. vittata*. The calls of *H. gigas* are typical of the *Hipposideridae* in being relatively short (12-15 ms) and of high frequency (ca 55 kHz), at least relative to the very large size of the bat. The calls also have the terminal FM-component typical of the *Hipposideridae* (Fig. 4A, Table 2).

***Macronycteris vittata* (Peters, 1852)**

This species is more common than *M. gigas* in Kenya and we found it in several caves along the coast and also in Meru and Isiolo counties inland. The echolocation calls are very similar to those of the larger *M. gigas*, except that the CF-components are consistently of higher frequencies (64-70 kHz as compared to ca 55 kHz; Fig. 4B, Table 2). The terminal FM-components are of variable amplitude and frequency extent and this applies to both species. As in *M. gigas*, the sexes use the same frequency despite a considerable size dimorphism (Table 3, Guillen-Servent 1996; in our sample $P > 0.05$, Mann-Whitney U-test).

Family *Rhinonycteridae*

***Cloeotis percivali* Thomas, 1901**

This is a very small bat and it uses the highest CF of any bat known. There is no previous information on the echolocation calls of this species from Kenya (Happold & Happold 2013). We obtained a single recording from a resting individual belonging to a colony in Fikirini caves and also captured and recorded a male and a female in the hand. The calls were short and emitted at high repetition rate and with a terminal FM-component. The CF-components of these individuals were at 217-225 kHz (Fig. 5A, Table 2).

The frequency of the CF-component of *C. percivali* in southern Africa is 208-213 kHz (Monadjem et al. 2010), slightly lower than in Kenya, perhaps indicating that there may be two forms. The species was named from an individual collected near Mombasa, so the Fikirini calls probably document the typical condition.

Table 2 - Means or range of means of echolocation sequences measurements of different species and localities in Kenya. N is the number of individuals and n the total number of sequences analysed.

Species	Locality	Recording conditions	Sex	Duration (ms)	Duty cycle (%)	F _{max} (kHz)	N (n)
<i>Hipposideros beatus</i>	Kakamega forest	Hand-held	Female	7.0-9.1	18-40	114.8-123.7	3 (8)
		Hand-held	Male	8.0-8.4	35-43	124.0	2 (3)
<i>Hipposideros caffer</i>	Fikirini caves, Kwale	Free-flying	-	8.2-9.7	44-63	148.9-143.5	5 (5)
	Kaboga cave, Watamu	Flight-cage	Male	5.4-8.9	34-65	147.4-150.2	2 (4)
	Lion Hill cave, Nakuru	Free-flying	-	6.7-7.7	43-83	151.1-153.6	2 (2)
	Nuu Dam, Kitui	Hand-held	Female	8.9-9.7	31-40	150.9	1 (3)
	Marsabit Forest	Hand-held	Male	9.0-10.6	20-35	155.8	1 (3)
	Makinyeny cave, Mt Elgon	Hand-held	Female	5.0-7.0	60-61	147.5	1 (2)
		Hand-held	Female	7.2-9.0	25-32	146.3	1 (3)
	Jaika cave, Thome	Hand-held	Male	7.1-9.5	27-62	145.7	1 (3)
		Hand-held	Male	6.9-8.2	33	145.0	1 (2)
	Nyamidi cave, Kirinyaga	Hand-held	Female	7.9-9.5	29-52	145.5-149.4	3 (3)
Hand-held		Male	8.5-9.6	38-50	145.6-149.3	3 (3)	
<i>Hipposideros ruber</i>	Mahiakalo mine, Kakamega	Hand-held	Male	7.4-8.8	15-32	132.6-134.5	3 (3)
	Lirhanda mine, Kakamega	Hand-held	Female	7.3-7.7	35	140.4-145.3	2 (2)
<i>Doryrhina camerunensis</i>	Kakamega forest	Hand-held	Female	24.5-27.7	23-35	50.8	1 (3)
		Hand-held	Male	23.1-27.1	37-49	51.1	1 (3)
<i>Macronycteris gigas</i>	Shimoni cave, Kwale	Resting	-	12.3-14.6	47	54.8-55.3	2 (2)
		Hand-held	Female	17.1-19.2	11-26	53.4-54.3	2 (2)
		Hand-held	Male	10.4-15.7	22-33	53.4-54.1	3 (3)
<i>Macronycteris vittata</i>	Arabuko-Sokoke forest	Flight cage	Female	10.6-16.5	18-49	69.3-69.7	2 (8)
		Hand-held	Female	14.6-17.6	24-42	68.2-69.2	2 (5)
	Kaboga cave, Watamu	Hand-held	Male	14.3-17.9	25-47	67.9-70.1	2 (6)
		Hand-held	Female	15.2-17.8	18-35	69.6	1 (3)
		Hand-held	Female	11.2-12.6	22-36	64.3-64.8	2 (3)
<i>Cloeotis percivali</i>	Fikirini caves, Kwale	Resting	-	3.9	28	217.1	1 (1)
		Hand-held	Female	4.0	29	225.3	1 (1)
		Hand-held	Male	4.0	40	219.6	1 (1)
<i>Triaenops afer</i>	Kaboga cave, Watamu	Flight-cage	Female	7.6-8.4	23-47	82.5	1 (3)
		Flight cage	Male	8.2-10.0	15-40	75.2	1 (4)
	Lolldaiga Hills, Laikipia	Hand-held	Male	9.0-10.4	13-20	75.7	1 (2)
		Hand-held	Female	12.2	9	83.9	1 (1)
		Hand-held	Male	8.4-12.2	5-25	30.1	1 (3)
		Free-flying	-	7.9-10.8	32-47	88.2-91.2	5 (5)

***Triaenops afer* Dobson, 1871**

This species uses rather short echolocation calls with high repetition rate, variable CF-component at 75-88 kHz and with a terminal FM-component (Fig. 5B, Table 2). The CF-component has a distinctly bimodal distribution, with females using higher frequencies (82-84 kHz in our sample)

than males (70-75 kHz). A similar bimodal distribution was also recorded in Kenya by Pye (1972), with males using 75-78 kHz and females 85-88 kHz. The situation is similar in Malawi (Happold & Happold 2013). Sexual differences in echolocation call frequency does not seem to be related to size, as the sexes are similar (Happold & Happold 2013).

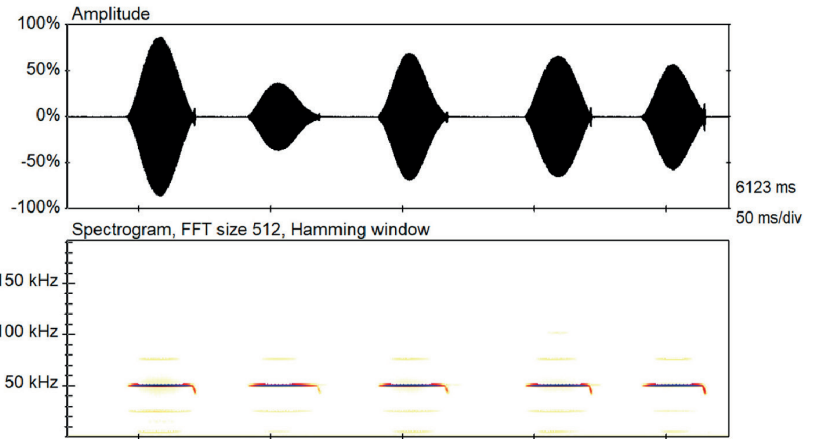


Fig. 3 - Portrait, oscillogram and spectrogram of echolocation calls of a hand-held *Doryrhina camerunensis* male from Kakamega forest. The panel is 250 ms.

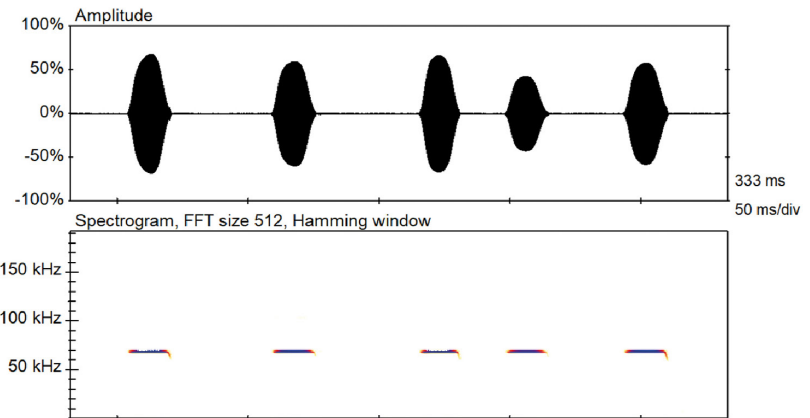
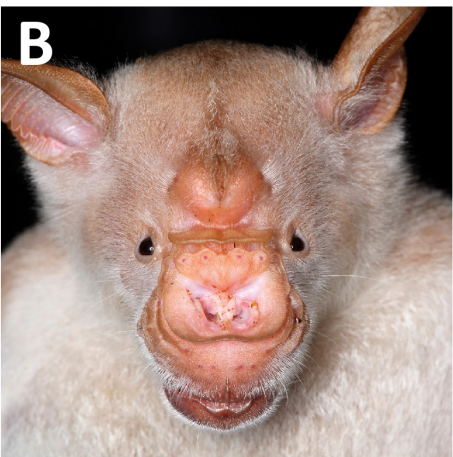
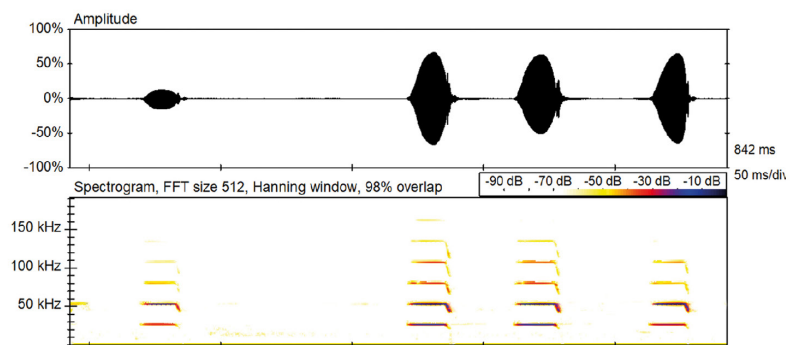
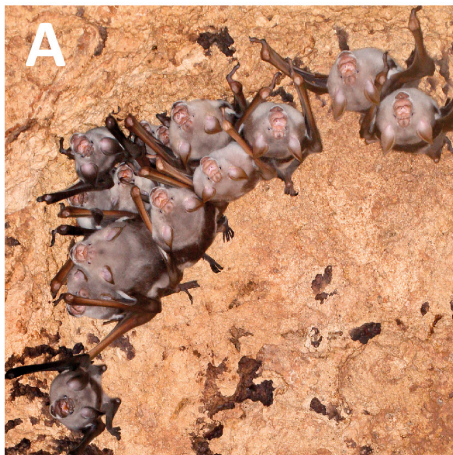


Fig. 4- Oscillogram and sonagram from a hand-held *Macronycteris gigas* at Shimoni cave (A) and a hand-held female *Macronycteris vittata* from Gede village (B). The panels are 250 ms. The pictures show a group of *M. gigas* in the ceiling of Shimoni cave (A) and a portrait of an adult male *M. vittata* from Sokoke Arabuko forest (B).

DISCUSSION

In accordance with other studies, our data show that the most useful feature in acoustic species determination in high duty-cycle bats is the frequency of the CF-component, which remains almost constant within an individual (Schnitzler & Kalko 2001, Denzinger & Schnitzler 2013, Fenton et al. 2012). Other features such as pulse duration, duty cycle and different frequency measurements are of much lower value for species recognition.

The echolocation calls of the Hipposideridae and Rhinonycteridae are much shorter than those used by sympatric horseshoe bats Rhinolophidae, and the pulse length can be used to recognize the former families. A consistent lack of an initial FM-component but presence of a terminal one is another diagnostic feature of hipposiderid and rhinonycterid calls. Rhinolophid calls usually have both (Henson et al. 1987). The FM-components are used for ranging and therefore, the bandwidth is broad when the bat is flying (e.g. Fig. 2) but weak and narrow when it hand-held or resting (e.g. Fig. 3).

Table 3 - Means and SD of the constant-frequency (CF) portion of the echolocation calls and forearm length (FA) of *Macronycteris gigas* and *M. vittata* from Shimoni and Similani caves in coastal Kenya, as recorded by others (data extracted from various sources by [Guillen-Servent 1996](#)). The two species were described as *Hipposideros gigas* and *H. commersoni*, respectively. However, *H. commersoni* is now considered to be restricted to Madagascar, and mainland African forms are referred to *M. vittata*.

Locality	Sex	CF	FA	Species
Shimoni	female	53.0+0 (<i>n</i> = 3)	109.2+2.5 (<i>n</i> = 43)	<i>M. gigas</i>
	male	53.9+1.4 (<i>n</i> = 14)	116.1+2.6 (<i>n</i> = 69)	<i>M. gigas</i>
	female	64.8+1.9 (<i>n</i> = 13)	93.0+2.3 (<i>n</i> = 59)	<i>M. vittata</i>
	male	64.2+1.1 (<i>n</i> = 13)	101.8+2.2 (<i>n</i> = 80)	<i>M. vittata</i>
Similani	male	54.0+0.5 (<i>n</i> = 10)	116.4+2.4 (<i>n</i> = 11)	<i>M. gigas</i>
	female	69.7+0.5 (<i>n</i> = 6)	90.9+2.0 (<i>n</i> = 68)	<i>M. vittata</i>
	male	67.5+1.3 (<i>n</i> = 4)	99.1+2.8 (<i>n</i> = 73)	<i>M. vittata</i>

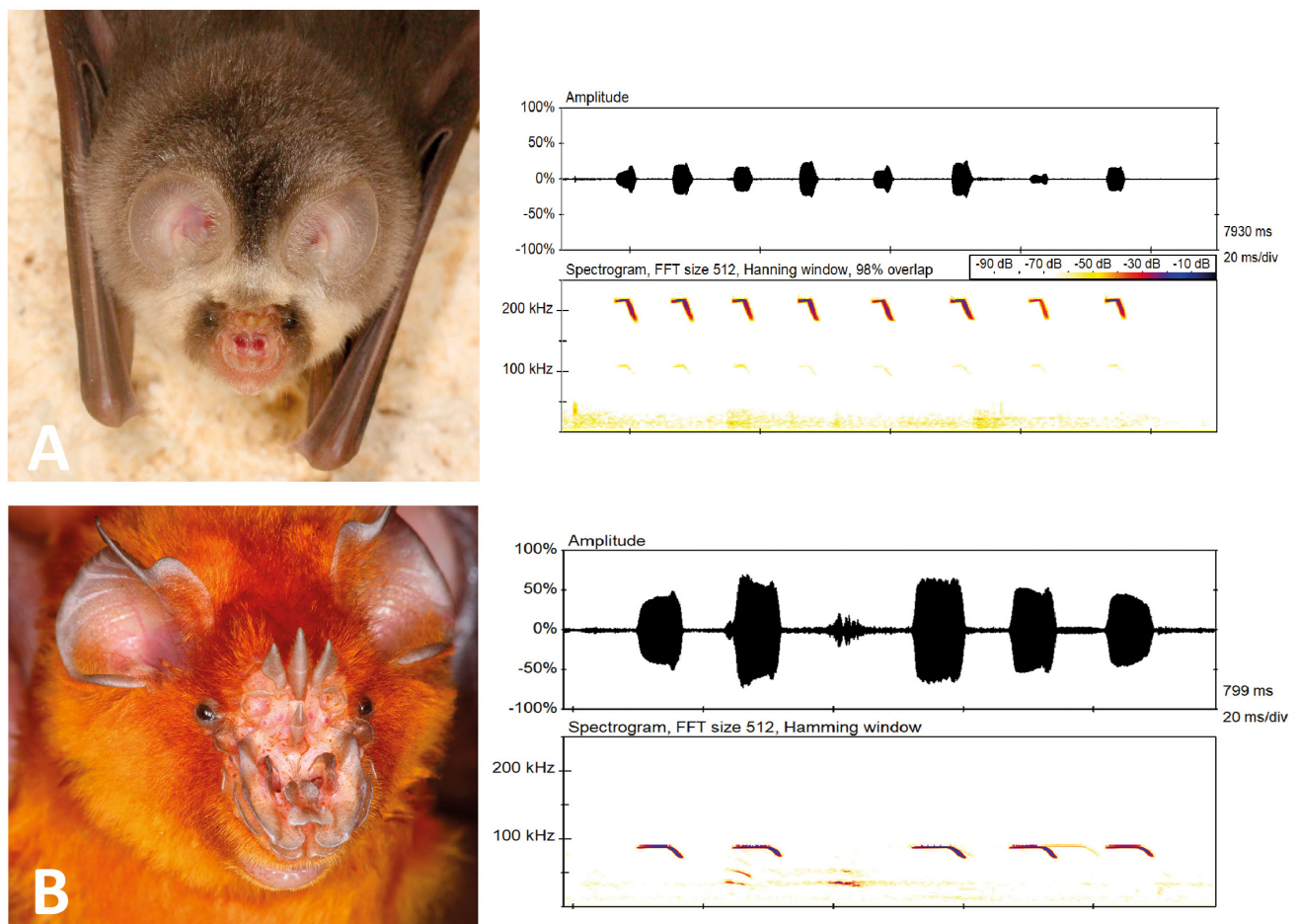


Fig. 5- Portrait, oscillogram and spectrogram from two free-flying Rhinonycteridae from Kenya; *Cloeotis percivali* from Fikirini caves (A) and *Trienops afer* from Kaboga cave (B). The sound panels are 100 ms.

We concentrated most of our attention on variations in the CF-frequency within and among species, and how it can be used to identify them. We used both the resting-frequencies, i.e. of hand-held individuals, and for some species also the frequency recorded in flight either in a flight cage or free-flying. The latter is expected to show more variation than the resting frequency, because it also includes the variation due to Doppler shift compensation ([Schnitzler 1973](#), [Neuweiler 1989](#)).

The CF-bands used by the different species are in most cases unique within Kenya, so the species can be

identified using this feature alone. The three species of small *Hipposideros* (*H. beatus*, *H. caffer* and *H. ruber*) can be distinguished by their high CF-frequencies (>110 kHz), very short pulses (<10 ms), and fast pulse repetition rates. *H. ruber* and *H. caffer* slightly overlap in frequency at ca 140 kHz, but the risk of misidentification is small, because the two species live in different habitats. While *H. ruber* is a rainforest species, occurring in western Kenya, *H. caffer* is distributed more generally, including savanna and bushland areas but also forest habitats throughout most of the country ([Happold & Happold 2013](#)). *D. camerunensis* is very different, being much larger. Its calls can easily be distinguished from

Table 4 - Summary of the frequencies of the CF-components (range of means) of bats obtained during this study, except *, which was cited from Happold and Happold (2013). N = the number of individuals analysed; 1-4 sequences per individual and 10 pulses per sequence.

Species	Resting CF (kHz)	Free-flying F _{max} (kHz)
<i>Hipposideros beatus</i>	114.5-124.0 (N = 5)	-
<i>Hipposideros caffer</i>	145.0-155.8 (N = 14)	147.3-153.6 (N = 7)
<i>Hipposideros ruber</i>	132.6-145.3 (N = 5)	-
<i>Doryrhina camerunensis</i>	50.8-51.2 (N = 2)	-
<i>Doryrhina cyclops</i> *	51.4±0.5 (Uganda)	-
<i>Macronycteris gigas</i>	54.8-55.3 (N = 7)	-
<i>Macronycteris vittata</i>	64.2-70.1 (N = 9)	-
<i>Cloeotis percivali</i>	217.1-225.3 (N = 3)	-
<i>Triaenops afer</i>	70.1-83.9 (N = 3)	75.2-91.2 (N = 7)

those of all other species in Kenya because it uses a much lower frequency band around 51 kHz, and its call frequency does not overlap with any other species of Hipposideridae in Kenya. Its calls are in fact more reminiscent of *Rhinolophus* calls than of *Hipposideros*. In Kenya, *D. camerunensis* is rare and probably restricted to the rainforests in Kakamega and adjacent Nandi counties in the west.

The two *Macronycteris* species, *M. gigas* and *M. vittata*, can easily be distinguished from each other by the difference in the frequency of the CF-component and from all other bats in Kenya by the relatively short calls (10-20 ms) with only a terminal FM-component.

The two species of Rhinonycteridae use calls similar to those of the Hipposideridae, but in both cases employ unique frequency bands that do not overlap with those of any other high duty-cycle bat in Kenya. It should be noticed that *Cloeotis percivali* is difficult to record because of its high frequency calls, which suffer extreme atmospheric attenuation and very short range (Lawrence & Simmons 1982). In practice, the maximum recording range is less than 1m for this species, which means that it is easily missed in acoustic surveys particularly when relying on passive sampling. To some extent, this problem also applies to the small *Hipposideros* species. The CF-frequencies of the species presented here are summarized in table 4.

CONCLUSION

Hipposiderid and rhinonycterid species in Kenya can be separated easily by their echolocation calls, particularly the frequency of the CF-component. The only exception is the two small *Hipposideros* species *H. caffer* and *H. ruber*, which, however, do not occur in the same habitat. The echolocation calls are usually loud and therefore easy to record and analyse. However, the small species have to be recorded at close range (a few metres) because of rapid attenuation of their high-frequency sounds in the air. The rare *H. megalotis* and *Doryrhina cyclops* were not encountered during our study. The calls of the former remain undescribed, while the latter's calls are known from outside Kenya.

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REFERENCES

- APOZNANSKI, G., SANCHEZ-NAVARRO, S., KOKUREWICZ, T., PETERSSON, S. & RYDELL, J. (2018). Barbastelles in wind farms: Are they at risk? *European Journal of Wildlife Research*, 64(4): 43. <https://doi.org/10.1007/s10344-018-1202-1>
- BARATAUD, M. (2015). Acoustic ecology of European bats. Species identification and studies of their habitats and foraging behaviour. Biotope - Muséum national d'Histoire naturelle, Paris, France. 340 pp.
- BELL, G.P. & FENTON, M.B. (1984). The use of Doppler shifted echoes as a flutter detection and clutter rejection system: the echolocation and feeding behavior of *Hipposideros ruber* (Chiroptera: Hipposideridae). *Behavioral Ecology and Sociobiology*, 15(2): 109-114. <https://doi.org/10.1007/BF00299377>

- DECHER, J. & FAHR, J. (2005). *Hipposideros cyclops*. *Mammalian Species*, 763: 1-7. [https://doi.org/10.1644/1545-1410\(2005\)763\[0001:HC\]2.0.CO;2](https://doi.org/10.1644/1545-1410(2005)763[0001:HC]2.0.CO;2)
- DENZINGER, A. & SCHNITZLER, H.-U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, 4: 164. <https://doi.org/10.3389/fphys.2013.00164>
- FENTON, M.B., FAURE, P.A. & RATCLIFFE, J.M. (2012). Evolution of high duty cycle echolocation in bats. *Journal of Experimental Biology*, 215: 2935-2944. <https://doi.org/2935-2944>. [10.1242/jeb.073171](https://doi.org/10.1242/jeb.073171)
- FOLEY, N.M., GOODMAN, S.M., WHELAN, C.V., PUECHMAILLE, S.J. & TEELING, E. (2017). Towards navigating the Minotaur's labyrinth: cryptic diversity and taxonomic revision within the speciose genus *Hipposideros* (Hipposideridae). *Acta Chiropterologica*, 19(1): 1-18. <https://doi.org/10.3161/15081109ACC2017.19.1.001>
- GUILLÉN-SERVENT, A. (1996). Ecolocación en murciélagos: estudios desde una perspectiva ecológica y evolutiva. PhD thesis, Universidad Complutense de Madrid, Madrid, Spain.
- HAPPOLD, M. & HAPPOLD, D.C.D. (2013). *Mammals of Africa IV: Hedgehogs, shrews and bats*. Bloomsbury Publishing, London, United Kingdom. 800 pp.
- HENSON, O. W. Jr., BISHOP, A., KEATING, A., KOBLER, J., HENSON, M., WILSON, B., & HANSEN, R. (1987). Biosonar imaging of insects by *Pteronotus parnellii*, the mustached bat. *National Geographic Research*, 3(1): 82-101.
- JONES, G., MORTON, M., HUGHES, P.M. & BUDDEN, R.M. (1993). Echolocation, flight morphology and foraging strategies of some West African hipposiderid bats. *Journal of Zoology*, 230(3): 385-400. <https://doi.org/10.1111/j.1469-7998.1993.tb02691.x>
- JONES, G. (1999). Scaling of echolocation call parameters in bats. *Journal of Experimental Biology*, 202(23): 3359-3367.
- JONES, G. & TEELING, E.C. (2006). The evolution of echolocation in bats. *Trends in Ecology and Evolution*, 21: 149-156. <https://doi.org/10.1016/j.tree.2006.01.001>
- LANZA, B., FUNAIOLI, U. & RICCUCCI, M. (2015). *The bats of Somalia and neighbouring areas*. Edition Chimaera, Frankfurt am Main, Germany. 566 pp.
- LARSEN, R.J., BOEGLER, K.A., GENOWAYS, H.H., MASEFIELD, W.P., KIRSCH, R.A. & PEDERSEN, S.C. (2007). Mist netting bias, species accumulation curves, and the rediscovery of two bats on Montserrat (Lesser Antilles). *Acta Chiropterologica*, 9(2): 423-435.
- LAWRENCE, B.D. & SIMMONS, J.A. (1982). Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *Journal of the Acoustical Society of America*, 71(3): 585-590.
- LAZURE, L. & FENTON, M.B. (2011). High duty cycle echolocation and prey detection by bats. *Journal of Experimental Biology*, 214: 1131-1137. <https://doi.org/10.1242/jeb.048967>
- MACSWINEY, M.C., CLARKE, F.M. & RACEY, P.A. (2008). What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in Neotropical bat assemblages. *Journal of Applied Ecology*, 45(5): 1364-1371. <https://doi.org/10.1111/j.1365-2664.2008.01531.x>
- MCWILLIAM, A. (1982). Adaptive responses to seasonality in four species of Microchiroptera in coastal Kenya. PhD thesis, University of Aberdeen, Aberdeen, United Kingdom.
- MEYER, C.F.J., AGUIAR, L.M.S., AGUIRRE, L.F., BAUMGARTEN, J., CLARKE, F.M., COSSON, J.-F., VILLEGAS, S.E., FAHR, J., FARIA, D., FUREY, N., HENRY, M., HODGKISON, R., JENKINS, R.K.B., JUNG, K.G., KINGSTON, T., KUNZ, T.H., GONZALEZ, M.C.M., MOYA, I., PATTERSON, B.D., PONS, J.-M., RACEY, P.A., REX, K., SAMPAIO, E.M., SOLARI, S., STONER, K.E., VOIGT, C.C., STADEN, D.V., WEISE, C.D. & KALKO, E.K.V. (2011). Accounting for detectability improves estimates of species richness in tropical bat surveys. *Journal of Applied Ecology*, 48(3): 777-787. <https://doi.org/10.1111/j.1365-2664.2011.01976.x>
- MONADJEM, A., TAYLOR, P.J., COTTERILL, F.D.P. & SCHOEMAN, M.C. (2010). *Bats of southern and central Africa: a biogeographic and taxonomic synthesis*. Wits University Press, Johannesburg, South Africa. 596 pp.
- MONADJEM, A., RASMUSSEN, M., & VAN DER MADE, D.C. (2011). Echolocation calls and wing morphology of selected bats in western Uganda. *Durban Museum Novitates*, 34: 29-34.
- MURRAY, K. L., RITZKE, E.R.B., ADLEY, B.M.H. & ROBBINS, L.W. (1999). Surveying bat communities: a comparison between mist nets and AnaBat II bat detector system. *Acta Chiropterologica*, 1(1): 105-112.
- MUSILA, S., BOGDANOWICZ, W., SYINGI, R., ZUHURA, A., CHYLARECKI, P. & RYDELL, J. (2019a). No lunar phobia in insectivorous bats in Kenya. *Mammalian Biology*, 95: 77-84. <https://doi.org/10.1016/j.mambio.2019.03.002>
- MUSILA, S., MONADJEM, A., WEBALA, P.W., PATTERSON, B.D., HUTTERER, R., JONG, Y.A., BUTYNSKI, T.M., MWANGI, G., CHEN, Z.Z. & JIANG, X.L. (2019b). An annotated checklist of mammals of Kenya. *Zoological Research*, 40(1): 3-52. <https://doi.org/10.24272/j.issn.2095-8137.2018.059>
- MWALE, S. (2000). Changing relationships: the history and future of wildlife conservation in Kenya. *Swara*, 22: 11-17. <https://doi.org/10.21690/foge/2017.60.2p>

- NEUWEILER, G. (1989). Foraging ecology and audition in echolocating bats. *Trends in Ecology and Evolution*, 4(6): 160-166. [https://doi.org/10.1016/0169-5347\(89\)90120-1](https://doi.org/10.1016/0169-5347(89)90120-1)
- NOVICK, A. (1958). Orientation in paleotropical bats. I. Microchiroptera. *Journal of Experimental Zoology*, 138(1): 81-153. <https://doi.org/10.1002/jez.1401380105>
- O'FARRELL, M. & GANNON, W. (1999). A comparison of acoustic versus capture techniques for the inventory of bats. *Journal of Mammalogy*, 80(1): 24-30. <https://doi.org/10.2307/1383204>
- OKELLO, M. & KIRINGE, J. (2004). Threats to biodiversity and their implications in protected and adjacent dispersal areas of Kenya. *Journal of Sustainable Tourism*, 12(1): 55-69. <https://doi.org/10.1080/09669580408667224>
- PARSONS, S. & SZEWCZAK, J.M. (2009). Detecting, recording, and analyzing the vocalizations of bats. In, *Ecological and behavioral methods for the study of bats*, 2nd ed. (Kunz, T.H. and Parsons, S. eds.), pp. 91–112. Johns Hopkins University Press, Baltimore, USA. 920 pp.
- PATTERSON, B.D. & WEBALA, P.W. (2012). Keys to the bats (Mammalia: Chiroptera) of East Africa. *Fieldiana, Life and Earth Sciences*, 6: 1-60. <https://doi.org/10.3158/2158-5520-12.6.1>
- PYE, J.D. (1972). Bimodal distribution of constant frequencies in some hipposiderid bats (Mammalia: Hipposideridae). *Journal of Zoology*, 166(3): 323-335. <https://doi.org/10.1111/j.1469-7998.1972.tb03102.x>
- RUSS, J. (2012) British bat calls: a guide to species identification. Pelagic Publishing, Exeter, United Kingdom. 204 pp.
- RYDELL, J., OTTVALL, R., PETTERSSON, S. & GREEN, M. (2017). Effects of wind power on birds and bats. An updated synthesis report 2017. Naturvårdsverket, Stockholm, Sweden. 132 pp.
- SCHNITZLER, H.-U. (1973). Control of doppler shift compensation in the greater horseshoe bat, *Rhinolophus ferrumequinum*. *Journal of Comparative Physiology*, 82(1): 79-92. <https://doi.org/10.1007/BF00714171>
- SCHNITZLER, H.-U. & KALKO, E.K.V. (2001). Echolocation by insect-eating bats. *Bioscience*, 51(7): 557–569. [https://doi.org/10.1641/0006-3568\(2001\)051\[0557:EBIEB\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2)
- SOKAL, R.R. & ROHLF, F.J. (1981). *Biometry*, 2nd ed. W. H. Freeman & Co, New York, USA. 859 pp.
- SUGA, N. (2018). Specialization of the auditory system for the processing of bio-sonar information in the frequency-domain: Mustached bats. *Hearing Research*, 361: 1-22. <https://doi.org/10.1016/j.heares.2018.01.012>
- TAYLOR, P.J., GEISELMAN, C., KABOCHI, P., AGWANDA, B. & TURNER, S. (2005). Intraspecific variation in the calls of some African bats (Order Chiroptera). *Durban Museum Novitates*, 30: 24-37.
- TAYLOR, P.J., STOFFBERG, S., MONADJEM, A., SCHOEMAN, M.C., BAYLISS, J. & COTTERILL, F.D.P. (2012). Four new bat species (*Rhinolophus hildebrandtii* Complex) reflect PlioPleistocene divergence of dwarfs and giants across an Afromontane archipelago. *PLoS ONE* 7(9): e41744. <https://doi.org/10.1371/journal.pone.0041744>
- VALLO, P., GUILLÉN-SERVENT, A., BENDA, P., OIRES, D.B. & KOUBEKI, P. (2008). Variation of mitochondrial DNA in the *Hipposideros caffer* complex (Chiroptera: Hipposideridae) and its taxonomic implications. *Acta Chiropterologica*, 10(2): 193–206. <https://doi.org/10.3161/150811008X414782>
- WEBALA, P.W., CRAIG, M.D., LAW, B.S., ARMSTRONG, K.N., WAYNE, A.F. & BRADLEY, J.S. (2010). Bat habitat use in logged jarrah eucalypt forests of south-western Australia. *Journal of Applied Ecology*, 48(2): 398-406. <https://doi.org/10.3161/150811008X414782>