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Forest bats of Madagascar: results of acoustic surveys

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Spectral and temporal features of echolocation calls produced by 15 insectivorous bat species in three families from Madagascar are described. In addition we provide a library of bat vocalizations that can be used for acoustic inventories involving heterodyne and time-expansion bat detectors. Time-expanded recordings of calls from 153 bats from 15 species were analyzed using five commonly used temporal and frequency variables measured from spectrographs. Echolocation calls for six species (*Scotophilus tandrefana*, *S. marovaza*, *Emballonura tiavato*, *Neoromicia* spp., *N. malagasyensis* and *Triaenops auritus*) are described for the first time. A discriminant function analysis revealed that a function based on the five measured variables provided a correct overall classification of 82.2%. Three groups of echolocation calls based upon the temporal and frequency characteristics of calls are recognized. The Constant Frequency group consists of hipposiderids and *Emballonura* spp., the Frequency Modulated/Quasi-Constant Frequency group is dominated by vespertilionids, and one species, *Myotis goudoti*, is in the Frequency Modulated group. Further we describe the utility of using acoustic sampling in inventory and monitoring studies, and in investigations of habitat use.

Key words: Chiroptera, echolocation calls, discrimination, Madagascar

INTRODUCTION

Bats are major components of mammalian biodiversity in temperate and tropical regions (Mickleburgh *et al.*, 1992; Hutson *et al.*, 2001; Simmons, 2005). In Madagascar however, the chiropteran fauna is relatively species-poor compared to other similar-sized islands but is distinctive for having a higher proportion of endemic species (Eger and Mitchell, 2003; Racey *et al.*, In press). Ongoing surveys continue to provide new information on the distribution and taxonomy of Malagasy Chiroptera with ten new species described in the last five years (Goodman and Cardiff, 2004; Goodman and Ranivo, 2004; Goodman *et al.*, 2005*a*, 2006*a*, 2006*b*, 2007; Bates *et al.*, 2006). There are now 38 species of insectivorous bats known from Madagascar. The rapid rise in new information about the distribution of Malagasy bats indicates a need for further survey work. A key question now facing conservationists in Madagascar is the extent to which insectivorous bats are dependant on intact forest (Goodman *et al.*, 2005*b*) and the impact of habitat degradation on their populations.

Although trapping and netting are widely used techniques for assessing bat diversity and habitat use, captures may not be representative in chiropteran communities dominated by vespertilionids and hipposiderids because these bats may detect and avoid traps and nets or forage in areas that are unsuitable for trap placement. Acoustic methods, which involve the analysis of echolocation calls, are used in nationwide monitoring programs (e.g., Walsh *et al.*, 2001; Rydell *et al.*, 2002; Russo and Jones, 2002; Roche *et al.*, 2005) and in biodiversity inventories (MacSwiney *et al.*, 2008). However, before acoustic methods can be used in assessments of habitat use, or to augment inventories, a library of authenticated calls is required to describe the echolocation characteristics of each species.

The aim of this paper is to present a description of the echolocation calls of some Malagasy bats most of which are associated with forest habitats, to provide a template for acoustic monitoring studies. In the first attempt to document the echolocation of Malagasy bats, Russ *et al.* (2003) presented sonograms of 15 microchiropteran species (including *Taphozous mauritianus* and five molossids). We have omitted the molossids and *T. mauritianus* from our analysis as they generally fly high and are difficult to record in captive situations that approximate natural flying conditions. Furthermore, recordings were unavailable for *Nycteris madagascariensis*, a species known only from two specimens (Peterson *et al.*, 1995; Eger and Mitchell, 2003; Goodman *et al.*, 2005*a*). We present here recordings from previously unsurveyed localities for some common species and descriptions of echolocation calls of six species not previously described. Furthermore, we will relate the acoustic results to the future needs for ecological research on the insectivorous bats of Madagascar.

MATERIALS AND METHODS

Study Sites

Recordings were made during chiropteran surveys of national parks, a community forest and other sites under consideration for protected area status between 2002 and 2006 (Fig. 1). Habitat types were mid-elevation dense humid forest, littoral forest, dry deciduous forest and a range of degraded or severely impacted habitats such as farmland and scrub thicket. A full list of study sites is given in Appendix.

Capture and Measurements

Bats were trapped in mist nets, harp traps or taken by hand directly from roosts over 4–6 nets nights during 4–33 nights spent at each site (Appendix). Most individuals were identified by morphological characteristics (Peterson *et al.*, 1995) but

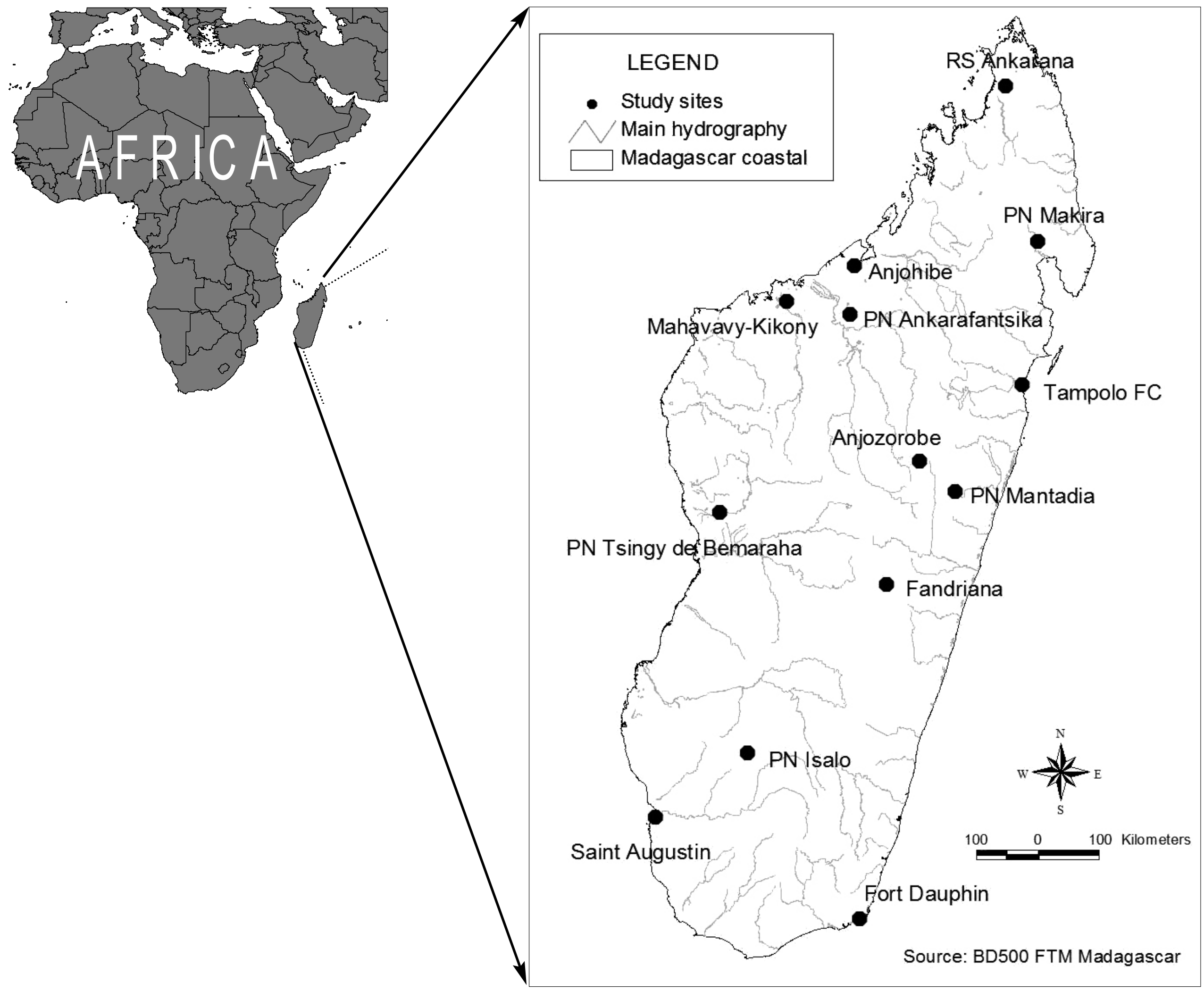

FIG. 1. Location of Madagascar relative to the African mainland; distribution, locality of the study sites

permitted voucher specimens were taken for bats that could not be reliably determined in the field and deposited in the collections housed in the Department of Animal Biology, University of Antananarivo. All individuals were sexed, weighed to the nearest 0.5 g and forearms measured to the nearest 0.1 mm with dial calipers.

Recording and Sound Analysis

Bats were recorded using bat detectors (D980 and D240X, Pettersson Elektronic, Uppsala, Sweden) in time-expansion mode (× 10), which retains the integrity of the original signal (Rydell *et al.*, 2002). Recordings were stored on mini-disks (Sony MZ-N505 Net MD Recorder/Player without compression) for later analysis. The recordings were analyzed with BatSound Pro software (Pettersson Elektronic) at a sampling rate of 44.1 kHz; with 16-bit resolution. The spectrogram and the power spectrum were created using an interpolated 512-point Fast Fourier Transform (FFT) in conjunction with a Hanning window and the threshold was set between 13 and 18%. Recordings were made from bats as they were released from the hand, or in flight cages and occasionally from hand held bats or those flying indoors. The advantage of flight cage recordings is that the bat can be retained, allowing the echolocation recording to be assigned to a voucher specimen. During 2005 we recorded bats using a zip-line (Szewczak, 2000), which allows the bat to fly in relatively uncluttered environments and may provide a recording more similar to natural flight than either release or flight cage recordings. This is especially important when a new species is described. A zip-line consists of 30–50 m of taut monofilament line stretched between two poles. A small loop at one end of a metre of elasticated thread is placed around the bat's neck and the other end is attached to the zip-line with a small snap swivel. Small stoppers are fixed to the zip-line about 2 m from either end to prevent the bat from becoming entangled with the poles. Hanging a miniature light stick from the swivel aids in tracking the bat's position on the zip-line, for recording calls and also for locating the bat when it stops flying. The length of the zip-line enables bats to achieve a regular pattern of flight before calls are recorded.

From each recording we measured five variables either from the dominant harmonic or the fundamental: (i) call duration (dur in ms: the duration from the onset of the call to the end of the call); (ii) the inter-pulse interval (IPI in ms: the duration between the onset of the call and the onset of a subsequent call); (iii) minimum frequency (Fmin in kHz: the minimum frequency of the call); (iv) maximum frequency (Fmax in kHz: the maximum frequency of the call); (v) the frequency that contains maximum energy (FmaxE in kHz).

Measurements were taken from sonograms (i, ii, iii and iv) and power spectrograms (v). The shapes of calls were also characterized as steep frequency modulation (FM), steep frequency modulation followed by shallow-frequency modulation or quasi constant frequency (FM/QCF), constant frequency followed by short frequency modulation (CF/FM) or constant frequency usually preceded with or followed by short frequency modulation sweeps (FM/CF/FM) (Russ, 1999). The number of harmonics present within the frequency response of our recording quipment (maximum = 120 kHz) was also noted. The duty cycle was determined by dividing call duration by interpulse interval and classified as low (< 10%) or high (> 10%) (Jennings *et al.*, 2004).

To avoid pseudoreplication (Hurlbert, 1984) and to ensure the most accurate possible description was obtained, a single call sequence from each individual bat was selected. The choice was based on call quality. We selected one of the last echolocation calls in each sequence, with a high signal to noise ratio (Jennings *et al.*, 2004), considered to be a search phase call (Betts, 1998) and which allowed the selected variables to be measured with confidence.

Multiple Discriminant Function Analysis

To test the validity of assigning echolocation calls to species groups, a multivariate discriminate function analysis (DFA) was performed using SPSS version 10.0.01 (SPSS Inc, 1999). The analysis determines which variables discriminate between groups or species using discriminant functions (Digby and Kempton, 1987). Canonical analysis produces eigenvalues which indicate the strength of the functions in differentiating one group from another. Wilk's lambda is used to test the significance of all the discriminating functions in separating groups of data. The significance level of lambda is determined from the distribution of Chi-square. To obtain a graphical representation of the separation of groups based on their discriminant functions, we plotted the group centroids with 95% confidence limits for separate functions and the canonical discriminant functions.

RESULTS

We recorded and analyzed echolocation calls produced by 153 bats of 15 species from three families (Emballonuridae, Hipposideridae and Vespertilionidae — Table 1). Sample sizes for individual species ranged from one to 28. Morphological measurements (forearm length, FA) are also given in Table 1. Depending on the species, there were 1–6 recording sites and 1–28 bats recorded (Table 2).

Emballonuridae

In Madagascar, this family is represented by four species, two of which are also found on the African mainland (*Taphozous mauritianus* and *Coleura afra*) and two endemic *Emballonura* species.

Emballonura tiavato
Goodman, Cardiff, Ranivo, Russell, and Yoder, 2006

Echolocation calls of six individuals of this recently described species (two from Antsalova and four from Bekopaka) were recorded using a zip line and in a flight cage. Echolocation calls were FM/CF/FM (Fig. 2A) with up to five harmonics. The fundamental (often calls recorded in a flight cage) or second harmonic (almost all calls recorded using a zip line) was the most intense. The species produced short calls with a medium IPI and a low duty cycle (Table 1).

We recorded the exit calls of some bats as they emerged from a cave roost near Bekopaka.

TABLE 1. Morphological measurements and frequency and temporal variables of echolocation calls produced by 153 bats of 15 taxa recorded using hand release, on zip lines, in flight cages, and during roost exits, in various sites within Madagascar, 2002–2006. FA: forearm length; FmaxE: frequency of maximum energy; Fmax: maximum frequency; Fmin: minimum frequency; dur: duration; IPI: interpulse interval. For each variable, $\bar{x} \pm SD$ (minimum – maximum) are shown and one echolocation call (i.e. sequence of pulses) per bat was analysed. Sample sizes shown are numbers of bats (*n* bats) and pulses analysed (*n* pulses). The maximum number of harmonics (including the fundamental) is shown. The harmonic with most energy is named as F and H2 (fundamental or second, respectively). Duty cycle values are also shown

Species	FA (mm)	*N* bats / *n* pulses	Maximum number of harmonics	Harmonic with most energy	Call structure	FmaxE (kHz)	Fmax (kHz)	Fmin (kHz)	Dur (ms)	IPI (ms)	Duty cycle (%)
Hipposideros commersoni	87.4 ± 6.07	28/153	3	H2	CF/FM	66.6 ± 7.09 (61.6–76.5)	67.7 ± 3.60 (62.3–77.8)	53.5 ± 4.36 (46.0–64.8)	12.3 ± 2.81 (7.3–19.3)	39.8 ± 19.79 (15.7–125.5)	31.2
Triaenops menamena	49.6 ± 1.72	15/82	3	H2	CF/FM	93.2 ± 1.01 (90.3–95.0)	94.2 ± 1.33 (92.0–98.0)	82.0 ± 3.77 (70.0–89.0)	10.1 ± 1.38 (6.5–13.5)	42.7 ± 13.91 (22.7–86.3)	25.5
T. furculus	45.5 ± 1.63	18/135	3	H2	FM/CF/FM	103.4 ± 7.09 (94.8–113.5)	104.7 ± 6.77 (97–114)	81.5 ± 4.94 (68–97)	12.2 ± 6.31 (8.70–18.7)	35.2 ± 14.37 (16.70–92.7)	52.4
T. auritus	46.7 ± 2.02	10/54	3	H2	CF/FM	100.3 ± 5.94 (91.3–108.5)	104.2 ± 7.02 (94.7–111.1)	82.9 ± 4.94 (80.1–107.6)	12.19 ± 4.42 (4.60–22.30)	37.65 ± 21.89 (17.80–101.0)	40.2
Emballonura tiavato	38.0 ± 0.66	6/25	5	H2	FM/CF/FM	54.2 ± 0.71 (52.4–55.8)	55.6 ± 0.88 (55.0–57.0)	37.2 ± 2.82 (33.0–42.0)	4.2 ± 1.13 (2.90–6.7)	92.2 ± 29.59 (68.4–183.2)	5.7
E. atrata	38.4 ± 0.53	2/7	3	H2	FM/CF/FM	52.9 ± 1.16 (50.0–54.3)	55.7 ± 0.95 (55.0–57.0)	39.1 ± 3.07 (36.0–43.0)	2.9 ± 0.44 (2.3–3.5)	82.8 ± 11.12 (69.9–96.2)	4.3
Miniopterus manavi sensu latissimo	36.2 ± 1.17	16/68	1	F	FM/QCF	58.1 ± 1.98 (53.7–61.5)	100.5 ± 17.11 (63.1–128.0)	51.7 ± 3.77 (44.0–57.0)	4.0 ± 0.73 (3–5.70)	71.4 ± 16.88 (48.8–121.9)	7.4
M. majori/ sororculus	43.7 ± 1.63	11/35	1	F	FM/QCF	48.5 ± 3.55 (44.2–54.5)	73.4 ± 9.10 (57.7–95.2)	45.4 ± 3.57 (40.3–51.6)	4.5 ± 0.71 (3–5.9)	78.8 ±17.89 (41–110.5)	8.2
M. gleni	47.6 ± 1.10	7/34	1	F	FM/QCF	44.8 ± 3.25 (38.4–50.5)	78.3 ± 7.18 (62.8–91.0)	40.0 ± 4.41 (30.0–46.8)	3.6 ± 0.51 (2.7–4.7)	65.4 ± 16.66 (34.8–101.2)	6.8
Myotis goudoti	37.3 ± 1.52	11/60	1	F	FM	64.4 ± 4.45 (55.3–72.1)	121.2 ± 9.47 (101.2–140)	45.4 ± 6.46 (23.7–55.0)	3.0 ± 0.76 (1.5–4.3)	51.8 ± 21.27 (13.7–92.1)	7.0
Neoromicia sp.	33.3 ± 1.12	6/26	1	F	FM/QCF	41.5 ± 1.68 (39.2–44.3)	69.2 ± 8.78 (60.3–88.2)	37.7 ± 0.98 (35.5–39.3)	5.7 ± 1.41 (3.8–8.0)	109.9 ± 45.07 (65.2–196.7)	7.7
N. malagasyensis	30.7 ± 1.15	6/20	1	F	FM/QCF	45.7 ± 2.94 (41.4–51.0)	79.8 ± 12.35 (60.3–100.0)	40.5 ± 3.77 (32.4–45.50)	4.9 ± 0.78 (3.6–6.3)	69.1 ± 17.57 (34.2–94.4)	9.7
Scotophilus robustus	63.0 ± 2.06	7/35	1	F	FM/QCF	38.0 ± 1.81 (34.6–42.8)	64.8 ± 3.34 (60.0–72.0)	32.4 ± 1.37 (30.0–35.0)	5.0 ± 0.87 (3.3–6.2)	77.8 ± 24.37 (26.3–109.6)	7.9
S. tandrefana	46.2 ± 0.00	1/7	1	F	FM/QCF	48.2 ± 1.52 (45.9–49.5)	91.2 ± 8.95 (76.8–100.0)	42.9 ± 0.72 (42.2–43.9)	3.0 ± 0.30 (2.6–3.3)	33.0 ± 10.33 (22.9–46.1)	9.2
S. marovaza	43.5 ± 1.33	9/21	1	F	FM/QCF	45.9 ± 1.2 (43.8–48)	68.9 ± 3.7 (58–72.6)	42.9 ± 1.3 (40.6–45.3)	6.4 ± 0.6 (6–8)	87.4 ± 24.4 (55–146)	7.8

They consisted of multiharmonic signals the fourth harmonic of which contains the maximum energy at about 55.2 kHz.

Emballonura atrata (Peters, 1874)

Echolocation calls of two *E. atrata* were recorded in a flight cage from Tolagnaro in south-eastern Madagascar. This species produced FM/CF/FM calls with the most energy in the second harmonic at 52.9 kHz (Table 1 and Fig. 2B).

Hipposideridae

In Madagascar, the family is represented by four species of which three are endemic. The echolocation calls of *Hipposideros commersoni*, *Triaenops menamena*, *T. furculus* and *T. auritus* were recorded during the study.

Hipposideros commersoni (E. Geoffroy, 1813)

This is the largest insectivorous bat in Madagascar. We recorded the echolocation calls of 28 individuals from six different sites (Parc National (PN) Tsingy de Bemaraha, PN Namoroka, Tolagnaro, PN Isalo, Tampolo CF and PN Ankarafantsika). This species produces narrowband and long CF calls which terminate with brief FM elements with a high duty cycle (31.2 %) and maximum energy at about 66.6 kHz (Table 1). The calls consisted of a maximum of three harmonics most energy in the fundamental or second harmonic (Fig. 3).

Triaenops menamena Goodman and Ranivo, 2009

Fifteen individuals of this medium-sized bat were recorded from Antsalova and Bekopaka within PN Tsingy de Bemaraha and the Saint

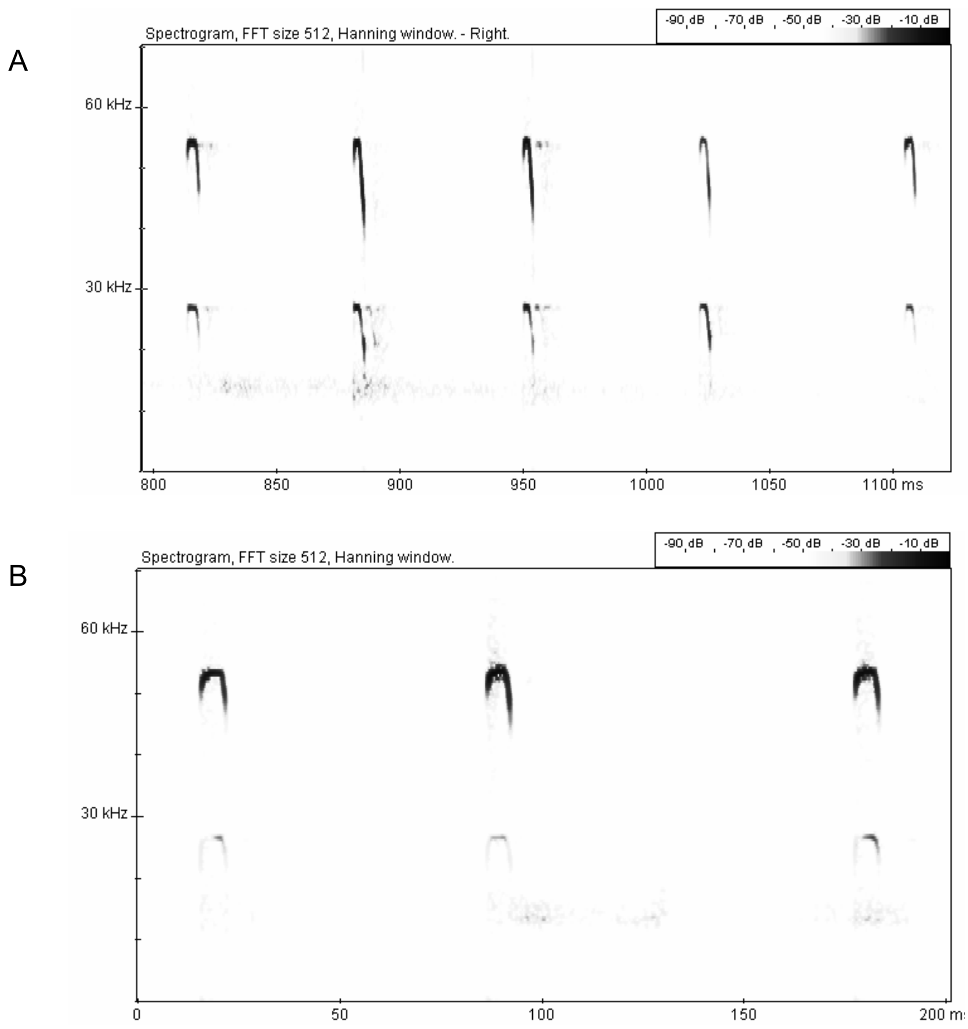

FIG. 2. Sonograms of: (A) *Emballonura tiavato* (Zip line, 22 October 2005, PN Tsingy de Bemaraha, western Madagascar) and (B) *E. atrata* (Flight cage, 23 May 2004, Mandena, south-eastern Madagascar)

TABLE 2. Species recorded numbers of recording sites and number of bats recorded. The numbers of bats recorded in each method are also shown

Species	*n* sites	*N* bats	Processing method				
			Hand release	Roost emergence	Free flight	Flight cage	Zip line
Hipposideros commersoni	6	28	16			9	3
Triaenops menamena	2	15	4			5	6
T. furculus	3	18	5			13	
T. auritus	1	10				10	
Emballonura tiavato	1	6	2	1*		2	2
E. atrata	1	2				2	
Miniopterus manavi sensu latissimo	4	16	6			7	3
M. majori/sororculus	1	11	11				
M. gleni	3	7	6			1	
Myotis goudoti	5	11	4			7	
Neoromicia sp.	2	6	2		3	1	
N. malagasyensis	1	6	6				
Scotophilus robustus	3	7	3	3			1
S. tandrefana	1	1				1	
S. marovaza	2	9	2				7
Total	14	153	67	4	3	58	22

* — These bats are not included to the analysis

Augustin region. The species produced echolocation calls with a relatively short CF component followed by brief FM components. The duty cycle was high (25.5% — Fig. 4A). The second harmonic generally contained most energy at about 93.2 kHz. A maximum of three harmonics were also observed.

Triaenops auritus (Grandidier, 1912)

Echolocation calls were recorded from 10 individuals in the Réserve Spéciale (RS) Ankarana. Calls consisted of a distinctive narrowband CF component that ended with short FM sweeps with a maximum energy of 100.3 kHz (Table 1 and Fig. 4B).

Triaenops furculus (Trouessart, 1906)

This medium sized bat was recorded in PN Tsingy de Bemaraha, PN Namoroka and near Saint Augustin village. Echolocation calls were recorded from eighteen individuals. Pulses were of longer duration than those of *T. menamena* and consisted of a narrowband CF component that, unlike *T. menamena*, began and ended with short FM sweeps with a high duty cycle (52.5 %) and with up to two harmonics. The second harmonic contains

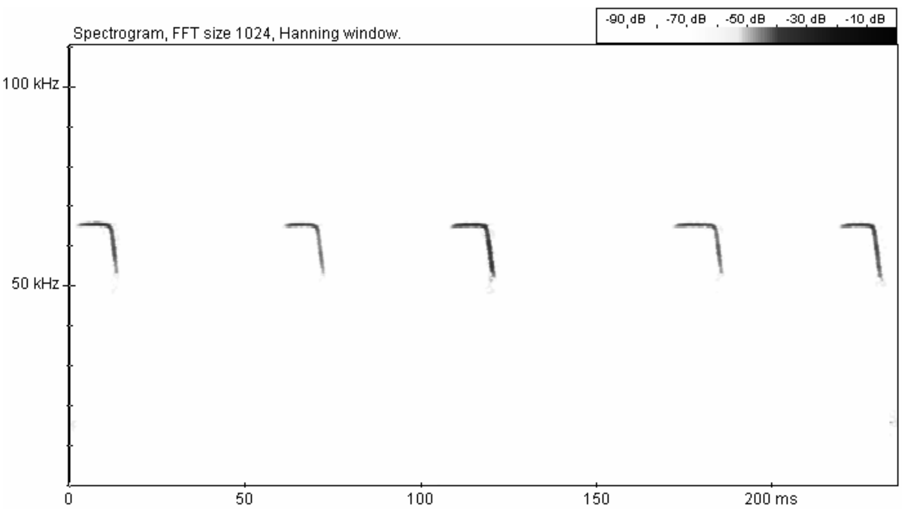

FIG. 3. Sonogram of *H. commersoni* (Zip line, 13 October 2005, PN Tsingy de Bemaraha, western Madagascar)

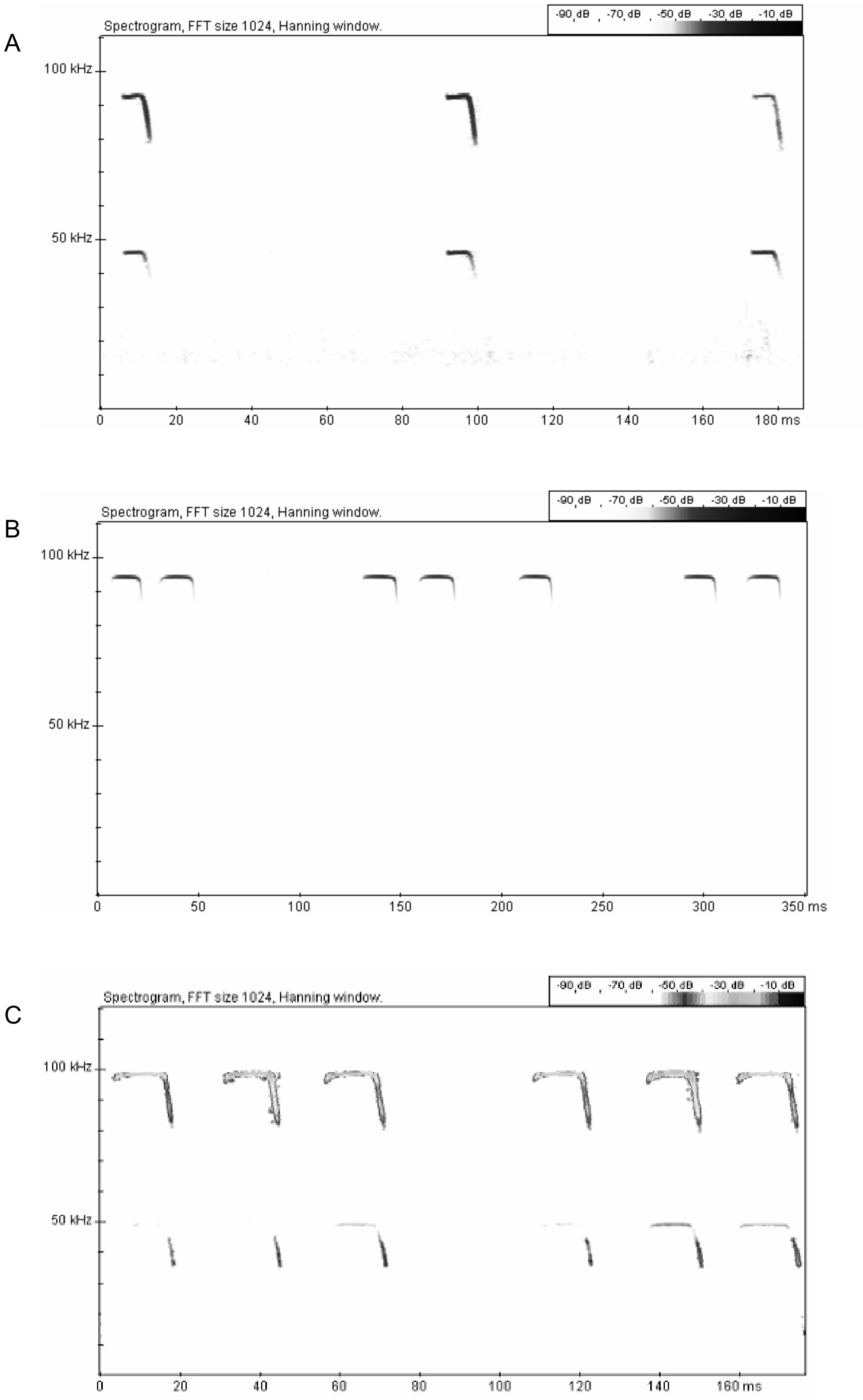

FIG. 4. Sonograms of: (A) *T. menamena* (Zip line, 31 October 2005, PN Tsingy de Bemaraha, western Madagascar), (B) *T. auritus* (Flight cage, 09 May 2003, RS Ankarana, Northern Madagascar), and (C) *T. furculus* (Hand release, 6 November 2005, PN Tsingy de Bemaraha, western Madagascar)

most energy at about 103.4 kHz (Table 1 and Fig. 4C).

Vespertilionidae

In Madagascar, the family is represented by six genera: *Hypsugo*, *Pipistrellus*, *Neoromicia*, *Myotis*, *Miniopterus* and *Scotophilus* of which the last four were the subject of the echolocation analysis.

Miniopterus manavi sensu latissimo (sen lat.)[1]

The echolocation calls of this small bat were recorded from individuals in flight cages, on zip lines and during hand release at PN Tsingy de Bemaraha, PN Namoroka, PN Isalo and PN Mantadia.

The calls were broadband FM/QCF sweeps produced at low duty cycle with most energy at about 58.1 kHz in the fundamental (Table 1 and Fig. 5A). The pulses were short in duration (ca. 4.0 ms).

Miniopterus majori (Thomas, 1906)
Miniopterus sororculus Goodman, Ryan, Maminirina, Fahr, Christidis and Appleton, 2007

Because separation of these species requires detailed description of crania, we refer to them as *Miniopterus majori/sororculus*. They were recorded from the Fandriana region, and they produced broadband FM/QCF echolocation calls at low duty cycle (Table 1 and Fig. 5B) but with a lower maximum energy, at about 48.5 kHz. The fundamental is always the most intense with short duration pulses (ca. 4.5 ms).

Miniopterus gleni
Peterson, Eger and Mitchell, 1995

This is the largest *Miniopterus* species in Madagascar. We recorded eight individuals from three sites: PN Isalo, PN Tsingy de Bemaraha and PN Namoroka. The calls are characterized by broadband FM/QCF pulses produced at low duty cycle (Table 1 and Fig. 5C) with a frequency of maximum energy at about 44.8 kHz. The fundamental is always the most intense call and pulses are of short duration.

Myotis goudoti (A. Smith, 1834)

This is the only *Myotis* species on Madagascar. We recorded 11 individuals of this small bat from five localities (Makira, Anjozorobe, PN Isalo, PN Tsingy de Bemaraha and PN Namoroka). Calls were characterized by broadband FM sweeps produced at low duty cycle (Fig. 6). The most energy is always found in the fundamental at about 64.4 kHz. The pulses were of very short duration (ca. 3.0 ms — Table 1).

Neoromicia spp.

Recordings made in Mantadia and Anjozorobe during release and roost emergence were revealed to be potentially from two species (*N. melckorum* and *N. matroka*). In the absence of attributed calls for each species we refer to these taxa together. Calls had a steep frequency modulation (FM) following by a shallow frequency modulation (QCF) pulse at a low duty cycle (Table 1 and Fig. 7A).

Neoromicia malagasyensis
Goodman and Ranivo, 2004

This recently described species (Goodman and Ranivo, 2004) is restricted to a small area around PN Isalo. Recordings from six individuals at PN Isalo revealed that calls consisted of FM/QCF components produced at low duty cycle (Tables 1 and 2, Fig. 7B). The maximum energy was present in the fundamental at about 45.8 kHz.

Scotophilus robustus (Milne-Edwards, 1881)

Three individuals of this widespread but rare endemic species were recorded from PN Tsingy de Bemaraha, PN Namoroka and Sainte Luce. Calls were characterized by a broadband steep frequency modulation (FM) followed by quasi constant frequency (QCF) calls at low duty cycle (Fig. 8A). The fundamental was always the most intense with peak energy at about 38.1 kHz (Table 1).

Scotophilus tandrefana
Goodman, Jenkins and Ratrimomanarivo, 2005

Only a single individual of this species was caught and 7 calls were recorded in a flight cage at PN Tsingy de Bemaraha. The bat emitted broadband FM/QCF calls at low duty cycle with frequency containing most energy at about 48.2 kHz (Table 1 and Fig. 8B).

[1] — Based on recent morphological and molecular phylogenetic studies, *M. manavi* (Thomas, 1906) is now considered to be at least three species: *M. manavi* sensu stricto, *M. aelleni* and *M. griveaudi* (Goodman *et al.*, 2009), which have a paraphyletic relationship and converge morphologically. We refer to them as *M. manavi* sensu latissimo (sen lat.) because some recordings were made without voucher specimens.

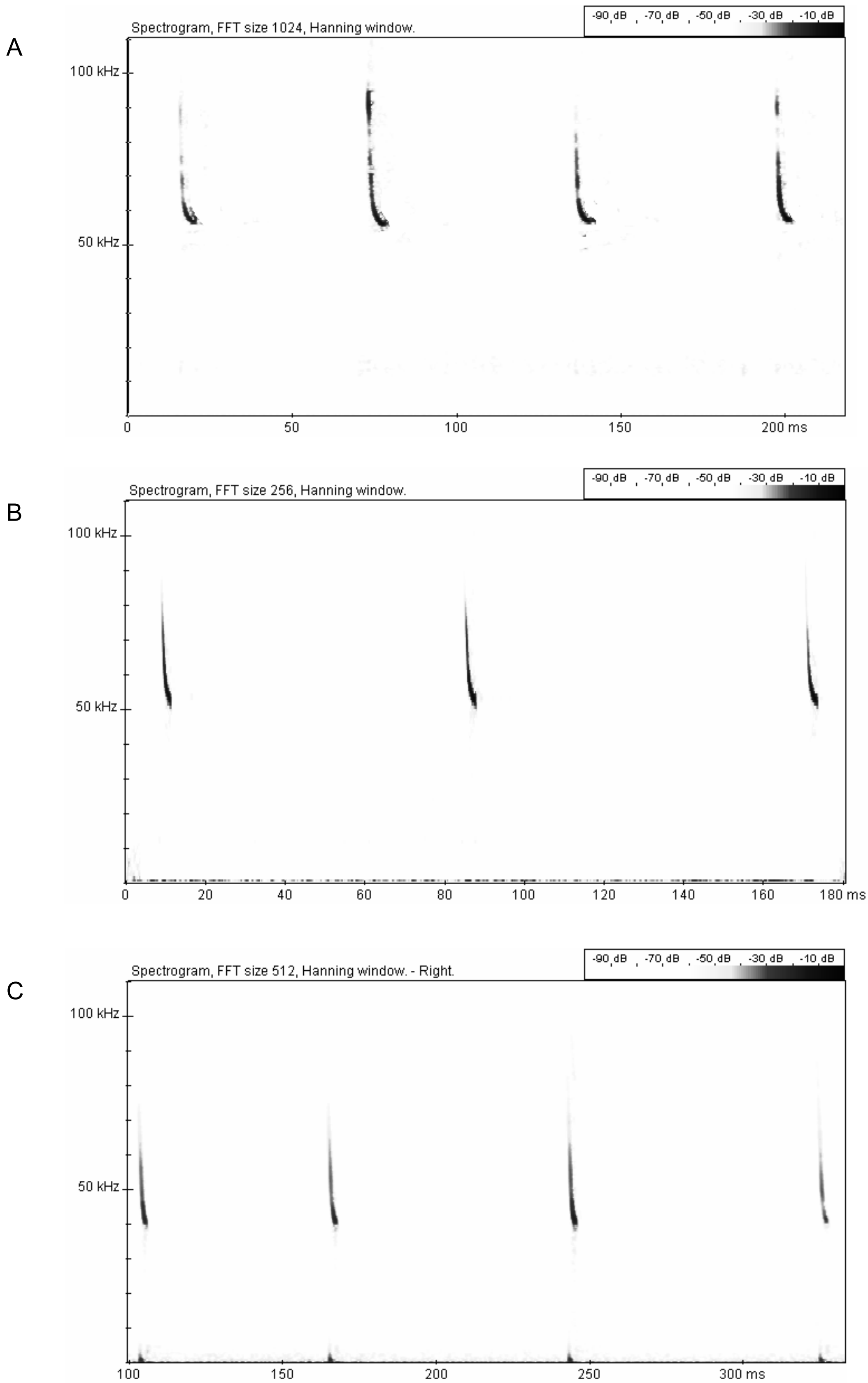

FIG. 5. Sonograms of (A) *M. manavi* sensu latissimo (Flight cage, 27 July 2003, PN Tsingy de Bemaraha, western Madagascar), (B) *M. majori/sororculus* (Hand release, 11 April 2003 Fandrianana, central-eastern Madagascar), and (C) *M. gleni* (Hand release, 3 April 2003, PN d'Isalo, central-southern Madagascar)

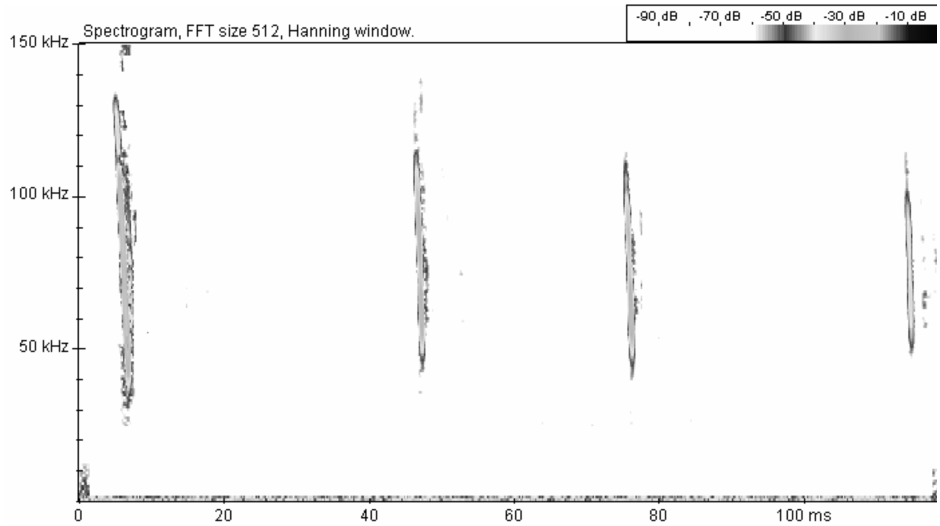

FIG. 6. Sonogram of *M. goudoti* (Flight cage, 08 September 2002, Anjozorobe, eastern Madagascar)

Scotophilus marovaza Goodman, Ratrimomanarivo and Randrianandrianina, 2006

Nine individuals of this species, the smallest in the genus *Scotophilus* were recorded from two sites in western Madagascar (Complexe Mahavavy-Kinkony and Anjohibe). Calls were characterized by broadband steep frequency modulation (FM) followed by a quasi constant frequency (QCF). The bat emitted low duty cycle calls with maximum energy at about 45.9 kHz (Table 1 and Fig. 8C).

Multiple Discriminant Function Analysis

Five canonical discriminant functions were obtained for the species groups. Function 1 was the strongest, accounting for 82.4% of the overall variation between groups (Table 3). Chi-square analysis suggested that species groups varied significantly in Functions 1, 2, 3, 4 and 5 and discriminated effectively between groups (Table 4).

The largest absolute correlation between each variable and any discriminant function are displayed in the structure matrix. For Function 1, FmaxE and Fmin were positively weighted as was Fmax for Function 2.

The plot of mean canonical scores with 95% confidence limits and the canonical discriminant functions (Figs. 10 and 11) demonstrates that the species groups are well separated in multidimensional space with the exception of *N. malagasyensis* and *M. gleni*. Vespertilionid species are most widely separated from each other in terms of Function 1. The furthest apart in terms of Function 2 are the hipposiderids and the emballonurids (Fig. 11). The number of individuals in each group was compared with those predicted by the multiple discriminant analysis, which indicates that 82.2% of the individuals were classified correctly into independently determined groups.

The CF echolocating species *H. commersoni* was 100% correctly classified. *T. menamena*, *T. furculus* and *T. auritus* were respectively 97.1%, 91.5% and 61.4% correctly classified, with the remaining calls assigned to each of the three *Triaenops* species. Calls of *E. atrata* and *E. tiavato* were respectively correctly assigned in 80% and 68.4% of cases while

TABLE 3. The results of discriminant function analysis of data from echolocation calls, including FmaxE, Fmin, Fmax, Dur, and IPI

Function	FmaxE	Fmin	Fmax	Dur	IPI	Eigen-values	Cumulative %	Wilks' lambda	χ^2	*d.f.*	*P*-value
1	**0.883***	**0.671***	0.213	0.200	-0.135	36.187[a]	82.4	0.001	4276.840	70	0.0001
2	0.232	0.185	**0.941***	-0.243	0.011	5.334[a]	94.5	0.032	2081.950	52	0.0001
3	0.074	-0.671	0.263	0.269	-0.226	1.657[a]	98.3	0.205	961.440	36	0.0001
4	0.237	-0.214	-0.021	-0.299	0.648	0.569[a]	99.6	0.545	368.264	22	0.0001
5	-0.324	0.144	0.005	**0.859***	**0.715***	0.169[a]	100.0	0.855	94.754	10	0.0001

* — Largest absolute correlation between each variable and any discriminant function
[a] — First five canonical discriminant functions were used in the analysis

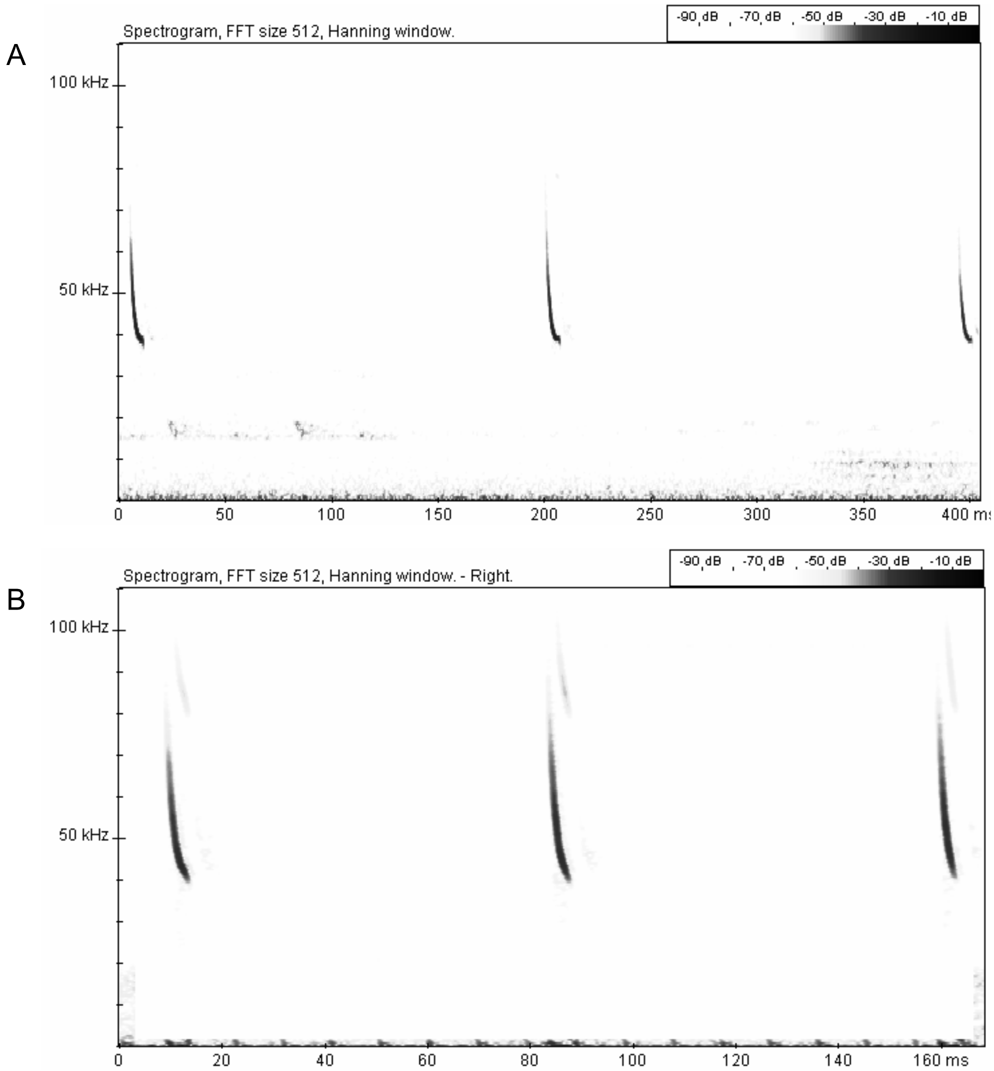

FIG. 7. Sonograms of: (A) *Neoromicia* spp. (Flight cage, 08 September 2002, Anjozorobe, eastern Madagascar), and (B) *N. malagasyensis* (Flight cage, 27 March 2003, PN Isalo, central-southern Madagascar)

the remaining percentages were shared by the other *Emballonura* species.

The FM echolocating bats *Myotis goudoti* was 98.0% correctly classified while 2.0% was assigned to *M. manavi* sen. lat. Calls of FM/QCF vespertilionid species were correctly classified from 40% (*Neoromicia* sp.) to 92.9% (*S. robustus*) of the cases. The remaining percentages formed an overlap between those vespertilionid bats. For example, calls of *M. manavi* sen. lat.were 67.3% correctly assigned to *M. manavi* sen. lat. with others calls of this species being classified to *M. majori/ sororculus* (13.5%), and *M. goudoti* (19.2%).

DISCUSSION

Descriptions of echolocation calls are important because they can be used to investigate behavioural ecology, habitat use and to supplement species inventories based on traditional capture methods. The fact that the echolocation calls of some species in Madagascar remain poorly known should not prohibit the application of acoustic techniques on the island. Rather, the descriptions we present here are essential prerequisites to future investigations. This study has demonstrated the additional contribution that acoustic sampling can make to survey and inventory for clarifying the distribution of Malagasy bats. Subjecting the call characteristics of 15 species (Fig. 9), including those of six species whose calls are described for the first time, to a DFA, revealed overall correct classifications of 82%.

Although Box's M test demonstrated that groups of taxa differed significantly in their covariance matrices, DFA is robust even when the assumption of homogeneity of covariances is not met, provided the

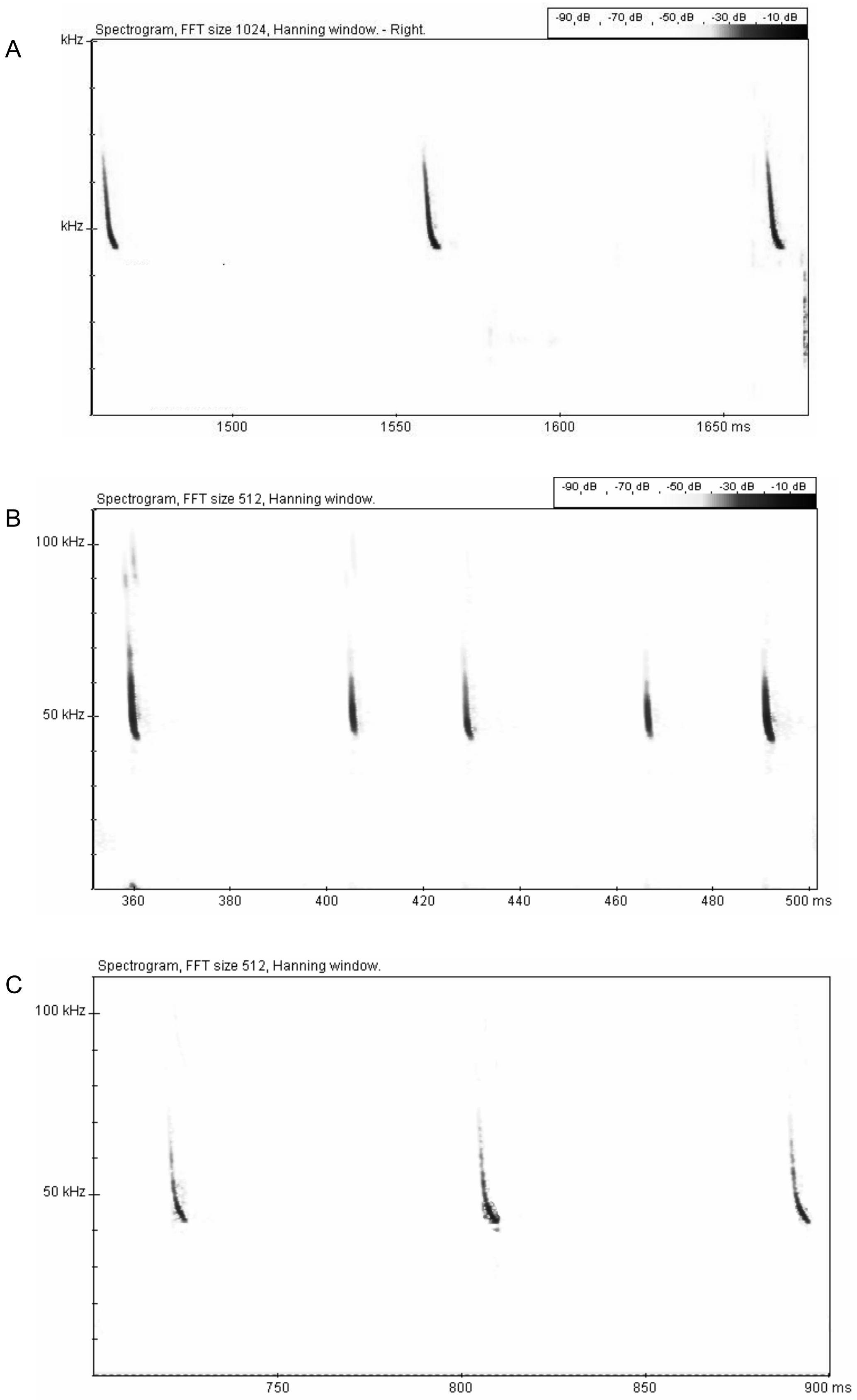

FIG. 8. Sonograms of: (A) *S. robustus* (Zip line, 13 October 2004, PN Tsingy de Bemaraha, western Madagascar), (B) *S. tandrefana* (Flight cage, 25 July 2003, PN Tsingy de Bemaraha, western Madagascar), and (C) *S. marovaza* (Zip line, 27 July 2006, Anjohibe, western Madagascar)

TABLE 4. Classification of individuals into species groups. 1 = *E. atrata* (Ea), 2 = E. *tiavato* (Et), 3 = *Neoromicia* sp. (Nsp), 4 = *H. commersoni* (Hc), 5 = *M. gleni* (Mgl), 6 = *M. majori/sororculus* (Mma), 7 = *M. manavi* sensu latissimo (Mmv), 8 = *M. goudoti* (Mgd), 9 = *N. malagasyensi* (Nm), 10 = *S. robustus* (Sr), 11 = *S. tandrefana* (St), 12 = *T. furculus* (Tfu), 13 = *T. menamena* (Truf), 14 = *T. auritus* (Taur) and 15 = *S. marovaza* (Sm), *n* = number of group

	Species code		Predicted group															Total
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Actual group	1	*n*	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	**5**
		%	**80.0**	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**100.0**
	2	*n*	6	13	0	0	0	0	0	0	0	0	0	0	0	0	0	**19**
		%	31.6	**68.4**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**100.0**
	3	*n*	0	0	8	0	1	0	0	0	5	1	0	0	0	0	5	**20**
		%	0.0	0.0	**40.0**	0.0	5.0	0.0	0.0	0.0	25.0	5.0	0.0	0.0	0.0	0.0	25.0	**100.0**
	4	*n*	0	0	0	122	0	0	0	0	0	0	0	0	0	0	0	**122**
		%	0.0	0.0	0.0	**100.0**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**100.0**
	5	*n*	0	0	0	0	11	4	0	0	9	0	1	0	0	0	2	**27**
		%	0.0	0.0	0.0	0.0	**40.7**	14.8	0.0	0.0	33.3	0.0	3.7	0.0	0.0	0.0	7.4	**100.0**
	6	*n*	0	0	1	0	1	13	0	0	3	0	0	0	0	0	6	**24**
		%	0.0	0.0	4.2	0.0	4.2	**54.2**	0.0	0.0	12.5	0.0	0.0	0.0	0.0	0.0	25.0	**100.0**
	7	*n*	0	0	0	0	0	7	35	10	0	0	0	0	0	0	0	**52**
		%	0.0	0.0	0.0	0.0	0.0	13.5	**67.3**	19.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**100.0**
	8	*n*	0	0	0	0	0	0	1	49	0	0	0	0	0	0	0	**50**
		%	0.0	0.0	0.0	0.0	0.0	0.0	2.0	**98.0**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**100.0**
	9	*n*	0	0	0	0	1	0	0	0	6	1	3	0	0	0	3	**14**
		%	0.0	0.0	0.0	0.0	7.1	0.0	0.0	0.0	**42.9**	7.1	21.4	0.0	0.0	0.0	21.4	**100.0**
	10	*n*	0	0	2	0	0	0	0	0	0	26	0	0	0	0	0	**28**
		%	0.0	0.0	7.1	0.0	0.0	0.0	0.0	0.0	0.0	**92.9**	0.0	0.0	0.0	0.0	0.0	**100.0**
	11	*n*	0	0	0	0	1	0	0	0	0	0	5	0	0	0	0	**6**
		%	0.0	0.0	0.0	0.0	16.7	0.0	0.0	0.0	0.0	0.0	**83.3**	0.0	0.0	0.0	0.0	**100.0**
	12	*n*	0	0	0	0	0	0	0	0	0	0	0	108	3	7	0	**118**
		%	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**91.5**	2.5	5.9	0.0	**100**
	13	*n*	0	0	0	0	0	0	0	0	0	0	0	2	66	0	0	**68**
		%	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.9	**97.1**	0.0	0.0	**100.0**
	14	*n*	0	0	0	0	0	0	0	0	0	0	0	12	5	27	0	**44**
		%	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	27.3	11.4	**61.4**	0.0	**100.0**
	15	*n*	0	0	3	0	2	1	0	0	0	0	0	0	0	0	15	**21**
		%	0.0	0.0	14.3	0.0	9.5	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	**71.4**	**100.0**

data do not contain outliers. When N is large however, as it is here, small deviations from homogeneity will be significant. The facts that log determinants were of similar magnitude indicated that it was acceptable to proceed with the analysis (Garson, 2006; Papadatou *et al.*, 2008).

The results presented here will encourage further work on those Malagasy bat species whose calls have yet to be recorded and described, particularly the molossids. It is noteworthy that none of the species descriptions for the recently described Malagasy bat taxa contain sonograms.

Madagascar is unique among tropical islands in that a quarter of the bat fauna has been described in the last decade. The description of 10 new species gives rise to the urgent need for information on the distribution and habitat requirements of these species at a time when plans for large increase in protected areas are well advanced (Kremen *et al.*, 2008).

Emballonuridae

There are as yet too few data to distinguish the two *Emballonura* species with confidence from their echolocation calls. *Emballonura atrata* and *E. tiavato* produced similar calls and we cannot rule out that differences in the recording environment influenced some of the parameters given in Table 1. Thus, Fmax varied from the first and second harmonics in the flight cage and on the zip-line respectively to the fourth in bats emerging from a cave. Further recordings of both species in similar situations are needed before these taxa can be identified with confidence from echolocation recordings although we note that, as expected, the FmaxE was higher for the smallest species, *Emballonura tiavato* (Jones, 1999). The sonograms however are distinctive from other bats in Madagascar and as the species are thought to be allopatric, time-expanded recordings could be attributable to species with confidence within their respective geographic ranges. As the only bats with a FmaxE of around 55 kHz, there is also considerable potential to use heterodyne detectors to conduct surveys. However, some recent surveys in the east (Randrianandrianina *et al.*, 2006.) and the west (Kofoky *et al.*, 2007) rarely recorded or netted *Emballonura* spp. despite their presence in caves, indicating that they may forage in zones (e.g., the forest canopy) that are outside the range of ground-level bat detectors and traps or that they are particularly adept at avoiding mist nets.

Hipposideridae

Jones (1999) reported an inverse linear relationship between bat size and echolocation frequency. In the present study *H. commersoni* echolocated at a lower frequency than the three *Triaenops* species. There was no overlap of FmaxE between

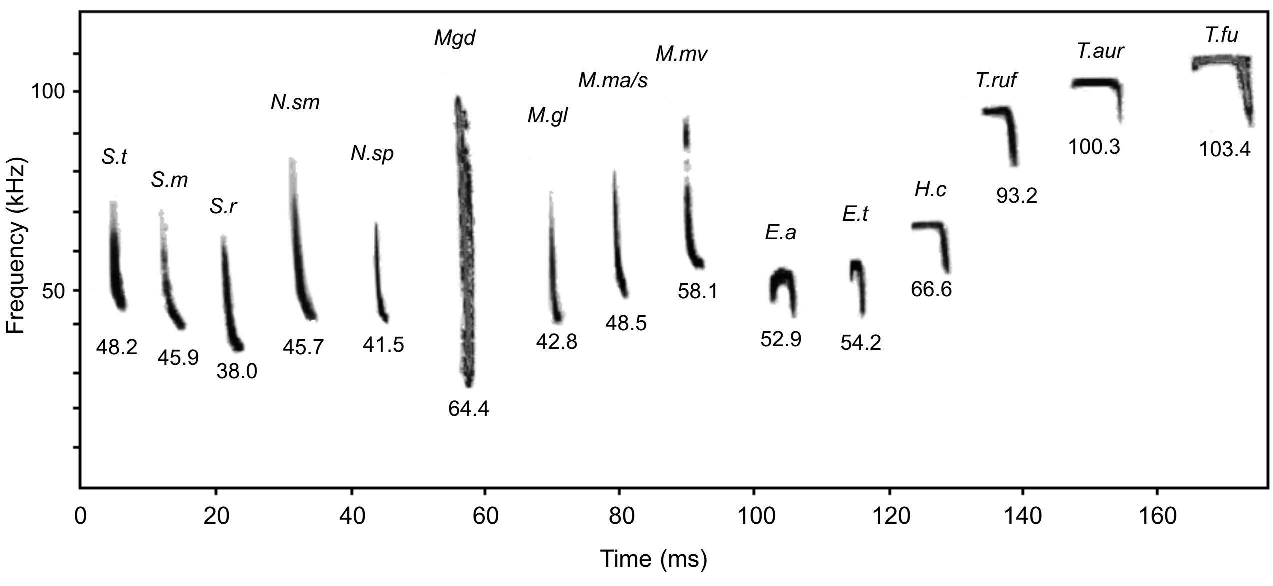

FIG. 9. Summary of acoustic identification of some Malagasy insectivorous bats. Values are the frequency with most energy (*S.t* = *S. tandrefana*, *S.r* = *S. robustus*, *S.m* = *S. marovaza, N.sm* = *N. malagasyensis, N.*spp = *Neoromicia* spp., *Mgd* = *M. goudoti*, *M.gl* = *M. gleni*, *M.ma/s* = *M. majori/sororculus*, *M.mv* = *M. manavi* sen lat., *E.a* = *E. atrata*, *E.t* = *E. tiavato*, *H.c* = *H. commersoni*, *T.ruf* = *T. menamena*, *T.aur* = *T. auritus* and *T.fu* = *T. furculus*)

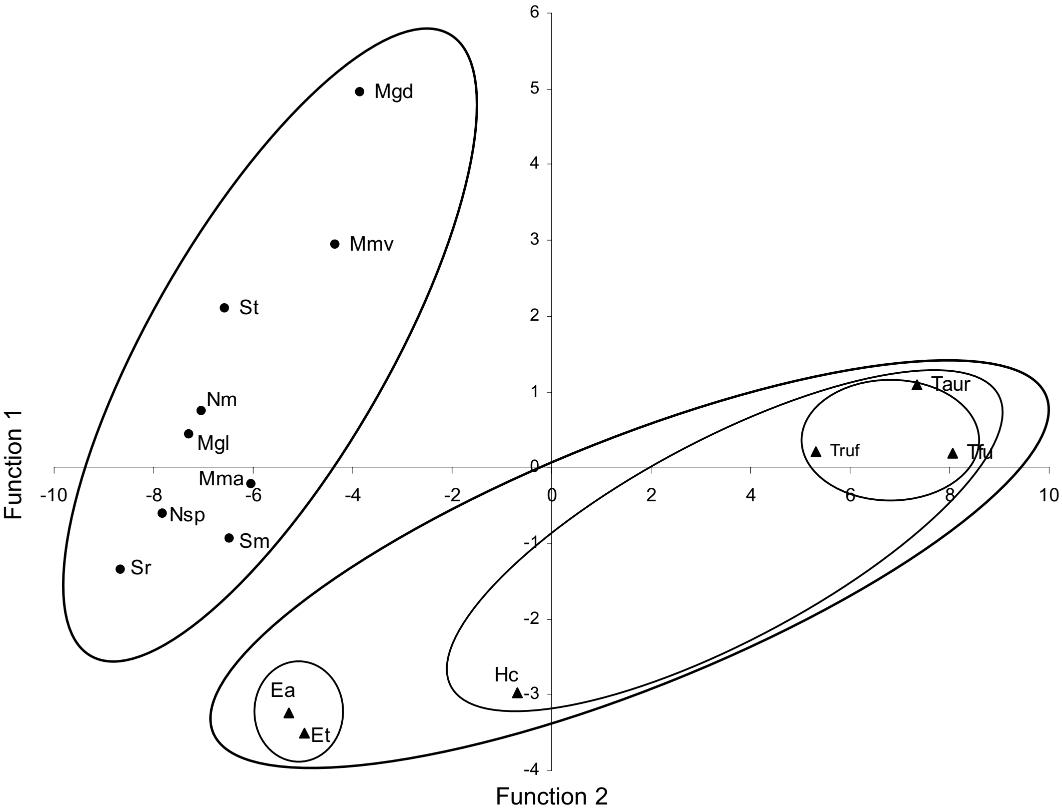

FIG. 10. Species group centroids (mean scores) with highest confidence intervals of the echolocations calls. (Ea) = *E. atrata*, (Et) = *E. tiavato*, (Nsp) = *Neoromicia* sp., (Hc) = *H. commersoni*, (Mgl) = *Miniopterus gleni*, (Mma) = *M. majori/ sororculus* (Mmv) = *M. manavi* sen. lat., (Mgd) = *M. goudoti*, (Nm) = *N. malagasyensi*, (Sr) = *S. robustus*, (St) = *S. tandrefana*, (Tfu) = *T. furculus*, (Truf) = *T. menamena*, (Taur) = *T. auritus*, and (Sm) = *S. marovaza*

H. commersoni and *T. menamena* and these species could be identified without ambiguity so that time-expansion and heterodyne detection methods are suitable for studying these species in natural conditions. Barclay and Brigham (2004) reported that calls with characteristics in the zone of overlap cannot be assigned to a particular species with 100% certainty. In the current study, this geographic overlap is apparent in *T. auritus* and *T. furculus* (Table 4). However these species occur allopatrically in western Madagascar and as their FmaxE is higher than both *H. commersoni* and *T. menamena*, they can be readily identified in the field using bat detectors within their respective ranges.

Vespertilionidae

Calls from this family (here defined as FM/QCF) were generally characterized by a steep frequency modulation (FM part) followed by a shallow frequency modulation (QCF part). In this respect, the Vespertilionidae have echolocation calls that resemble the Molossidae but are distinct from the Hipposideridae, Emballonuridae and Myzopodidae (Russ *et al*., 2003). The family produced echolocation calls of similar design but different in frequencies between species except *M. goudoti* which produced broadband and short, steep FM echolocation calls.

Habitat clutter influences the echolocation calls of some taxa including the Vespertilionidae; *Miniopterus* calls become more broadband and shorter in duration in open habitats, and bats of the genus *Myotis* often alter their echolocation calls in different foraging conditions (Russ *et al*., 2003). Greater effort is required in Madagascar to document how habitat clutter influences the echolocation of vespertilionids especially as the number of species in this family reported from the island has risen dramatically in the previous five years (Racey *et al*., In press). Moreover, based on multivariate analysis of measured parameters of echolocation calls, 40.0% to 92.5% of individuals were correctly classified to species, indicating that these parameters can be used to identify individuals to species level with varying degrees of accuracy.

Griffin (1958) originally drew attention to differences between nasal emitting bats, with their characteristic noseleaves, and oral emitting bats.

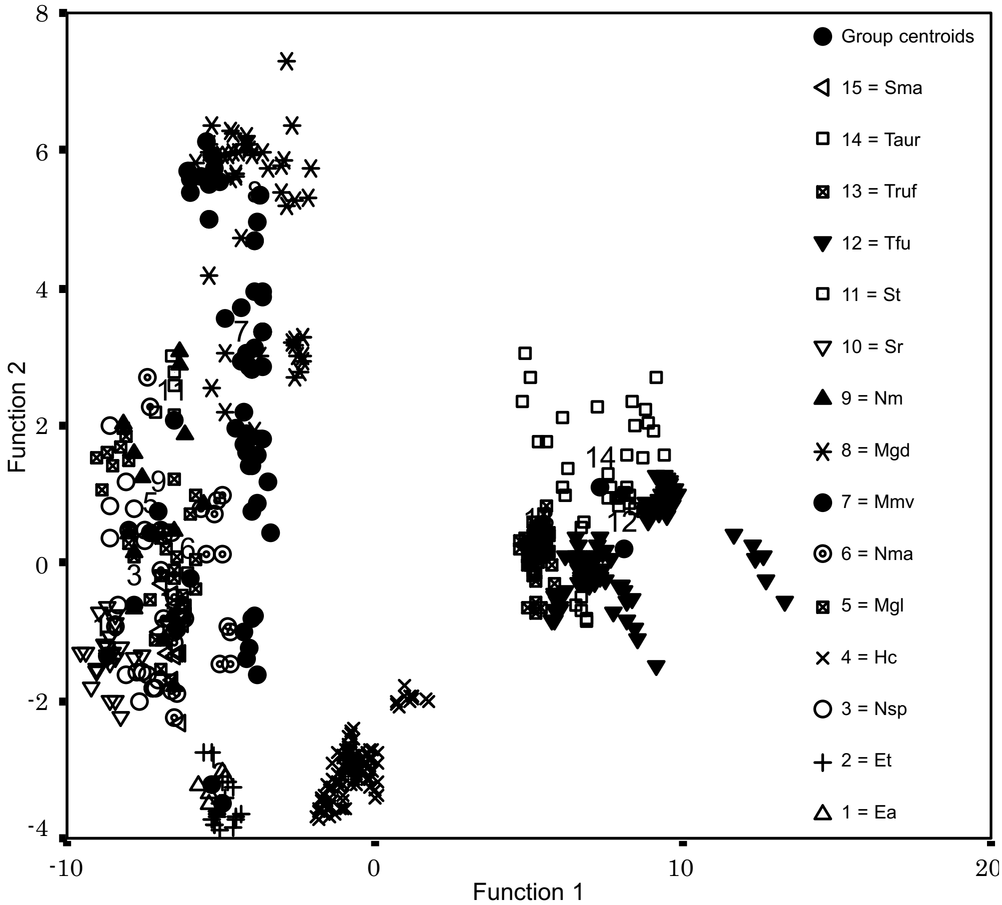

FIG. 11. Canonical Discriminant Functions. 1 = *E. atrata* (Ea), 2 = *E. tiavato* (Et), 3 = *Neoromicia* sp. (Nsp), 4 = *H. commersoni* (Hc), 5 = *M. gleni* (Mgl), 6 = *M. majori/sororculus* (Mma), 7 = *M. manavi* sen lat. (Mmv), 8 = *M. goudoti* (Mgd), 9 = *N. malagasyensis* (Nm), 10 = *S. robustus* (Sr), 11 = *S. tandrefana* (St), 12 = *T. furculus* (Tfu), 13 = *T. menamena* (Truf), 14 = *T. auritus* (Taur), and 15 = *S. marovaza* (Sm)

Our observations confirm that all hipposiderid (nasal emitting) bats produced echolocation calls of similar structure, different in frequencies but distinct from those of oral emitting bats (vespertilionids and emballonurids) which produced calls more varied in structure and frequency (Figs. 9, 10 and 11). Moreover, of the seven echolocation call types described by Jones and Teeling (2006), only two were represented in the present study. The short, broadband calls with a dominant fundamental harmonic are mainly observed within the Vesperilionidae and constant frequency signals are emitted by bats in the Hipposideridae and Emballonuridae.

Over the space of a few years, taxonomic research on the malagasy bat fauna has revealed many new and cryptic species, and it is likely that more remain to be described. In addition, as echolocation call structure combined with wing morphology are important indicators of foraging ecology (Jennings *et al.*, 2004), the continued study of these parameters is required for a better understanding of the ecology of Madagascar's bats.

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