Building evidence for conservation globally

Journal of Threatened Taxa

10.11609/jott.2023.15.10.23931-24150
www.threatenedtaxa.org

26 October 2023 (Online & Print)
15(10): 23931–24150
ISSN 0974-7907 (Online)
ISSN 0974-7893 (Print)

Open Access

ISSN 0974-7907 (Online); ISSN 0974-7893 (Print)

Publisher
Wildlife Information Liaison Development Society
www.wild.zooreach.org

Host
Zoo Outreach Organization
www.zooreach.org

43/2 Varadarajulu Nagar, 5th Street West, Ganapathy, Coimbatore, Tamil Nadu 641006, India
Registered Office: 3A2 Varadarajulu Nagar, FCI Road, Ganapathy, Coimbatore, Tamil Nadu 641006, India
Ph: +91 9385339863 | www.threatenedtaxa.org
Email: sanjay@threatenedtaxa.org

For Focus, Scope, Aims, and Policies, visit https://threatenedtaxa.org/index.php/JoTT/aims_scope
For Article Submission Guidelines, visit https://threatenedtaxa.org/index.php/JoTT/about/submissions
For Policies against Scientific Misconduct, visit https://threatenedtaxa.org/index.php/JoTT/policies_various

continued on the back inside cover

Cover: Orange Oakleaf *Kallima inachus* with colour pencils and watercolor wash by Elakshi Mahika Molur adapted from a workshop by Lenin Raj.

Journal of Threatened Taxa | www.threatenedtaxa.org | 26 October 2023 | 15(10): 23931–23951
ISSN 0974-7907 (Online) | ISSN 0974-7893 (Print)
https://doi.org/10.11609/jott.8597.15.10.23931-23951
#8597 | Received 16 June 2023 | Final received 24 July 2023 | Finally accepted 01 September 2023

ARTICLE

Echolocation call characterization of insectivorous bats from caves and karst areas in southern Luzon Island, Philippines

Renz Angelo Duco [1], Anna Pauline de Guia [2], Judeline Dimalibot [3†], Phillip Alviola [4] & Juan Carlos Gonzalez [5]

[1] Biodiversity Research Laboratory, Institute of Biology, University of the Philippines Diliman, Quezon City 1101, Philippines.
[1,2,3,4,5] Museum of Natural History, CFNR Quadrangle, Upper Campus, University of the Philippines, Los Baños College, Laguna 4031, Philippines.
[2,3,4,5] Institute of Biological Sciences, College of Arts and Sciences, University of the Philippines, Los Baños, College, Laguna 4031, Philippines.
[1] rjduco@up.edu.ph (corresponding author), [2] aodeguia@up.edu.ph, [3] jcdimalibot@up.edu.ph, [4] paalviola@up.edu.ph, [5] jtgonzalez@up.edu.ph
† deceased.

Abstract: Bats are excellent bioindicators and are increasingly used to assess ecosystem health and monitor changes in the environment. Due to increased awareness of the potential transmission of pathogens from bats to humans and recognizing the limitations of traditional bat sampling methods, the use of of non-invasive sampling techniques such as bat recorders were recommended for field-based monitoring studies. In the Philippines, however, bat bioacoustics is still a growing field, and the scarcity of acoustic data hinders the use of echolocation calls to conduct accurate inventories and population monitoring of echolocating bats. Here, we recorded and characterized echolocation calls of insectivorous bats from caves and karst areas located in southern Luzon Island, Philippines. In addition, we compared our results with other studies performed within and outside the country to identify possible regional and local variation in acoustic characters for some species. A total of 441 echolocation calls were recorded from six bat families: Hipposideridae (five species), Rhinolophidae (five species), Vespertilionidae (three species), Miniopteridae (two species), Megadermatidae (one species), and Emballonuridae (one species). Discriminant function analyses (DFA) with leave-one-out cross validation correctly classified bats emitting calls dominated with a constant frequency (CF) component (rhinolophids and hipposiderids) with >97% success and those producing frequency modulated (FM) calls (Miniopteridae and Vespertilionidae) with 88.9% success. We report echolocation calls for Philippine population of two species (*Megaderma spasma* and *Hipposideros lekaguli*) for the first time. Moreover, we present geographical variations in call frequencies for some species by comparing previously reported acoustic data elsewhere across the species' range. This underscores the importance of establishing a readily accessible and comprehensive local reference library of echolocation calls which would serve as a valuable resource for examining taxonomic identities of echolocating bats, particularly those whose calls exhibit biogeographic variations.

Keywords: Bat recorders, call frequencies, call library, discriminant function analysis, echolocating bats, ecotourism, limestone forest.

Editor: Chelmala Srinivasulu, Osmania University, Hyderabad, India. **Date of publication:** 26 October 2023 (online & print)

Citation: Duco, R.A., A.P. de Guia, J. Dimalibot, P. Alviola & J.C. Gonzalez (2023). Echolocation call characterization of insectivorous bats from caves and karst areas in southern Luzon Island, Philippines. *Journal of Threatened Taxa* 15(10): 23931–23951. https://doi.org/10.11609/jott.8597.15.10.23931-23951

Funding: This study was funded by the DOST Philippines (Department of Science and Technology) through the NICER-CAVES (Center for Cave Ecosystems Research) Program of the UPLB Museum of Natural History.

Competing interests: The authors declare no competing interests.

Author details: RAD is currently a research associate of the Biodiversity Research Laboratory at the Institute of Biology, University of the Philippines DIliman. APOdG is a Professor at the Animal Biology Division (ABD) of the Institute of Biological Sciences (IBS) and the curator for small mammals of the University of the Philippines Los Baños Museum of Natural History (UPLB MNH). JCD served as a curator for tree shrews and other mammals at UPLB MNH and also a faculty member of ABD. PAA is currently the MNH's curator for small mammals and other wildlife and an Associate Professor at IBS. JCTG is MNH's curator for birds and Professor of Zoology at ABD.

Author contributions & **Acknowledgements:** See end of this article.

INTRODUCTION

Bats are of great importance because they maintain ecosystem balance in tropical forests and their sensitivity to anthropogenic disturbances makes them excellent bioindicators in assessing ecosystem health and monitoring changes in the environment (Jones et al. 2009). Traditionally, bats are studied by capturing them using mist nets (Kunz & Kurta 1988; Sedlock 2001), although some studies found that the use of harp traps are more effective in capturing echolocating bats (Tidemann & Woodside 1978; Francis 1989). Sampling bats using mist nets provides a more standardized method of measuring bat abundance; however, this method is prone to sampling biases since mist nets are usually placed below the canopy. This practice underestimates bat diversity of an area since there are relatively more species of bats on the upper forest layers (O'Farrell & Gannon 1999; Larsen et al. 2007; Gonzalez et al. 2020). Moreover, mist nets are more biased towards larger–bodied bats which do not have the ability to evade mist nets like most echolocating bats (Larsen et al. 2007).

There has been a growing global trend in utilizing ultrasonic detectors and recording echolocation calls as an alternative approach for a non-invasive and passive means to document the occurrence of echolocating bats, investigate their ecology, behavior, and responses to various anthropogenic pressures, and identify habitat and important areas for conservation of these species (Rydell 1991; Siemers & Schaub 2011; Pauwels et al. 2019). Species-specific acoustic cues and characteristics allowed the accurate classification of species and the use of automatic classifiers have enabled rapid species identification using computer software programs (Adams et al. 2010; Agranat 2013; Amberong et al. 2021). Further, continuous advancements in ultrasonic bat recorders to cater the need for this growing field have led to improved features that facilitate the collection and analysis of larger datasets. These advancements have contributed to increased inventory completeness in studies focused on bat assemblages and have made long-term monitoring experiments feasible (Lausen & Barclay 2006; MacSwiney et al. 2008). Lastly, considering the recent Covid-19 pandemic and the potential transmission of bat-borne viruses and other zoonotic pathogens, the use of acoustic surveys offers a means of studying bats without direct contact, thereby reducing the risk of zoonotic transmissions (Nuñez et al. 2020; Pekar et al. 2022).

While acoustically monitoring bats ensures researchers' safety and significantly cuts the time and effort in surveying, there is still paucity of comprehensive and reliable bat call libraries in many regions which is an essential component for accurate species identification of echolocating bats (Karine & Kalko 2001). In the Philippines, bat bioacoustics is still in its infancy, and a comprehensive bat call library is still lacking. Relevant studies based on bioacoustics of bats are limited to very few localities and islands such as in Luzon (Sedlock 2001; Sedlock & Weyandt 2009; Esselstyn et al. 2012; Dimaculangan et al. 2019; Sedlock et al. 2019; Amberong et al. 2021; Taray et al. 2021), Panay Island (Mould 2012), Bohol Island (Phelps et al. 2018; Sedlock et al. 2014a), and Siquijor Island (Sedlock et al. 2014b). Previous works have focused on examining taxonomy (Sedlock & Weyandt 2009; Sedlock et al. 2014b) and studying behaviour, cave emergence, and activity (Dimaculangan et al. 2019; Sedlock et al. 2019) using few available acoustic data. Meanwhile, the works of Sedlock (2001), Amberong et al. (2021), and Taray et al. (2021) have delved into the characterization of acoustic calls of echolocating bats, aiming to establish a foundational dataset for creating a local bat call library for the Philippines. The archipelagic nature of the Philippines also provides an avenue to examine possible local echolocation variation or dialects, especially for endemic species with limited population dispersion.

Caves provide specific and stable microclimatic conditions, including temperature, relative humidity, and air quality, along with physical structures that are crucial for the survival of many bat populations. These factors provide a suitable environment for protection, roosting, and feeding (McCracken 1989; Murray & Kunz 2005). Among the 79 bat species present in the Philippines, 49 are known to roost in caves (Heaney et al. 2010). However, threats to these resident cave fauna are still rampant, including hunting, habitat destruction, and disturbances caused by unregulated human visits, leading to roost abandonment and rapid population decline (Mould 2012; Domingo & Buenavista 2018; Alcazar et al. 2020). Moreover, caves are also often overlooked and unprotected due to harsh conditions for proper assessment, research, and mapping of these landscapes (Tanalgo et al. 2022). Out of the 3500 caves identified in the Philippines, only approximately 40% have been adequately assessed and protected (BMB CAWED 2021). The lack of protection exposes these caves to potential exploitation, resulting in adverse long-term impacts on wildlife populations, such as reduced species richness and diversity, as well as the destruction of cave features. To address these challenges, rapid and cost-effective methods for surveying and monitoring cave bat populations, such as acoustic surveys, would be instrumental in assessing more caves in the country and protecting cave bats.

Here we describe echolocation calls of some insectivorous bat species we recorded from caves and karst areas in southern Luzon Island, Philippines and evaluate the potential of utilizing acoustic characters in identifying echolocating bat species. In addition, we want to assess possible geographic variation in echolocation call characteristics of some species by examining other existing acoustic data and studies done within and outside the country. Threats observed in the study areas and conservation implications of our results are also discussed. With this study, we aim to contribute to the building of a comprehensive reference library of bat echolocation calls for the Philippines and provide a non-intrusive and cost-effective tool for monitoring insectivorous bats.

MATERIALS AND METHODS

Study Site and Bat Sampling

Study sites were located in the Calabarzon Region, southern Luzon Island, Philippines. Four caves and surrounding karst forest areas were sampled between 2021 and 2023: (1) Cathedral Cave in Cavinti, Laguna Province, (2) Sungwan Cave in Tayabas City, Quezon Province, (3) Kamantigue Cave in Lobo, Batangas Province, and (4) Pamitinan Cave inside the Pamitinan Protected Landscape (PPL), Rodriguez, Rizal Province (Figure 1). We captured bats from sunset (1800 h) until 2000 h using mist-nets (12 x 2.6 m with 36 mm mesh). Nets were set up in cave openings, forest interior, and across water bodies and were checked at 10 min intervals.

Bat captures were identified to species level using external characters and morphometric measurements such as forearm length (FA), following an identification guide by Ingle & Heaney (1992). Wing biopsy tissue samples from released individuals or muscle tissues from voucher specimens were also collected for molecular analysis. All voucher specimens were deposited at

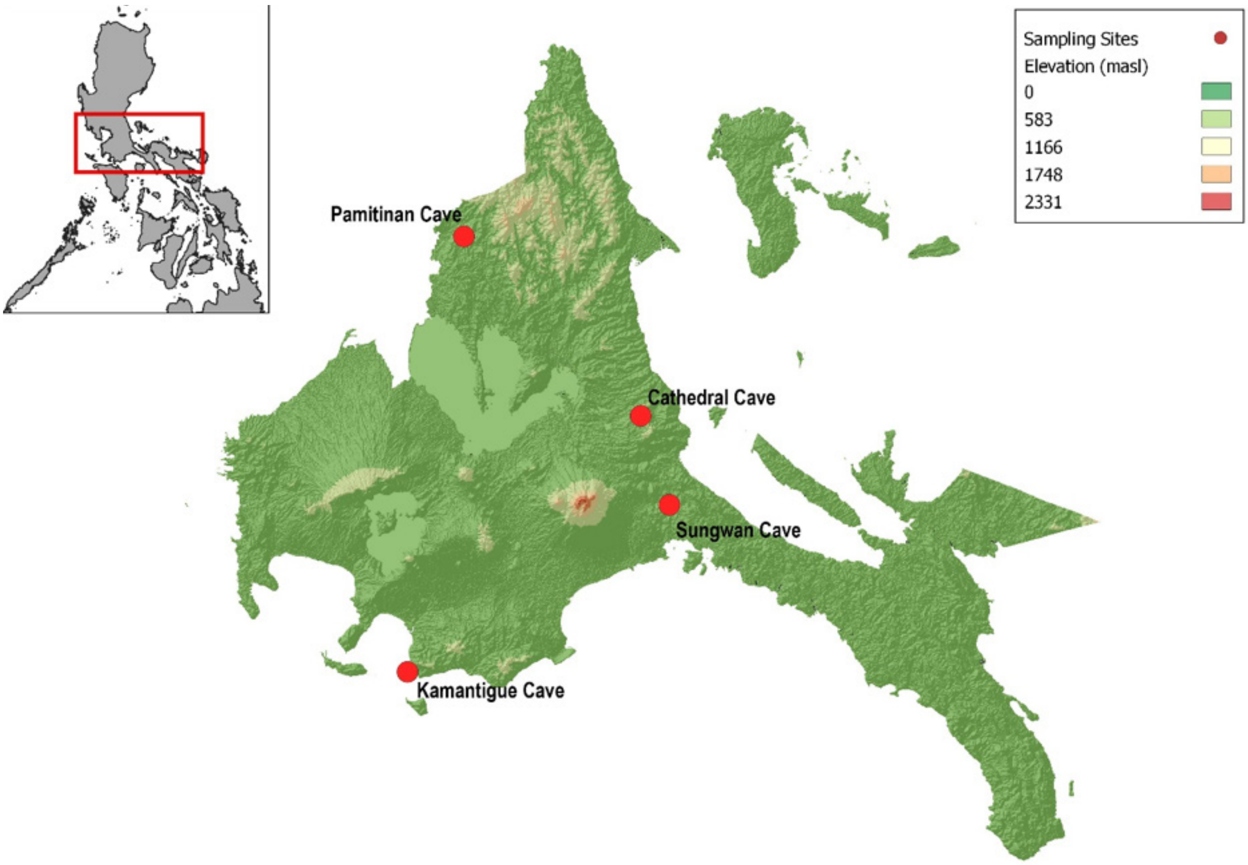

Figure 1. CALABARZON Region depicting locations of caves surveyed for sampling during this study.

University of the Philippines Los Baños-Museum of Natural History Zoological Collection. Field sampling was covered by Wildlife Gratuitous Permit numbers R4A-WGP-2021-LAG-004, R4A-WGP-2021-QUE-005, R4A-WGP-2021-BAT-006, and R4A-WGP-2021-RIZ-010.

Acoustic recording and description of echolocation calls

Echolocation calls were recorded using M500 USB Ultrasound Microphone attached to a laptop PC (Pettersson Elektronic AB, Upsala, Sweden) with a sampling rate of up to 768 kHz and a frequency range of 5–235 kHz. Recordings were made from adult bats released in an enclosure (polyester camping tent with dimensions 2.74 x 2.1 x 1.5 m) to allow recording of echolocation call of bats on free flight for maximum of one minute per individual. Calls were recorded near the sampling site within two hours after retrieval. Call recordings were saved in WAV format on a flash card and call files were displayed as spectrograms using BatSound v. 4.2.1 (Pettersson Elektronik AB) with a sampling rate of 500 kHz with 16 bits/sample. Spectrograms were examined using 512-size fast fourier transformation (FFT) in a Hanning window. Three high quality search calls with high signal-to-noise ratio were chosen for analysis from each individual.

The following call parameters were measured from the spectrograms of each selected call (Figure 2): maximum frequency (Fmax), minimum frequency (Fmin), initial frequency (Fini), terminal frequency (Fter), call duration (D); frequency is given in kilohertz (kHz) while time is expressed in millisecond (ms). In addition, frequency at maximum energy (FmaxE) was measured from the power spectra.

Based on spectrograms, calls were described on the basis of their shape: (1) CF/FM call – consists of a constant frequency component terminated by a frequency modulation, (2) FM/CF/FM – constant frequency

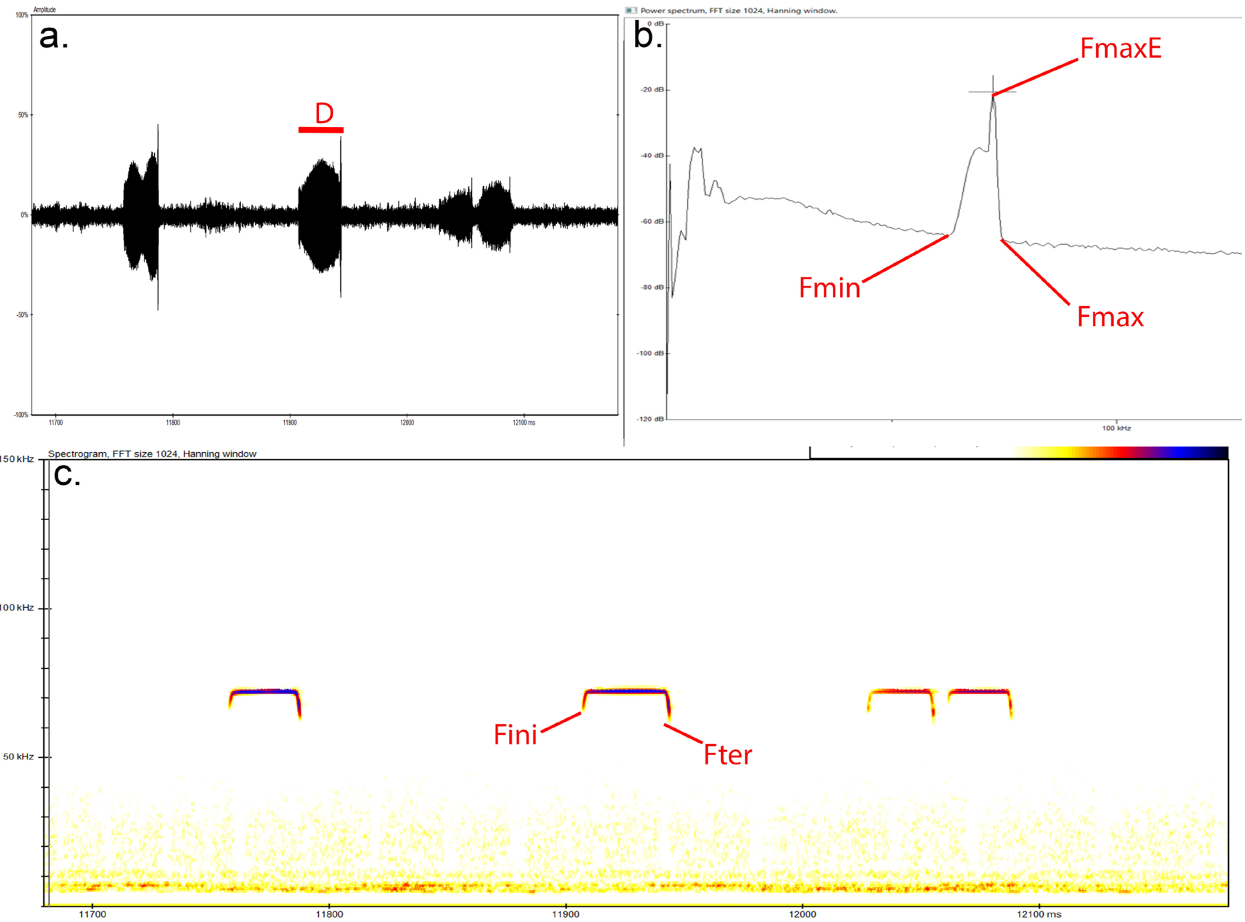

Figure 2. Call parameters extracted from call recordings of bats collected. a. Oscillogram of BatSound software where call duration (D) was measured; b. Power spectrum of the software showing the call variables frequency at maximum energy (FmaxE), minimum frequency (Fmin), and maximum frequency (Fmax); c. Spectrogram where initial frequency (Fini) and terminal frequency (Fter) were measured.

preceded and terminated by frequency modulation component, (3) FM – composed mainly of a steep pure frequency modulated sweep, and (4) Multiharmonic – pulses composed of two or more harmonics.

To investigate inter- and intraspecific variation in echolocation calls for the species we have sampled, we tabulated and analyzed available acoustic metrics reported elsewhere. This includes published research papers, bat acoustic identification guides, and local bat call libraries.

Statistical analysis

Intraspecific variation in call frequency across our samples was first investigated by performing Kruskal-Wallis test with post-hoc Mann-Whitney test. We compared echolocation call parameters between sexes and across the four study areas. No significant difference in the call parameters was observed for all species analyzed ($p < 0.05$), thus, data were pooled in subsequent analyses.

Discriminant function analysis (DFA) with leave-one-out cross-validation was used to determine whether species could be separated in independent groups and to test the extent to which the measured call parameters could be used to identify species (Fils et al. 2018). Except for bats with multiharmonic calls, we carried out DFA separately for each of the three call types identified: CF/FM bats (Hipposideridae), CF/FM/CF bats (Rhinolophidae), and FM-dominated bats (Vespertilionidae and Miniopteridae). Wilk's lambda values were obtained to test for statistical significance of the discriminant functions in discriminating calls between species (Pedro & Simonetti 2013). We also plotted group centroids with 95% confidence limits to present a graphical representation of the separation of species within families based on their discriminant functions.

Lastly, descriptive statistics (mean ± SE) for all call parameters were also computed for each species. All analyses were performed using IBM SPSS Statistics for Windows v 20.0.

RESULTS

Echolocation call descriptions

In total, we recorded and analyzed 441 echolocation pulses belonging to 147 individuals from six bat families: Hipposideridae (five species), Rhinolophidae (five species), Vespertilionidae (three species), Miniopteridae (two species), Megadermatidae (one species), and Emballonuridae (one species) (Table 1).

Hipposideridae calls showed the typical CF/FM call characteristic of the family wherein calls begin with a constant frequency component then terminate with a descending frequency modulated component (Figure 3A). Call frequency values were highest for *Hipposideros antricola*, followed by *Hipposideros bicolor*, and *Hipposideros pygmaeus* (Table 1). Call duration was longest for *H. diadema* (13 ms). All of the call parameters measured did not overlap between the five species.

Rhinolophidae calls were characterized by a long CF component preceded and terminated by an FM component (Table 1, Figure 3B). FmaxE values ranged from 28.2–40.0 kHz in *Rhinolophus philippinensis* to 73.3–76.3 kHz in *R. macrotis*. Most of the call parameters measured showed little to no overlap in values between species.

Vespertilionidae produced predominantly frequency-modulated (FM) calls (Figure 3C). Two species of the genus *Myotis* had calls characterized by a steep FM sweep of short duration (<4 ms). Based on the call parameters analyzed, the two *Myotis* species can easily be distinguished from one another; *Myotis horsfieldii* had lower call frequency values for all the parameters measured than *Myotis muricola* (Table 1). Meanwhile, calls of species within genus *Miniopterus* and *Tylonycteris* have steep FM components terminated by a short narrowband tail (Figure 3C). Between the two *Miniopterus* species, *M. paululus* emitted higher frequency for all call parameters measured (Table 1). Call measurements of *Tylonycteris pachypus* meanwhile overlapped with those of *M. paululus*.

Megadermatidae call was characterized by broadband FM, multi-harmonic signals of short duration. In contrast, calls of *Taphozous melanopogon* are characterized by having long multiharmonic call signals with most energy contained on the first three harmonics (Figure 3D).

Discriminant function analysis (DFA)

Hipposideridae (CF/FM)

In total, 97.8% of the original grouped cases were correctly classified to the five hipposiderid species (Wilk's $\lambda = 0.003$, $p < 0.001$) with Discriminant functions (DF) 1 and 2 explaining 97.1% and 2.9% of the total variance observed, respectively (Figure 4). Among the call parameters used in DFA, FmaxE was the most useful in discriminating between the species (Wilk's $\lambda = 0.042$, $p < 0.001$). Classification rates for the *Hipposideros* species are high based on the results of DFA; all species except *H. antricola* can be identified unambiguously with 100% success classification rate.

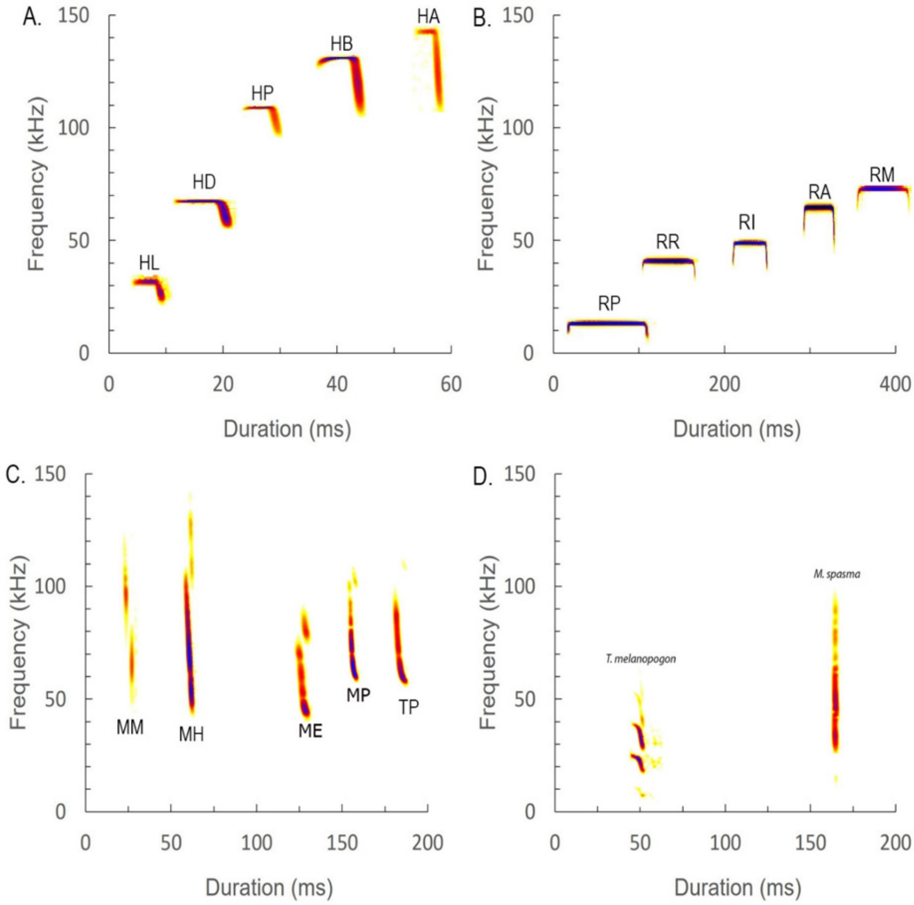

Figure 3. Spectrograms of representative echolocation calls of insectivorous bats recorded from caves and karst areas in southern Luzon Island, Philippines: A. Hipposideridae (HA: *H. antricola*, HB: *H. bicolor*, HD: *H. diadema*, HL: *H. lekaguli* HP: *H. pygmaeus*), B. Rhinolophidae (RP: *R. philippinensis*, RR: *R. rufus*, RI: *R.* inops, RA: *R. arcuatus*, RM: *R. macrotis*), C. Vespertilionidae (MM: *M. muricola*, MH: *M. horsfieldii*, MP: *M. paululus*, ME: *M. eschscholtzii*, TP: *T. pachypus*), and D. Multiharmonic bat calls.

Rhinolophidae (FM/CF/FM)

DFA analysis using the six acoustic parameters gave an overall correct classification of 99.4% of the calls after cross-validation (Wilk's $\lambda = 0.006$, $p < 0.001$) (Figure 5). Further, 99.1% of the variation was explained by the first two discriminant functions, with FmaxE being the most important parameter in discriminating between species (Wilk's $\lambda = 0.03$, $p < 0.001$). Calls emitted by all rhinolophids were 100% correctly identified and grouped independently of the rest of the species, except for *R. philippinensis* with 93.3% correct classification rate.

Vespertilionidae and Miniopteridae (FM-dominated)

Cross-validated DFA analysis resulted in 86.7% correct classification rate (Wilk's $\lambda = 0.046$, $p < 0.001$) (Figure 6). The most important variable in discriminating between the three species was minimal frequency (Wilk's $\lambda = 0.169$, $p < 0.001$) and terminal frequency (Wilk's $\lambda = 0.136$, $p < 0.001$). Correct classification rates (100%) were achieved for the three vespertilionids: *M. horsfieldii*, *M. muricola*, and *M. eschscholtzii*. Meanwhile, cross validated DFA for *M. paululus* and *T. pachypus* showed <20% misclassification rate to each other.

DISCUSSION

Acoustic identification and DFA Classification success

Reference calls were collected from 147 bat individuals across 17 species and six families. These calls provided additional data and contributed to efforts in building a call library for the acoustic identification of bats in the Philippines (Amberong et al. 2021). Moreover, these acoustic data will also be of great help in developing acoustic classifiers in the future, to utilize passive acoustic monitoring more effectively.

Table 1. List of insectivorous bats collected in four caves sampled in southern Luzon Island, Philippines including their call structure and summary statistics (mean ± SE) for all echolocation call parameters measured (D: Duration, FmaxE: frequency at maximum energy, Fini: initial frequency, Fter: terminal frequency, Fmax: Maximum frequency, Fmin: minimum frequency, n: number of calls analyzed, nInd: number of individual bats recorded). "+" indicates the presence of the species in the study areas (CC: Cavinti Cave, SC: Sungwan Cave, PC: Pamitinan Cave, KC: Kamantigue Cave).

Species	n	nInd	Call structure	D (ms)	FmaxE (kHz)	Fini (kHz)	Fter (kHz)	Fmax (kHz)	Fmin (kHz)	CC	SC	PC	KC
Hipposideridae													
Hipposideros antricola	21	7	CF/FM	6.03 ± 0.25	146.00 ± 1.6	144.21 ± 1.2	124.73 ± 2.5	146.09 ± 0.9	124.15 ± 2.9			+	+
Hipposideros bicolor	42	14	CF/FM	4.93 ± 0.7	133.24 ± 8.4	131.65 ± 9.3	111.64 ± 14.7	133.57 ± 7.2	109.59 ± 15.9				+
Hipposideros diadema	15	5	CF/FM	13.41 ± 2.8	69.05 ± 3.1	67.89 ± 2.7	57.48 ± 4.2	70.21 ± 2.0	55.78 ± 4.6		+		
Hipposideros lekaguli	33	11	CF/FM	8.48 ± 2.6	37.18 ± 1.8	36.15 ± 2.5	31.48 ± 3.0	38.09 ± 1.7	30.56 ± 2.5	+	+		
Hipposideros pygmaeus	24	8	CF/FM	3.93 ± 1.6	110.5 ± 0.8	109.13 ± 1.9	94.27 ± 1.9	112.23 ± 0.7	93.30 ± 0.2	+			
Rhinolophidae													
Rhinolophus arcuatus	108	36	FM/CF/FM	36.82 ± 0.9	65.76 ± 0.2	58.47 ± 0.3	53.51 ± 0.3	66.36 ± 0.9	50.96 ± 0.3	+	+	+	+
Rhinolophus inops	6	2	FM/CF/FM	49.10 ± 2.19	49.55 ± 0.22	43.13 ± 0.88	41.78 ± 0.76	50.37 ± 0.16	37.35 ± 0.51		+		
Rhinolophus macrotis	6	2	FM/CF/FM	36.65 ± 2.07	74.60 ± 0.42	66.40 ± 0.96	64.23 ± 0.74	74.38 ± 0.63	61.56 ± 0.59		+		
Rhinolophus philippinensis	15	5	FM/CF/FM	73.01 ± 3.30	30.73 ± 0.71	26.23 ± 0.44	24.50 ± 0.46	31.47 ± 0.63	22.44 ± 0.56	+	+		
Rhinolophus rufus	30	10	FM/CF/FM	47.74 ± 2.15	42.05 ± 7.1	34.75 ± 1.4	33.03 ± 1.0	42.39 ± 0.9	31.7 ± 1.3	+	+		
Vespertilionidae													
Myotis horsfieldii	9	3	FM	3.65 ± 0.11	70.02 ± 0.77	106.6 ± 0.79	42.37 ± 0.28	109.47 ± 0.71	39.33 ± 0.22	+	+		
Myotis muricola	6	2	FM	3.43 ± 0.18	82.37 ± 0.82	108.22 ± 1.45	44.27 ± 1.28	112.2 ± 2.00	42.17 ± 1.04		+		
Tylonycteris pachypus	6	2	FM/QCF	3.15 ± 0.5	69.37 ± 1.4	111.21 ± 11.6	59.52 ± 3.1	115.96 ± 11.6	55.8 ± 4.1			+	
Miniopteridae													
Miniopterus paululus	57	19	FM/QCF	2.68 ± 0.10	70.77 ± 0.27	109.38 ± 1.70	61.82 ± 0.37	120.42 ± 2.16	60.94 ± 0.31	+	+	+	
Miniopterus eschscholtzii	12	4	FM/QCF	3.26 ± 0.40	53.13 ± 0.39	97.25 ± 1.27	45.88 ± 0.33	99.9 ± 1.38	44.25 ± 0.71		+	+	
Emballonuridae													
Taphozous melanopogon	45	15	Multiharmonic	4.01 ± 0.40	28.4 ± 0.31	29.4 ± 0.22	20.16 ±0.65	29.9 ± 0.21	22.18 ± 0.16				+
Megadermatidae													
Megaderma spasma	6	2	Multiharmonic	2.90 ± 0.21	48.0 ± 0.23	72.0 ± 0.62	40.0 ± 3.01	115.1 ± 2.63	17.2 ± 1.61	+	+		

Our results demonstrate accurate classification of bat calls to families by considering their call structure, and identification to species level to some extent by analyzing several echolocation call parameters using DFA. Among the CF emitting bats, families Hipposideridae and Rhinolophidae could be distinguished from each other with the presence of an FM sweep preceding the CF component in the latter. Calls of *Hipposideros* species are also generally of shorter duration (<20 ms) compared to rhinolophids (Hughes et al. 2010). Most of the call parameters measured showed little to no overlap in values between species, indicating the reliability of utilizing these variables for acoustic identification of these bats in our study site.

Meanwhile, calls of FM bats can easily be distinguished from the other families by having calls of short duration and a steep FM component. Within this group, calls could further be classified into those which have pure and steep FM sweep (genus *Myotis*) and with a narrowband tail terminating the FM sweep (genus *Miniopterus* and *Tylonycteris*). Lastly, *Taphozous melanopogon* (Emballonuridae) and *Megaderma*

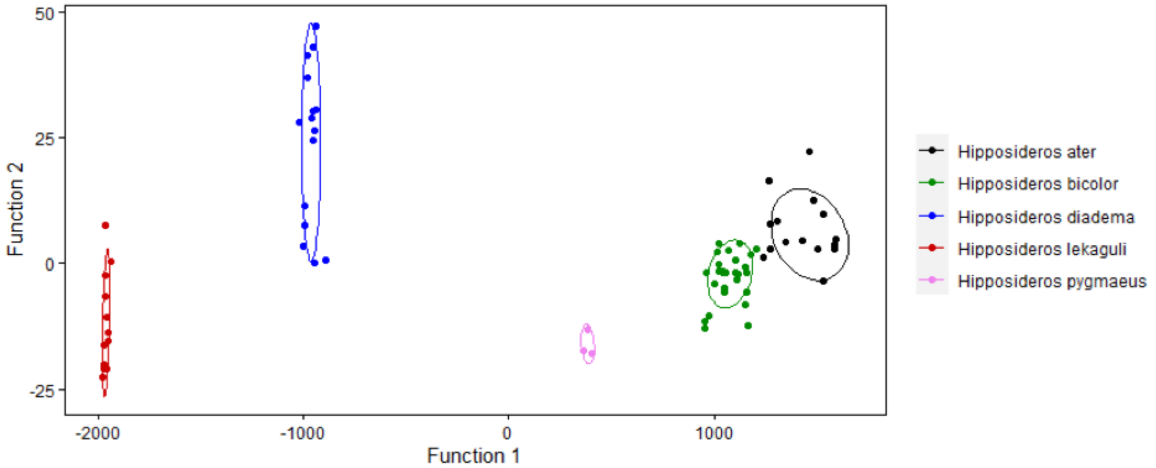

Figure 4. Canonical discriminant function biplots showing groupings of echolocation calls for the five *Hipposideros* species sampled in Luzon Island.

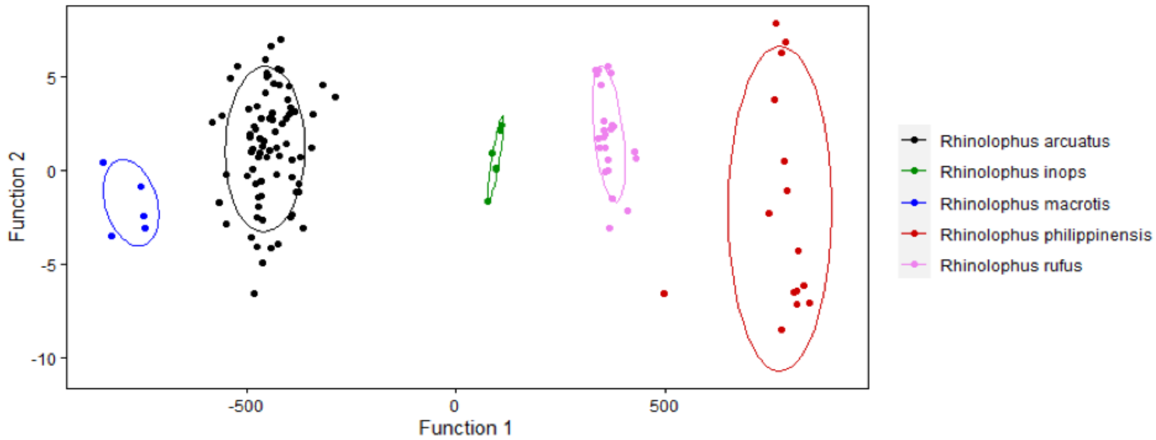

Figure 5. Canonical discriminant function biplots showing groupings of echolocation calls for the five phonic groups of *Rhinolophus* sampled in Luzon Island.

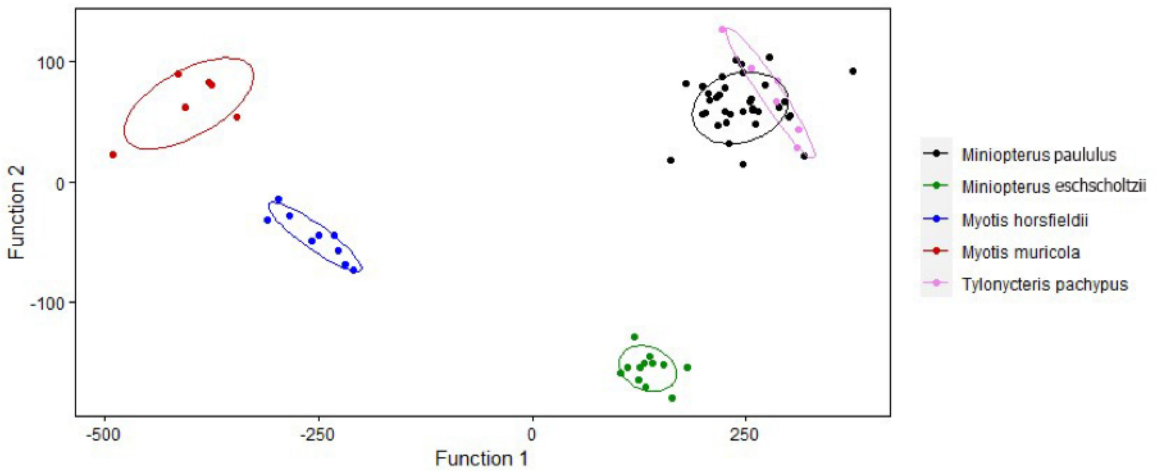

Figure 6. Canonical discriminant function biplots showing groupings of echolocation calls for the FM bats sampled in Luzon Island.

spasma (Megadermatidae) could be unambiguously identified by the presence of multiharmonic calls, the latter emitting broadband FM signals of short duration while the former having longer call duration at lower frequency.

Overall cross-validated DFA resulted in >88% correct classification to species for each family. Calls within each family have high rates (>80%) of classification to species, with most of the species (11 out of 15 species subjected to DFA) classified correctly. However, considering morphology for species discrimination is still important to avoid the risk of misidentification for some species which have overlapping call measurements. For instance, calls of *M. paululus* and *T. pachypus* have relatively lower rate of correct classification to each respective species based on the DFA (80.7% and 83.3%, respectively) but can easily be distinguished based on morphometrics.

Examining geographic variation in echolocation call characteristics based on previous records

As intraspecific variation in call frequency due to geographic location has been observed in many species of echolocating bats, it is essential to collect reference recording from as many locations as possible to reliably identify species whose call parameters overlap with those of others across their known distribution range, determine the accuracy of existing reference call data from different regions and localities, and help in identifying potential novel and cryptic species which have great implications in conservation management (Hughes et al. 2010; Wordley et al. 2014). Based on the compiled list of available acoustic data for the species we recorded, most of the species exhibited variation in their echolocation call frequencies across their range (Table 2), although very few data are publicly available for some species such as *R. inops*, *R. rufus*, and *H. lekaguli*. Further, echolocation call data for most islands and biogeographic regions in the Philippines are virtually absent, with most studies concentrated on Greater Luzon and central Philippine islands. This highlights the need for more acoustic studies in the country to generate a more reliable call library for Philippine bats.

CF bats (Hipposideridae and Rhinolophidae)

This study provided additional acoustic data for some endemic species of CF bats within the Philippines, which is useful for examining possible local variation in their call frequencies across the archipelago. For instance, acoustic data for *H. pygmaeus* are limited to those captured in central Philippine Islands such as Cebu, Bohol, and Siquijor (Sedlock et al. 2014a,b; Phelps et al. 2018). *H. pygmaeus* in these islands have average FmaxE values ranging from 93–102 kHz, which is relatively lower compared to the FmaxE value of 110 kHz recorded in this study. There is still great uncertainty on the taxonomic validity of Philippine hipposiderids which is evident in the recent molecular phylogenetic study done by Esselstyn et al. (2012) which suggested *H. pygmaeus* may comprise of three species.

Meanwhile, the two endemic rhinolophids in this study have little acoustic data reported to date. For instance, call data for *R. rufus* is limited to those collected in Bohol Island; frequency was well within the range with our samples (Sedlock et al. 2014a; Phelps et al. 2018). *R. rufus* is one of the largest insectivorous bats and currently under near threatened category by the IUCN (IUCN 2022). Little is known about its taxonomy due to lack of genetic and acoustic data for this species. Meanwhile, this is the third study to document and measure the echolocation call of *R. inops*; the first was by Sedlock et al. (2014b) in Bohol Island which recorded an average FmaxE value of 54 kHz, while Dimaculangan et al. (2019) recorded an average FmaxE value of 54.3 kHz for this species in Mt. Makiling in Luzon Island. Meanwhile, FmaxE of *R. inops* collected from this study averages at 50 kHz, which is slightly lower than the previous records. Additional acoustic data for these poorly known endemic species recorded from different localities in the country may be needed to further examine possible local dialects.

Meanwhile, the widespread species of CF bats recorded in this study are believed to comprise of species-complexes and may show variation in their call characteristics over their wide range. Cryptic species producing calls at different frequencies have been a recurring theme among CF bats (Kingston et al. 2001). For instance, FA length and FmaxE values of *R. philippinensis* recorded in the Philippines (Luzon Island: 28–30 kHz, Bohol Island: 31–32 kHz) (Sedlock et al. 2014a; Phelps et al. 2018; Amberong et al. 2021; this study) closely resemble the 'large form' (FA length: 52–59 mm) of *R. philippinensis* recorded in Australia (28–34 kHz) than the 'small form' (FA length: 50–53.5 mm, FmaxE: 40 kHz) (Pavey & Kutt 2008). Further, calls of *R. philippinensis* samples from the Philippines is close or well within the range of call frequencies of the species recorded in Borneo (32.8–34.8 kHz) (McArthur & Khan 2021) and in Sulawesi, Indonesia (27.2 kHz) (Kingston & Rossiter 2004) but are significantly lower compared to the other morphotypes discovered for the species: the 'small morph' emitting calls with an average of 53.6 kHz

Table 2. Echolocation call frequencies of bats recorded from this study and in other regions and localities.

Species	*n* individuals	Average FmaxE in kHz (range)	Fmax in kHz (range)	Fmin in kHz (range)	Country/ Region	Locality	Reference	Remarks
Hipposideridae								
Hipposideros antricola	7	146.00 ± 1.6	-	-	Philippines	Batangas	This study	-
	6	134.6 (128.5 – 138.1)	-	-	Philippines	Bulacan	Amberong et al. 2021	-
	6	138.6 ± 4.84	-	-	Philippines	Camarines Sur	Esselstyn et al. 2012	-
	9	140.3 ± 2.6 (134–143)	-	-	Philippines	Laguna	Sedlock 2001	-
	1	142	-	-	Philippines	Bohol	Esselstyn et al. 2012	-
	-	138.6	-	-	Philippines	Bohol	Phelps et al. 2018	-
	1	140	-	-	Philippines	Bohol	Sedlock et al. 2014a	-
Hipposideros bicolor	14	133.24 ± 8.4	-	-	Philippines	Batangas	This study	-
	1	136.2	-	-	Philippines	Quezon	Esselstyn et al. 2012	-
	2	126.4 ± 7.9 (119.0 – 133.7)	-	-	Philippines	Bulacan	Amberong et al. 2021	-
	2	111.1 ± 2.76	-	-	Philippines	Bohol	Esselstyn et al. 2012	-
	2	109.5 ± 2.1 (108.0–111.0)	-	-	Philippines	Bohol	Sedlock et al. 2014a	-
	-	133.13	-	-	Thailand	-	Hughes et al. 2010	-
	-	138	-	-	Indonesia	Sumatra	Huang et al. 2019	-
	-	133.3–143.1	-	-	Thailand	Satun	Bumrungsri 2010	-
	39	132.4 ± 2.4 (121.5 – 135.5)	-	-	Borneo	-	McArthur & Khan 2021	-
	-	136	-	-	Malaysia	-	Heller & Helversen 1989	-
	-	163.1–169.5	-	-	India	Madurai	Jones et al. 1994	-
Hipposideros diadema	5	69.05 ± 3.1	-	-	Philippines	Quezon	This study	-
	6	67 ± 0.9 (66–68)	-	-	Philippines	Makiling	Sedlock 2001	-
	1	69.5	-	-	Philippines	Quezon	Esselstyn et al. 2012	-
	<10	(68.0–70.0)	-	-	Philippines	Laguna	Sedlock et al. 2019	-
	6	70.0 ± 0.9 (66.5 – 72.0)	-	-	Philippines	Bulacan	Amberong et al. 2021	-
	164	69.4±0.1 (66.9–70.8)	-	-	Philippines	Panay	Mould 2012	-
	1	69.3	-	-	Philippines	Bohol	Phelps et al. 2018	-
	12	68.8 ± 1.1 (66.5–70.0)	-	-	Philippines	Bohol	Sedlock et al. 2014a	-
	12	69.5 ± 1.02	-	-	Philippines	Bohol	Esselstyn et al. 2012	-
	5	59.08 ± 0.24 (58.82–59.26)	-	-	India	Andaman Islands	Srinivasulu et al. 2016	-
	-	54.6–55.3	-	-	Thailand	Satun	Bumrungsri 2010	-
	-	61.45	-	-	Thailand	-	Hughes et al. 2010	-
	-	60	-	-	Thailand	-	Robinson 1996	-
	-	57.6	-	-	Indonesia	Sumatra	Huang et al. 2019	-
	2	67.52±2.26 (65.26–69.78)	-	-	Malaysia	Sarawak	Jinggong & Khan 2022	-
	21	67.5 ± 1.2 (65.1 – 69.4)	-	-	Borneo	-	McArthur & Khan 2021	-

Species	*n* individuals	Average FmaxE in kHz (range)	Fmax in kHz (range)	Fmin in kHz (range)	Country/ Region	Locality	Reference	Remarks
	3	65 ± 0.7 (64.5 – 66.7)	-	-	Brunei	-	Aylen 2021	-
	-	54.9	-	-	Australia	-	Fenton 1982	-
	1	56.94 (54–59)	-	-	PNG	Libano Sok	Leary & Pennay 2011	-
Hipposideros lekaguli	11	37.18 ± 1.8	-	-	Philippines	Laguna	This study	-
	-	49.73	-	-	Thailand	-	Hughes et al. 2010	-
	-	45–46	-	-	Malaysia	-	Wilson & Mittermeier 2019	-
Hipposideros pygmaeus	8	110.5 ± 0.8	-	-	Philippines	Laguna	This study	-
	15	111.4 ± 3.3 (105.5 – 115.7)	-	-	Philippines	Bulacan	Amberong et al. 2021	-
	17	93.0 ± 1.4 (90.0–95.0)	-	-	Philippines	Bohol	Sedlock et al. 2014a	-
	13	93.0 ± 1.35	-	-	Philippines	Bohol	Esselstyn et al. 2012	-
	-	95.5	-	-	Philippines	Bohol	Phelps et al. 2018	-
	11	102 (90.8–105.4)	-	-	Philippines	Cebu	Sedlock et al. 2014b	-
Rhinolophidae								
Rhinolophus arcuatus	36	65.76 ± 0.2	-	-	Philippines	Southern Luzon	This study	-
	13	71.2± 0.4 (71–72)	-	-	Philippines	Laguna	Sedlock 2001	-
	<10	(46.8–50.0)	-	-	Philippines	Laguna	Sedlock et al. 2019	-
	16	71.9 ± 1.5	-	-	Philippines	Laguna	Dimaculangan et al. 2019	-
	21	69.84 ± 1.70	-	-	Philippines	Quezon	Sedlock & Weyandt 2009	Narrow sella morph
	15	65.92 ± 2.30	-	-	Philippines	Quezon	Sedlock & Weyandt 2009	Wide sella morph
	29	66.81 ± 2.04 (62.17–69.34)	-	-	Philippines	Polilio Island	Taray et al. 2021	-
	23	65.0 ± 1.8 (61.8 –67.0)	-	-	Philippines	Bulacan	Amberong et al. 2021	-
	10	69.2±0.1 (68.3–69.3)	-	-	Philippines	Panay	Mould 2012	-
	11	67.48 (66.7–68.5)	-	-	Philippines	Cebu	Sedlock et al. 2014b	-
	-	68.7	-	-	Philippines	Bohol	Phelps et al. 2018	-
	32	68.7 ± 1.4 (67.0–72.0)	-	-	Philippines	Bohol	Sedlock et al. 2014a	-
	1	71.3 (70–72)	-	-	PNG	Libano Sok	Leary & Pennay 2011	-
	62	66.5 (58–69)	-	-	Malaysia	-	Novick 1958	-
Rhinolophus inops	2	49.55 ± 0.22	-	-	Philippines	Quezon	This study	FA length: 53mm
	9	54.3 ± 1.3	-	-	Philippines	Laguna	Dimaculangan et al. 2019	-
	12	54 (52.7– 55)	-	-	Philippines	Cebu	Sedlock et al. 2014b	-
Rhinolophus macrotis	2	74.60 ± 0.42	-	-	Philippines	Quezon	This study	FA length: 40mm
	2	74.0 ± 0.3 (73.7 – 74.4)	-	-	Philippines	Bulacan	Amberong et al. 2021	FA length: 41
	9	52.1 ± 0.80 (51–53)	-	-	Philippines	Laguna	Sedlock 2001	FA length: 44.1 – 46.4
	12	50.9 ± 1.1	-	-	Philippines	Laguna	Dimaculangan et al. 2019	FA length: 43 – 47

Species	*n* individuals	Average FmaxE in kHz (range)	Fmax in kHz (range)	Fmin in kHz (range)	Country/ Region	Locality	Reference	Remarks
	<10	(46.8–50.0)	-	-	Philippines	Laguna	Sedlock et al. 2019	-
	2	50	-	-	Philippines	Bohol	Sedlock et al. 2014a	FA length:44.1 – 46.3 (45.2)
	1	50	-	-	Philippines	Bohol	Phelps et al. 2018	-
	-	48	-	-	Philippines	-	Heller & Helversen 1989	FA length: 46.5
	1	75.1	-	-	Vietnam	Cu Lao Cham and Ly Son Archipelagos	Thong et al. 2019	FA length: 39.1
	-		-	-	Vietnam	Phia Oac	Tu et al. 2017	FA length: 48.6
	11	66.4 ± 0.9 (65.2–67.7)	-	-	Vietnam	-	Furey et al. 2009	-
	10	48.8 ± 0.6	-	-	China	Jiangxi	Sun et al. 2008	"large form", FA length: 45.2 ± 3.7
	2	64.7 ± 0.3	-	-	China	Jiangxi	Sun et al. 2008	"small form", FA length: 39.5–40
	9	57.3 ± 0.6	-	-	China	Yunnan	Sun et al. 2008	FA length: 42–43.5
	28	57.10 ± 0.68 (65.2–67.7)	-	-	China	Yunnan	Shi et al. 2009	FA length:41.8 ± 0.16
	6	66.7 ± 0.6	-	-	China	Guangxi	Sun et al. 2008	FA length: 39–40.5
	6	(47.2–53.9)	-	-	China	-	Zhang et al. 2009	FA length: 46.9–49.9
Rhinolophus philippinensis	5	30.73 ± 0.71	-	-	Philippines	Laguna, Quezon	This study	FA length:54–57mm
	2	28.9 ± 0.6 (28.2 – 29.5)	-	-	Philippines	Bulacan	Amberong et al. 2021	-
	5	31.2 ± 0.5 (31.0–32.0)	-	-	Philippines	Bohol	Sedlock et al. 2014a	-
	-	31.2	-	-	Philippines	Bohol	Phelps et al. 2018	-
	6	27.2 ± 0.2	-	-	Indonesia	Sulawesi	Kingston & Rossiter 2004	"large morph" FA length: 56.1 ± 1.5 mm
	3	39.0 ± 0.8	-	-	Indonesia	Buton Island	Kingston & Rossiter 2004	"Buton intermediate" FA length: 50.6 ± 1.4 mm
	1	41.7	-	-	Indonesia	Kabaena Island	Kingston & Rossiter 2004	"Kabaena intermediate" FA length: 48.4 mm
	11	53.6 ± 0.6	-	-	Indonesia	Sulawesi	Kingston & Rossiter 2004	"small morph" FA length: 47.0 ± 0.4 mm
	32	33.8 ± 0.5 (32.8 – 34.8)	-	-	Borneo	-	McArthur & Khan 2021	-
	-	36.6	-	-	Borneo	-	Francis & Habersetzer 1998	-
	-	(28–34)	-	-	Australia	-	Pavey & Kutt 2008	Large form FA length: 52–59mm
	-	40	-	-	Australia	-	Pavey & Kutt 2008	Small form FA length: 50–53mm
Rhinolophus rufus	10	42.05 ± 7.1	-	-	Philippines	Southern Luzon	This study	-
	-	39.5	-	-	Philippines	Bohol	Phelps et al. 2018	-
	9	39.5 ± 1.1 (39.0–41.9)	-	-	Philippines	Bohol	Sedlock et al. 2014a	-

Species	*n* individuals	Average FmaxE in kHz (range)	Fmax in kHz (range)	Fmin in kHz (range)	Country/ Region	Locality	Reference	Remarks
Vespertilionidae								
Myotis horsfieldii	3	70.02 ± 0.77	109.47 ± 0.71	39.33 ± 0.22	Philippines	Laguna, Quezon, Rizal	This study	-
	9	-	91.4 ± 14.1 (67–108)	47.6 ± 5.6 (38–58)	Philippines	Laguna	Sedlock 2001	-
	<10	(47.8–59.5)			Philippines	Laguna	Sedlock et al. 2019	-
	-	47.6	-	-	Philippines	Bohol	Phelps et al. 2018	-
	8	56.93 ± 7.98	134.25 ± 9.60	38.38 ± 3.46	Thailand	-	Hughes et al. 2011	-
	59	53.8 ± 5.14 (37.9–101)	-	-	India	Western Ghats	Wordley et al. 2014	-
	4	64.77 ± 3.91 (58.8–72.4)	104.29 ± 5.13 (94.1–113.5)	42.28 ± 4.29 (37.2–52.1)	India	Andaman Islands	Srinivasulu et al. 2017	-
	3	70.32 ± 17.58 (52.74–87.90)	100.61 ± 11.67 (88.94–112.28)	43.81 ± 6.26 (37.55–50.07)	Malaysia	Sarawak	Jinggong & Khan 2022	-
	5	58.0 ± 6.0 (48.4 – 63.1)	-	-	Borneo	-	McArthur & Khan 2021	-
	5	64 ± 7.2 (54.9–101.8)	103.2 ± 10.6 (78.5–122.9)	43.8 ± 3.7 (37.7–51.7)	Vietnam		Nguyen et al. 2021	-
	10	99 ± 7 (86 – 112)	134	79	Brunei		Aylen 2021	-
Myotis muricola	2	82.37 ± 0.82	112.2 ± 2.00	42.17 ± 1.04	Philippines	Quezon	This study	-
	3		67.2± 3.0 (63–71)	51.8± 0.8 (51–53)	Philippines	Laguna	Sedlock 2001	-
	-		105.2 ± 10.2 (87.8–127.7)	63.3 ± 1.3 (61.1–65.8)	Vietnam	Quang Binh	Thong et al. 2022b	-
	4	66.2 ± 0.9 (62.0–73.6)	59.7 ± 0.9 (57–63.6)	54.5 ± 0.9 (51.5–59.2)	Vietnam	-	Furey et al. 2009	-
	2	64.2–76.5	-	-	Thailand	Satun	Bumrungsri 2010	-
	49	82.27 ± 16.63	137.14 ± 12.79	55.33 ± 6.81	Thailand	-	Hughes et al. 2011	-
	4	66.4 ± 2.6 (63.1 – 69.1)	-	-	Borneo		McArthur & Khan 2021	-
	11	64.39 (63.39 –66.15)	126.07 (119.75 –132.62)	50.29 (45.49–54.08)	Borneo	-	Yoon & Park 2016	-
	-	(40–45)	-	-	Nepal		Csorba et al. 1999	-
	18	57.2 ± 0.0	79.9 ± 1.0	53.7 ± 0.48	Singapore		Pottie et al. 2005	-
	2	51.9 ± 2.51	104.7 ± 2.09	47.8 ± 3.66	India	Uttarakhand	Chakravarty et al. 2020	-
	-	63.5	108.2	40.7	Indonesia	Sumatra	Huang et al. 2019	-
	10	56 ± 1 (54 – 59)	118	48	Brunei		Aylen 2021	-
Tylonycteris pachypus	2	69.37 ± 1.4	115.96 ± 11.6	55.8 ± 4.1	Philippines	Rizal	This study	-
	-	69.8 ± 5.6 (76.7 – 61.1)	124.1 ± 7.1 (111.0 – 137.0)	54.2 ± 5.5 (46.0 – 61.0)	Philippines	Bulacan	Amberong et al. 2021	-
	3	63.38±4.07 (59.31–67.45)	97.03±4.90 (92.13–101.93)	54.75±0.98 (53.77–55.73)	Malaysia	Sarawak	Jinggong & Khan 2022	-
	-	-	-	53.5 (51–56)	Malaysia	-	Novick 1958	-
	1	48.2	-	-	Thailand	Satun	Bumrungsri 2010	-
	5	50.46 ± 13.05	134.4 ± 6.69	39.4 ± 4.39	Thailand	-	Hughes et al. 2011	-
	-	61.8	111.7	52.8	Indonesia	Sumatra	Huang et al. 2019	-
	126	65.1±2.8	129.2±7.4	58.3±1.8	China	Guangxi	Zhang et al. 2006	-
	78	76.5±2.1 (62.4–91.6)	91.6±4.5	62.4±3.8	China	Guangxi	Zhang et al. 2002	-
	4	64.7 ± 1.2 (63.9–66.5)	68.5 ± 3 (65–71)	46.3 ± 1.5 (45–48)	Cambodia		Phauk et al. 2013	-

Species	*n* individuals	Average FmaxE in kHz (range)	Fmax in kHz (range)	Fmin in kHz (range)	Country/ Region	Locality	Reference	Remarks
Miniopteridae								
Miniopterus paululus	19	70.77 ± 0.27	120.42 ± 2.16	60.94 ± 0.31	Philippines	Laguna, Quezon, Rizal	This study	-
	10		76.3± 4.7 (73–80)	61.3± 0.64 (60–62)	Philippines	Laguna	Sedlock 2001	-
	<10	(62.0–73.0)	-	-	Philippines	Laguna	Sedlock et al. 2019	-
	-	(55–80)	-	-	Philippines	Laguna	Sedlock et al. 2021	-
	25	69.68 ± 2.14 (66.24–74.06)	125.35 ± 5.72 (112.14–136.39)	58.29 ± 1.86 (53.71–60.71)	Philippines	Polilio Island	Taray et al. 2021	-
	14	72.9 ± 4.1 (63.7 – 90.0)	115.2 ± 12.1 (76.0 – 134.0)	60.7 ± 2.7 (52.0 – 65.0)	Philippines	Bulacan	Amberong et al. 2021	-
	-	65.18	-	-	Philippines	Bohol	Phelps et al. 2018	-
	4	65.5 ± 4.8 (60.7 – 70.4)	-	-	Borneo	-	McArthur & Khan 2021	-
Miniopterus eschscholtzii	4	53.13 ± 0.39	99.9 ± 1.38	44.25 ± 0.71	Philippines	Quezon, Rizal	This study	-
	2	-	69.6± 3.8 (63–77)	45.6 ± 0.7 (44–46)	Philippines	Laguna	Sedlock 2001	-
	4	51.68 ± 1.08 (50.62–52.90)	100.42 ± 3.63 (97.49–105.31)	41.99 ± 1.47 (39.88–43.29)	Philippines	Polilio Island	Taray et al. 2021	-
	1	53.1 ± 2.9 (49.7 – 55.0)	101.7 ± 1.2 (101.0 – 103.0)	44.3 ± 0.6 (44.0 – 45.0)	Philippines	Bulacan	Amberong et al. 2021	-
	1	48.5	-	-	Philippines	Bohol	Phelps et al. 2018	-
Emballonuridae								
Taphozous melanopogon	15	28.4 ± 0.31	-	-	Philippines	Batangas	This study	-
	<10	(26.0–30.0)	-	-	Philippines	Laguna	Sedlock et al. 2019	-
	-	(20–30)	-	-	Philippines	Laguna	Sedlock et al. 2021	-
	6	29.8 ± 0.9 (28.5 – 31.9)	-	-	Philippines	Bulacan	Amberong et al. 2021	-
	-	29.1	-	-	Philippines	Bohol	Phelps et al. 2018	-
	33	29.71 ± 2.67	76.15 ± 20.18	20.37 ± 6.2	Thailand	–	Hughes et al. 2011	-
	2	28.16 ± 1.70 (25.8–32.5)	34.01 ± 0.54 (32.9–35.2)	26.47 ± 0.95 (25.3–28.6)	India	Andaman Islands	Srinivasulu et al. 2017	-
	10	-	32.5 ± 1.7 (30.1–35.2)	20.6 ± 0.6 (19.7–21.6)	Vietnam	Quang Ninh	Thong et al. 2022a	-
	6	27.9 ± 0.56	28.7 ± 1.24	25.2 ± 0.82	Singapore	–	Pottie et al. 2005	-
	1	28.9	–	–	Thailand	Satun	Bumrungsri 2010	-
	12	30.10 ± 3.41	30.14 ± 2.58	22.72 ± 2.62	China	Guangxi	Wei et al. 2008	-
Megadermatidae								
Megaderma spasma	2	48.0 ± 0.23	-	-	Philippines	Quezon	This study	-
	32	20 (17–22)	-	-	Malaysia	-	Novick 1958	-
	2	47.5–58.8	-	-	Thailand	Satun	Bumrungsri 2010	-
	1	83.2	-	-	Thailand	Rawi Island	Bumrungsri 2010	-
	44	72.99 ± 12.52	108.93 ± 8.24	20.8 ± 12.44	Thailand	-	Hughes et al. 2011	-
	59	55.9 ± 12.3 (38.3–91.4)	99.79 ± 12.37 (65.3–113.1)	38.87 ± 2.30 (34.6–44.3)	India	Western Ghats	Wordley et al. 2014	-
	3	21.87 ± 2.36 (18.1–25.2)	67.03 ± 1.86 (64.0–70.0)	14.90 ± 0.68 (14.0–16.0)	India	Andaman Islands	Srinivasulu et al. 2017	-
	-	63	82.9	47.6	Indonesia	Sumatra	Huang et al. 2019	-
	1	69.0 ± 23.3 (52.5 – 85.5)	-	-	Borneo	-	McArthur & Khan 2021	-
	5	65.4 ± 3.1 (61.6–69.3)	70.8 ± 4.3 (65–74)	62.5 ± 2.1 (60–65)	Cambodia	-	Phauk et al. 2013	-

in Sulawesi, Indonesia and 'intermediate forms' calling at 39.0–42.0 kHz in Indonesia (Kingston & Rossiter 2004).

Initial analysis of morphological and acoustic data of *R. macrotis* available in the Philippines revealed that at least two morphs are present: a small morph (FA: 40–41 mm) and a large morph (FA: 43–46 mm) with dominant frequency at 75 kHz and 50 kHz, respectively (Table 2). An extensive morphological and call frequency variation is present in *R. macrotis* populations in the Philippines and thus considered a species complex (Heaney et al. 2016). The *R. macrotis* samples collected in this study as well as those collected in Bulacan (Amberong et al. 2021) resembles the small morph of this species. Interestingly, the frequency values obtained from *R. macrotis* in this study are also closely similar to those collected in Vietnam (75.1 kHz) (Thong et al. 2019).

Meanwhile, different morphotypes and phonic types of *R. arcuatus* have been observed to occur sympatrically in different localities within Luzon Island. For instance, Sedlock et al. (2019) recorded calls of *R. arcuatus* from Mt. Makiling with FmaxE values ranging from 46.8–50 kHz whereas those recorded by Dimaculangan et al. (2019) and Sedlock (2001) from the same locality ranged from 70–72 kHz. Meanwhile, the FmaxE value obtained from *R. arcuatus* in our study (65.76 kHz) is closely similar to the calls obtained from the 'wide-sella' morph (65.98 kHz), one of the noseleaf morphs observed by Sedlock and Weyandt (2009) to occur sympatrically with 'narrow-sella' morph (FmaxE = 69.84 kHz) in Mt. Banahaw, Luzon Island.

Hipposideros antricola and *H. bicolor* are often misidentified in the field due to similar morphological characteristics and overlapping measurements (Heaney et al. 2016; Amberong et al. 2021). In contrast with the recent survey done by Amberong et al. (2021), this study showed higher correct classification rate of calls to each respective species using DFA but found to emit relatively higher frequencies. Meanwhile, the calls of *H. bicolor* reported from Bohol Island are relatively lower (ca. 111 kHz) compared to those in Luzon Island, and may need additional studies.

For *H. diadema*, there appears to be not much variation in its FmaxE when Philippine populations are considered (Table 2). This is consistent with the molecular phylogeny of *H. diadema* presented by Esselstyn et al. (2012) which suggests that only one species is referred to *H. diadema* in the Philippines. However, the same study suggests that there are three species within *H. diadema* throughout its global range and previous records of the echolocation call for this species outside the Philippines showed variation in terms of FmaxE values. For instance, southern and southeastern Asian populations have average FmaxE values ranging from 58–62 kHz (Robinson 1996; Hughes et al. 2010; Srinivasulu et al. 2016) while those in Australia have FmaxE values ranging from 55–57 kHz (Fenton 1982; Leary & Pennay 2011).

This study is the first to report acoustic data for *Hipposideros lekaguli* from the Philippines. This species is generally poorly known in the country, with only few ecological and distribution records reported to date. Previous records of this species from southeastern Asian countries such as Thailand and Peninsular Malaysia showed FmaxE ranging from 45–50 kHz which is relatively higher than those recorded in this study (37 kHz) (Hughes et al. 2010; Wilson & Mittermeier 2019). Further study is needed to assess the taxonomy of the Philippine population of *H. lekaguli*.

FM bats (Miniopteridae and Vespertilionidae)

Among the vespertilionids with calls characterized by a steep broadband FM, acoustic data for *M. horsfieldii* is closely similar to those recorded from Mt. Makiling, Luzon Island (Sedlock 2001) and Thailand (Hughes et al. 2011). Similarly, our acoustic measurements for *M. muricola* showed similarities with other southeastern Asian forms in Malaysia, Vietnam, and Philippines (Sedlock 2001; Furey et al. 2009; Yoon & Park 2016) (Table 2).

Currently, the distribution of *M. paululus* is limited to Indonesia, Malaysia, the Philippines, and Timor-Leste. In the Philippines, there have been recorded call frequencies (FmaxE) for *M. paululus* on Luzon Island ranging from 62.0–73.0 kHz in Mt. Makiling (Sedlock et al. 2019), 73 kHz in Bulacan (Amberong et al. 2021), and an average of 65.9 kHz on Bohol Island (Phelps et al. 2018). However, no acoustic data has been obtained from other areas where this species is known to occur, although McArthur & Khan (2021) reported an average FmaxE value of 65.5 ± 4.8 kHz for individuals they identified as *M. australis* in Borneo.

Miniopterus eschscholtzii was formerly acknowledged as a subspecies of *M. schreibersii*. However, subsequent molecular studies resulted in its reclassification as a distinct species (Akmali et al. 2015; MMD 2021; Kusuminda et al. 2022; Simmons & Cirranello 2023). FmaxE values of the Philippine endemic *Miniopterus eschscholtzii* recorded in this study were within the range of obtained values recorded from other localities within the Philippines: 48.5 kHz in Bohol Island (Phelps et al. 2018), 45.6 kHz in Mt. Makiling, Luzon Island (Sedlock 2001), and 53.1 kHz in Bulacan, Luzon Island (Amberong et al. 2021).

Multiharmonic bats (Emballonuridae and Megadermatidae)

The calls of *Taphozous melanopogon* can easily be distinguished from other species, containing multiharmonic signals of long duration. The fundamental harmonic of its call is often weakly discerned while the first harmonic is the strongest component (Heller 1989). Calls of this species recorded in this study is well within the range of call measurements recorded from other localities such as in Luzon Island (Amberong et al. 2021), Malaysia (Heller 1989; Kruskop & Borisenko 2013), Vietnam (Pham et al. 2021), and Thailand (Thong et al. 2018).

We report the first echolocation call parameters for *Megaderma spasma* in the Philippines. Except for FmaxE, all call parameters are consistent with those reported before by other studies from Thailand (Hughes et al. 2011) and India (Raghuram et al. 2014). FmaxE values recorded in this study (48 kHz) are relatively lower than those recorded from the abovementioned areas (69–73 kHz). As the measurement of calls from this study is limited to only one individual, more samples are needed to evaluate the observed variation in the FmaxE values recorded.

Bat community of caves and karst areas in southern Luzon: conservation status and current threats

Owing to its unique microhabitat and complex terrains, karst forests are recognized as regions of significant biological significance due to the abundance of unique flora and fauna (Duco et al. 2021). Extensive small to large cave systems are present in these landscapes, making them an important habitat for many cave dwelling species such as bats. However, despite their ecological and economic importance, many caves in the Philippines remain vulnerable and continually being subjected to exploitation. Collection of speleothems, guano mining, vandalism, unregulated visitations, and littering pose significant threats to caves and their inhabitants in the Philippines (Tanalgo et al. 2016).

The present study accounts for 17 species of insectivorous bats (Image 1) from the four caves and surrounding karst forest surveyed in southern Luzon Island. Interestingly, new locality records and species of conservation concern were documented. For instance, three endemic species (*R. rufus*, *R. inops*, and *H. pygmaeus*) were recorded from the study areas while eight species were recorded to be new locality records for Batangas province (*T. melanopogon*, *H. antricola*, *H. bicolor*, and *R. arcuatus*), Cavinti, Laguna (*R. philippinensis*, *H. lekaguli*, *H. pygmaeus*, and *M. spasma*), and Tayabas, Quezon (*M. spasma*). In addition, potential novel or cryptic species of insectivorous bats such as *R. macrotis*, *H. bicolor*, and *H. pygmaeus* were also recorded based on observed acoustic divergence between island populations.

Of the species documented in our study areas, two species (*R. rufus* and *H. lekaguli*) are currently under Near Threatened category by the IUCN (IUCN 2022). Both species are highly associated with caves and limestone areas. The occurrence of these species underscores the importance of the caves surveyed as crucial habitat for species of conservation concern. The caves and karst areas within Calabarzon region are subject to human-induced pressure due to rapid deforestation driven by urban development (Fallarcuna & Perez 2015). Thus, protection and proper management is needed to ensure the availability of suitable habitat for these species.

In addition, the IUCN conservation status assessment for most of the species recorded in this study may require an updated revision. For instance, the last conservation assessment for The IUCN Red List of Threatened Species for 10 out of the 17 species recorded (*T. melanopogon*, *H. bicolor*, *H. lekaguli*, *H. pygmaeus*, *R. macrotis*, *R. rufus*, *R. inops*, *M. horsfieldii*, *M. muricola*, and *T. pachypus*) was done in 2018 (IUCN 2022). Additionally, no evaluation or assessment has been conducted for *H. antricola* and *M. eschscholtzii*. Currently, the Red List assessments are considered outdated after 10 years, although more current assessments (ideally 4–5 years) are recommended to ensure best possible information to conservationists are provided (Rondinini et al. 2014; IUCN 2023). With the rapid deforestation and deterioration of environmental conditions in many critical habitat areas in the Philippines, providing an up-to-date evaluation of population status and conservation assessment for these species is warranted to guide critical conservation management actions.

Majority of the bat community of the caves and karst forest visited in this study are also cave dependent species. In general, bat populations in the Philippines are steadily declining and forest degradation, habitat loss, and hunting are considered primary drivers for this trend (Raymundo & Caballes 2016; Quibod et al. 2019; Tanalgo & Hughes 2019). However, as most of our study areas are locally designated ecotourism areas, the most common threats to bats observed include human disturbance due to frequent human visits as well as

Image 1. Insectivorous bats recorded in caves and karst areas of Southern Luzon. A—*H. antricola* | b—*H. bicolor* | c—*H. diadema* | d—*H. lekaguli* | e—*H. pygmaeus* | f—*R. arcuatus* | g—*R. inops* | h—*R. macrotis* | i—*R. philippinensis* | j—*R. rufus* | k—*M. horsfeldii* | l—*M. muricola* | m—*T. pachypus* | n—*M. paululus* | o—*M. eschscholtzii* | p—*T. melanopogon* | q—*M. spasma*. © RADuco, JCTGonzalez, and JAParcon.

land-use changes resulting from development of these tourism areas. For instance, a project to pave the road going to Cathedral Cave in Cavinti, Laguna has recently been completed resulting in evident fragmentation in the karst landscape. Moreover, the project allowed accessibility resulting in increased tourist visits as well as rapid development and construction of human settlements. Meanwhile, in Pamitinan Cave, low population of bats and roost abandonment is apparent probably due to past human activities (tourist visits, removal of speleothems, hunting, vandalism) done inside the cave. Indeed, ecotourism is a rapidly expanding industry and contributes significantly to economic growth (Clements et al. 2006; Tolentino et al. 2020). Further, the essential role of communities in long–term conservation and protection of caves and its resources is well recognized. Thus, careful planning and proper management of these caves as well as strengthening community involvement are needed for this industry to be sustainable, balancing livelihoods as well as protecting wildlife and cave resources.

CONCLUSION

We successfully described echolocation calls of 17 species of insectivorous bats belonging to five families (Hipposideridae, Rhinolophidae, Verpertillionidae, Emballonuridae, and Megadermatidae). Discriminant function analysis (DFA) was able to correctly identify species with high classification rate, providing a feasible and effective tool for conducting future acoustic surveys in the Philippines.

In addition, we provided evidence of possible regional differences in echolocation calls for some of the species we recorded as well as the presence of unrecognized morphs and potential novel cryptic species. This highlights the importance of conducting more acoustic surveys from as many localities as possible because of the observed geographical variations in call frequencies within a species as well as to confirm the presence of local dialects (Hughes et al. 2010). Acoustic analysis can be utilized in conjunction with morphometric and molecular analysis to accurately determine species' taxonomic identities, especially those which are acoustically divergent and morphologically cryptic species. Our results contribute to the growing field of bat bioacoustics in the Philippines and in the development of a robust and well–developed echolocation call library for the country.

Further, this study identified several anthropogenic activities that may pose threat to the bat population in the study areas. Utilizing bat recorders, this study recommends bat emergence watching as an alternative to conventional ecotourism activities, such as visiting roost sites inside the cave, which could potentially disturb bats during sensitive periods like pregnancy, lactation, and weaning (Sheffield 1992; Tanalgo & Hughes 2021). This recreational night activity occurs at cave entrances, allowing tourists to observe bats emerging from their roosts (Kasso & Balakrishnan 2013). Integrating bat recorders to make bat calls audible to visitors will also enhance the tour experience (Wolf & Croft 2012). These activities present avenues to raise local awareness about bat conservation and the importance of caves and present novel guidelines for managing ecotourism activities in caves and karst landscapes.

REFERENCES

Adams, M.D., B.S. Law & M.S. Gibson (2010). Reliable automation of bat call identification for eastern New South Wales, Australia, using classification trees and AnaScheme software. *Acta Chiropterologica* 12(1): 231–245. https://doi.org/10.3161/150811010X504725

Agranat, I. (2013). Bat species identification from zero crossing and full spectrum echolocation calls using Hidden Markov Models, Fisher scores, unsupervised clustering and balanced winnow pairwise classifiers. *Proceedings of Meetings on Acoustics* 19: 010016. https://doi.org/10.1121/1.4799403

Akmali, V., R. Mehdizadeh, K. Chaghamirza, M. Moradi & M. Sharifi (2015). Taxonomic evaluation of the bent-winged bat (*Miniopterus*) populations occurring in Iran inferred from mitochondrial cytochrome-b sequences. *Mammalia* 79(4): 449–455. https://doi.org/10.1515/mammalia-2014-0002

Alcazar, S.M.T., I.L. Lit, C.M. Rebancos, A.L.B. Dupo, A.P.O. De Guia, N.C. Bantayan & J.D. Alvarez (2020). Diversity of cave-dwelling bats in Cebu Island, Philippines. *Biodiversitas Journal of Biological Diversity* 21(7): 3249–3254. https://doi.org/10.13057/biodiv/d210747

Amberong, A.G., J. Fidelino, R.A. Duco, M. Ledesma, M. Duya, P. Ong & M.R. Duya (2021). Toward a Philippine Bat Call Library: Acoustic Characterization of Insectivorous Bats in Bulacan, Luzon Island, Philippines. *Philippine Journal of Science* 150(S1): 473–485. https://doi.org/10.56899/150.S1.36

Aylen, O. (2021). Bats, Bioacoustics, & Bat Lures in Brunei Darussalam. Doctoral Dissertation. Department of Zoology, University of Otago.

BMB CAWED (2021). Number of Caves and Wetlands. Biodiversity Management Bureau-Caves and Wetlands Division. https://bmb.gov.ph/statistics/. Accessed on 20 July 2023.

Bumrungsri, S., B. Doungboupha, P. Soisook, A. Dejtaradol & U. Pimsai (2010). Species diversity of bats (Mammalia: Chiroptera) in Tarutao National Park, Satun province, Thailand. Prince of Songkla University, Thailand, 41 pp.

Chakravarty, R., M. Ruedi & F. Ishtiaq (2020). A recent survey of bats with descriptions of echolocation calls and new records from the western Himalayan region of Uttarakhand, India. *Acta Chiropterologica* 22: 197–224. http://doi.org/10.3161/15081109acc2020.22.1.019

Clements, R., N.S. Sodhi, M. Schilthuizen & P.K.L. Ng (2006). Limestone karsts of Southeast Asia: imperiled arks of biodiversity. *BioScience* 56: 733–742. https://doi.org/10.1641/0006-

3568(2006)56[733:LKOSAI]2.0.CO;2

Csorba, G., S.V. Kruskop & A.V. Borissenko (1999). Recent records of bats (Chiroptera) from Nepal, with remarks on their natural history. *Mammalia* 63: 61–78. http://doi.org/10.1515/mamm.1999.63.1.61

Dimaculangan, F.D., A. Jacobson, P. Alviola, J. Alvarez & J.L. Sedlock (2019). Seasonal emergence counts from a multispecies horseshoe bat (Chiroptera: Rhinolophidae) roost in the Philippines. *Journal of Bat Research & Conservation* 12(1): 46–51. https://doi.org/10.14709/barbj.12.1.2019.06

Domingo, K.L.B. & D.P. Buenavista (2018). Anthropogenic Impacts on Cave-roosting Bats: A Call for Conservation Policy Implementation in Bukidnon, Philippines. *Suan Sunandha Science and Technology Journal* 5(1): 28–34.

Duco, R.A.J., J.S. Fidelino, M.V. Duya, M.M. Ledesma, P.S. Ong & M.R.M. Duya (2021). Bird Assemblage and Diversity along Different Habitat Types in a Karst Forest Area in Bulacan, Luzon Island, Philippines. *Philippine Journal of Science* 150(S1): 399–414. https://doi.org/10.56899/150.S1.30

Esselstyn, J.A., B.J. Evans, J.L. Sedlock, F.A. Anwarali Khan & L.R. Heaney (2012). Single–locus species delimitation: a test of the mixed Yule–coalescent model, with an empirical application to Philippine round–leaf bats. *Proceedings of the Royal Society B: Biological Sciences* 279: 3678–3686. https://doi.org/10.1098/rspb.2012.0705

Fallarcuna, B. & G.J. Perez (2015). Quantifying forest cover changes in the Philippines from 2000–2012 from landsat-derived global forest cover dataset. Proceedings from 36th Asian Conference on Remote Sensing: Fostering Resilient Growth in Asia; 2015 October 24-28; Quezon City, Metro Manila Philippines: Asian Association on Remote Sensing (AARS). http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.741.1502. Accessed on 20 July 2023.

Fenton, M. (1982). Echolocation Calls and Patterns of Hunting and Habitat Use of Bats (Microchiroptera) from Chillagoe, North Queensland. *Australian Journal of Zoology* 30: 417. https://doi.org/10.1071/zo9820417.

Fils, E.M.B., A.M. Mongombe, D.E. Tsala & J.L. Tamesse (2018). Acoustic identification of five insectivorous bats by their echolocation calls in the Sahelian zone of Far North Cameroon. *The Journal of Basic and Applied Zoology* 79: 28. https://doi.org/10.1186/s41936-018-0041-7

Francis, C.M. (1989). A Comparison of Mist Nets and Two Designs of Harp Traps for Capturing Bats. *Journal of Mammalogy* 70: 865–870. https://doi.org/10.2307/1381730

Francis, C.M. & J. Habersetzer (1998). Interspecific and intraspecific variation in echolocation call frequency and morphology of horseshoe bats, *Rhinolophus* and *Hipposideros*, pp. 169–179. In: Kunz T.H. & P.A. Racey (eds.). *Bat Biology and Conservation*. Smithsonian Institution Press, Washington, D.C., xvi+365 pp.

Furey, N.M., I.J. Mackie & P.A. Racey (2009). The role of ultrasonic bat detectors in improving inventory and monitoring surveys in Vietnamese karst bat assemblages. *Current Zoology* 55: 327–341. https://doi.org/10.1093/czoolo/55.5.327

Gonzalez, J.C., A.P. de Guia, J. Dimalibot, K. Pantua, W. Gustilo & N. Bantayan (2020). Understorey to canopy vertebrate fauna of a lowland evergreen forest in Mt. Makiling Forest Reserve, Philippines. *Biodiversity Data Journal* 8:e56999. https://doi.org/10.3897/bdj.8.e56999

Heaney, L.R., D.S. Balete & E.A. Rickart (2016). *The mammals of Luzon Island: biogeography and natural history of a Philippine fauna*. Johns Hopkins University Press, Maryland, 304 pp.

Heaney, L.R., M.L. Dolar, D.S. Balete, J.A. Esselstyn, E.A. Rickart & J.L. Sedlock (2010). Synopsis of Philippine mammals. http://fieldmuseum.org/explore/ synopsis-philippine-mammals. Accessed on 20 July 2023.

Heller, K.-G. (1989). The echolocation calls of Malaysian bats. *Zeitschrift für Säugetierkunde* 54: 1–8.

Heller, K.-G. & O.V. Helversen (1989). Resource partitioning of sonar frequency bands in rhinolophoid bats. *Oecologia* 80: 178–186. https://doi.org/10.1007/bf00380148

Huang, J.C., E.L. Rustiati, M. Nusalawo & T. Kingston (2019). Echolocation and roosting ecology determine sensitivity of forest-dependent bats to coffee agriculture. *Biotropica* 51: 757–768. https://doi.org/10.1111/btp.12694

Hughes, A.C., C. Satasook, P.J.J. Bates, P. Soisook, T. Sritongchuay, G. Jones & S. Bumrungsri (2010). Echolocation Call Analysis and Presence–Only Modelling as Conservation Monitoring Tools for Rhinolophoid Bats in Thailand. *Acta Chiropterologica* 12: 311–327. https://doi.org/10.3161/150811010x537891

Hughes, A.C., C. Satasook, P.J.J. Bates, P. Soisook, T. Sritongchuay, G. Jones & S. Bumrungsri. (2011). Using Echolocation Calls to Identify Thai Bat Species: Vespertilionidae, Emballonuridae, Nycteridae and Megadermatidae. *Acta Chiropterologica* 13: 447–455. https://doi.org/10.3161/150811011x624938

Ingle, N.R. & L.R. Heaney (1992). A key to the bats of the Philippine Islands. *Fieldiana: Zoology* 69: 1–44. https://doi.org/10.5962/bhl.title.3504

IUCN (2022). The IUCN Red List of Threatened Species. Version 2022–2. https://www.iucnredlist.org. Accessed on 10 December 2022.

IUCN (2023). What's New Archive. https://www.iucnredlist.org/resources/whatsnewarchive. Accessed on 20 July 2023.

Jinggong, E.R. & F.A.A. Khan (2022). Bats of Mount Silabur, Sarawak, and Its Potential for Conservation. *Borneo Journal of Resource Science and Technology* 12: 141–156. https://doi.org/10.33736/bjrst.4235.2022

Jones, G., D. Jacobs, T. Kunz, M. Willig & P. Racey (2009). Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research* 8: 93–115. https://doi.org/10.3354/esr00182

Jones, G., K. Sripathi & D.A. Waters (1994). Individual variation in the echolocation calls of three sympatric Indian Hipposiderid bats, and an experimental attempt to jam bat echolocation. *Folia Zoologica* 43(4): 347–362.

Karine, C. & E.K.V. Kalko (2001). Toward a global bat–signal database. *IEEE Engineering in Medicine and Biology Magazine* 20: 81–85. https://doi.org/10.1109/51.932730

Kasso, M. & M. Balakrishnan (2013). Ecological and economic importance of bats (Order Chiroptera). *ISRN Biodiversity* 2013: 1–9. https://doi.org/10.1155/2013/187415

Kingston, T. & S.J. Rossiter (2004). Harmonic–hopping in Wallacea's bats. *Nature* 429: 654–657. https://doi.org/10.1038/nature02487

Kingston, T., M.C. Lara, G. Jones, Z. Akbar, T.H. Kunz & C.J. Schneider (2001). Acoustic divergence in two cryptic *Hipposideros* species: a role for social selection? *Proceedings of the Royal Society of London. Series B: Biological Sciences* 268: 1381–1386. https://doi.org/10.1098/rspb.2001.1630

Kruskop, S.V. & A.V. Borisenko (2013). A New Species of South–East Asian *Myotis* (Chiroptera: Vespertilionidae), with Comments on Vietnamese 'Whiskered Bats.' *Acta Chiropterologica* 15:293–305. https://doi.org/10.3161/150811013x678937

Kunz, T.H. & A. Kurta (1988). Capture methods and holding devices, pp. 1–29. In: T. H. Kunz (ed.). *Ecological and Behavioral Methods for the Study of Bats*. Smithsonian Institution Press, Washington, D.C.

Kusuminda, T., A. Mannakkara, K.D. Ukuwela, S.V. Kruskop, C.J. Amarasinghe, U. Saikia, P. Venugopal, M. Karunarathna, R. Gamage, M. Ruedi, G. Csorba, W.B. Yapa & B.D. Patterson (2022). DNA barcoding and morphological analyses reveal a cryptic species of *Miniopterus* from India and Sri Lanka. *Acta Chiropterologica* 24(1):1–17.

Larsen, R.J., K.A. Boegler, H.H. Genoways, W.P. Masefield, R.A. Kirsch & S.C. Pedersen (2007). Mist netting bias, species accumulation curves, and the rediscovery of two bats on Montserrat (Lesser Antilles). *Acta Chiropterologica* 9:423–435. https://doi.org/10.3161/150811007783528031

Lausen, C.L. & R.M.R. Barclay (2006). Winter bat activity in the Canadian prairies. *Canadian Journal of Zoology* 84(8):1079–1086. https://doi.org/10.1139/z06-093

Leary, T. & M. Pennay (2011). Echolocation calls of eight microchiroptera from Papua New Guinea. *The Biology and Conservation of Australasian Bats* 35:106–127. https://doi.

org/10.7882/fs.2011.014

MacSwiney G.M.C., F.M. Clarke & P.A. Racey (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

MMD (Mammal Diversity Database) (2021). *Miniopterus eschscholtzii.* Retrieved from www.mammaldiversity.org.

McArthur, E. & F.A.A. Khan (2021). Towards a regional call library: Classifying calls of a species–rich bat assemblage in a Bornean karst rainforest. *Barbastella* 14:95–117. https://doi.org/10.14709/barbj.14.1.2021.11

McCracken, G.F. (1989). Cave conservation: Special problems of bats. *American National Speleological Society Bulletin* 51: 47–51.

Mould, A. (2012). Cave bats of the central west coast and southern section of the Northwest Panay Peninsula, Panay Island, the Philippines. *Journal of Threatened Taxa* 4:2993–3028. https://doi.org/10.11609/jott.o3104.2993–3028

Murray, S.W. & T.H. Kunz (2005). Bats. In: David, C.C. & W.B. White (eds.). *Encyclopedia of Caves*. Elsevier Academic Press, Burlington/California, London, 661pp.

Nguyen, S.T., T.J. O'Shea, J.A. Gore, K.V. Nguyen, T.T. Hoang, M. Motokawa, P.H. Dang, M.D. Le, T.T. Nguyen, T. Oshida, H. Endo, T.A. Tran, H.T. Bui, T.N. Ly, D.T. Vu, H.T. Chu & T.T. Vuong (2021). Bats (Chiroptera) of Bidoup Nui Ba National Park, Dalat Plateau, Vietnam. *Mammal Study* 46(1):53–68. https://doi.org/10.3106/ms2020–0024

Novick, A. (1958). Orientation in paleotropical bats. I. Microchiroptera. *Journal of Experimental Zoology* 138(1):81–153.

Nuñez, G.B., A. Cunningham, E.M.B Fils, W. Frick, M.N. Islam, T. Jolliffe, R. Kading, A. Kepel, T. Kingston, S. Leopardi, R. Medellín, I. Mendenhall, S. Parsons, P. Racey, D. Russo, J.T. Shapiro, A. Vicente–Santos, R.A. Víquez & T.V. Dinh (2020). IUCN SSC Bat Specialist Group (BSG) Recommended Strategy for Researchers to Reduce the Risk of Transmission of SARS–CoV–2 from Humans to Bats. https://www.iucnbsg.org/uploads/6/5/0/9/6509077/amp_recommendations_for_researchers_final.pdf. Accessed on 15 October 2022

O'Farrell, M.J. & W.L. Gannon (1999). A Comparison of Acoustic Versus Capture Techniques for the Inventory of Bats. *Journal of Mammalogy* 80:24–30. https://doi.org/10.2307/1383204

Pauwels, J., I. Le Viol, C. Azam, N. Valet, J.F. Julien, Y. Bas, C. Lemarchand, A. Sanchez de Miguel & C. Kerbiriou (2019). Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning. *Landscape and Urban planning* 183:12–25. https://doi.org/10.1016/J.LANDURBPLAN.2018.08.030

Pavey, C.R. & A.S. Kutt (2008). Large–eared horseshoe bat *Rhinolophus philippinensis,* pp. 454–456. In: Van Dyck, S. & R. Strahan (eds.). *The mammals of Australia.* 3rd edition. Reed New Holland, Sydney, Australia, 887pp.

Pedro, A.R.-S. & J.A. Simonetti (2013). Acoustic identification of four species of bats (Order Chiroptera) in central Chile. *Bioacoustics* 22:165–172. https://doi.org/10.1080/09524622.2013.763384

Pekar, J.E., A. Magee, E. Parker, N. Moshiri, K. Izhikevich, J.L. Havens, K. Gangavarapu, L.M.M. Serrano, A. Crits-Christoph, N.L Matteson, M. Zeller, J.I. Levy, J.C. Wang, S. Hughes, J. Lee, H. Park, M-S. Park, K.C.Z. Yan, R.T.P. Lin, M.N.M. Isa, Y.M. Noor, T.I. Vasylyeva, R.F. Garry, E.C. Holmes, A. Rambaut, M.A. Suchard, K.G. Andersen, M. Worobey & J. O. Wertheim (2022). The molecular epidemiology of multiple zoonotic origins of SARS-CoV-2. *Science* 377(6609):960–966. https://doi.org/0.1126/science.abp8337

Pham, L.K., B.V. Tran, Q.T. Le, T.T. Nguyen & C.C. Voigt (2021). Description of Echolocation Call Parameters for Urban Bats in Vietnam as a Step Towards a More Integrated Acoustic Monitoring of Urban Wildlife in Southeast Asia. *Diversity* 13:18. https://doi.org/10.3390/d13010018

Phauk, S., S. Phen & N.M. Furey (2013). Cambodian bat echolocation: a first description of assemblage call parameters and assessment of their utility for species identification. *Cambodian Journal of Natural History* 2013(1):16–26.

Phelps, K., R. Jose, M. Labonite & T. Kingston (2018). Assemblage and Species Threshold Responses to Environmental and Disturbance Gradients Shape Bat Diversity in Disturbed Cave Landscapes. *Diversity* 10:55. https://doi.org/10.3390/d10030055

Pottie, S.A., D.J.W. Lane, T. Kingston & B.P.Y.–H. Lee (2005). The microchiropteran bat fauna of Singapore. *Acta Chiropterologica* 7:237–247. https://doi.org/10.3161/150811005775162632

Quibod, Ma.N.R.M., P.A. Alviola, A.P.O. de Guia, V.C. Cuevas, I.L. Lit & B.O. Pasion (2019). Diversity and threats to cave–dwelling bats in a small island in the southern Philippines. *Journal of Asia–Pacific Biodiversity* 12:481–487. https://doi.org/10.1016/j.japb.2019.06.001

Raghuram, H., M. Jain, & R. Balakrishnan (2014). Species and acoustic diversity of bats in a palaeotropical wet evergreen forest in southern India. *Current Science* 107(4):631–641. https://www.jstor.org/stable/24103535

Raymundo, M.L. & C.F. Caballes (2016). An Insight into Bat Hunter Behavior and Perception with Implications for the Conservation of the Critically Endangered Philippine Bare–Backed Fruit Bat. *Journal of Ethnobiology* 36:382–394. https://doi.org/10.2993/0278–0771–36.2.382

Robinson, M.F. (1996). A relationship between echolocation calls and noseleaf widths in bats of the genera *Rhinolophus* and *Hipposideros*. *Journal of Zoology* 239:389–393. https://doi.org/10.1111/j.1469–7998.1996.tb05459.x

Rondinini, C., M. Di Marco, P. Visconti, S.H.M. Butchart & L. Boitani (2014). Update or outdate: long-term viability of the IUCN Red List. *Conservation Letters* 7:126–130. https://doi.org/10.1111/conl.12040

Rydell, J. (1991). Seasonal use of illuminated areas by foraging northern bats *Eptesicus nilssonii. Holarctic Ecology (Ecography)* 14(3): 203-207. https://doi.org/10.1111/j.1600-0587.1991.tb00653.x

Sedlock, J.L. (2001). Inventory of insectivorous bats on Mount Makiling, Philippines using echolocation call signatures and a new tunnel trap. *Acta Chiropterologica* 2(3): 163–178.

Sedlock, J.L., D.G.E. Gomes, J.J. Rubin, S. Woody, B.A.R. Hadi & J.R. Barber (2021). A phantom ultrasonic insect chorus repels low-flying bats, but most are undeterred. *Functional Ecology* 35:2743–2752. https://doi.org/10.1111/1365–2435.13933

Sedlock, J.L., R.P. Jose, J.M. Vogt, L.M.J. Paguntalan & A.B. Cariño (2014a). A Survey of Bats in a Karst Landscape in the Central Philippines. *Acta Chiropterologica* 16:197–211. https://doi.org/10.3161/150811014x683390

Sedlock, J.L., F. Krüger & E.L. Clare (2014b). Island bat diets: does it matter more who you are or where you live? *Molecular Ecology* 23:3684–3694. https://doi.org/10.1111/mec.12732

Sedlock, J.L., A.M. Stuart, F.G. Horgan, B. Hadi, A. Como Jacobson, P.A. Alviola & J.D.V. Alvarez (2019). Local–Scale Bat Guild Activity Differs with Rice Growth Stage at Ground Level in the Philippines. *Diversity* 11:148. https://doi.org/10.3390/d11090148

Sedlock, J.L. & S.E. Weyandt (2009). Genetic divergence between morphologically and acoustically cryptic bats: novel niche partitioning or recent contact? *Journal of Zoology* 279:388–395. https://doi.org/10.1111/j.1469–7998.2009.00634.x

Sheffield, S.R., J.H. Shaw, G.A. Heidt & L.R. McQenaghan (1992). Guidelines for the protection of bat roosts. *Journal of Mammalogy* 73:707–710. https://doi.org/10.2307/1382051

Shi, L., J. Feng, Y. Liu, G. Ye & X. Zhu (2009). Is food resource partitioning responsible for deviation of echolocation call frequencies from allometry in *Rhinolophus macrotis*? *Acta Theriologica* 54:371–382. https://doi.org/10.4098/j.at.0001–7051.099.2008

Siemers, B.M. & A. Schaub (2011). Hunting at the highway: Traffic noise reduces foraging efficiency in acoustic predators. *Proceedings of the Royal Society B: Biological Sciences* 278(1712):1646–1652. https://doi.org/10.1098/rspb.2010.2262

Simmons, N.B. & A.L. Cirranello (2023). Bat Species of the World: A taxonomic and geographic database. Version 1.4. Accessed on 22 July 2023.

Srinivasulu, B., A. Srinivasulu, C. Srinivasulu, T.H. Dar, A. Gopi & G. Jones (2016). First record of the Diadem Leaf–Nosed Bat *Hipposideros diadema* (E. Geoffroy, 1813) (Chiroptera: Hipposideridae) from the Andaman Islands, India with the possible occurrence of a hitherto unreported subspecies. *Journal of Threatened Taxa* 8:9316. https://doi.org/10.11609/jott.2862.8.11.9316–9321

Srinivasulu, C., A. Srinivasulu, B. Srinivasulu, A. Gopi, T.H. Dar, P.J.J. Bates, S.J. Rossiter & G. Jones (2017). Recent Surveys of Bats from the Andaman Islands, India: Diversity, Distribution, and Echolocation characteristics. *Acta Chiropterologica* 19:419–437. https://doi.org/10.3161/15081109acc2017.19.2.018

Sun, K.–P., J. Feng, T.–L. Jiang, J. Ma, Z.–Z. Zhang & L.–R. Jin (2008). A new cryptic species of *Rhinolophus macrotis* (Chiroptera: Rhinolophidae) from Jiangxi Province, China. *Acta Chiropterologica* 10:1–10. https://doi.org/10.3161/150811008x331045

Tanalgo, K.C. & A.C. Hughes (2019). Priority–setting for Philippine bats using practical approach to guide effective species conservation and policy–making in the Anthropocene. *Hystrix, the Italian Journal of Mammalogy* 30(1): 74–83. https://doi.org/10.4404/hystrix–00172–2019

Tanalgo, K.C. & A.C. Hughes (2021). The potential of bat-watching tourism in raising public awareness towards bat conservation in the Philippines. *Environmental Challenges* 4, 100140. https://doi.org/10.1016/j.envc.2021.100140

Tanalgo, K.C., H.F. Oliveira & A.C. Hughes (2022). Mapping global conservation priorities and habitat vulnerabilities for cave-dwelling bats in a changing world. *Science of The Total Environment* 843, 156909. https://doi.org/10.1016/j.scitotenv.2022.156909

Tanalgo, K.C., R.D. Teves, F.R.P. Salvaña, R.E. Baleva & J.A.G. Tabora (2016). Human-bat interactions in caves of South Central Mindanao, Philippines. *Wildlife Biology in Practice* 12(1):1–14. https://doi.org/10.2461/wbp.2016.12.2

Taray, K., P. Alviola, F. Cruz, I. Lit & J.C. Gonzalez (2021). Characterization of Echolocation Calls from Insectivorous Bats in Puting Bato Cave 5, Burdeos, Polillo Island, Philippines. *Philippine Journal of Science* 150. https://doi.org/10.56899/150.6b.10

Thong, V.D., A. Denzinger, V. Long, N.V. Sang, N.T.T. Huyen, N.H. Thien, N.K. Luong, L.Q. Tuan, N.M. Ha, N.T. Luong & H.–U. Schnitzler (2022a). Importance of Mangroves for Bat Research and Conservation: A Case Study from Vietnam with Notes on Echolocation of *Myotis hasselti*. *Diversity* 14:258. https://doi.org/10.3390/d14040258

Thong, V.D., H. Limbert & D. Limbert (2022b). First Records of Bats (Mammalia: Chiroptera) from the World's Largest Cave in Vietnam. *Diversity* 14:534. https://doi.org/10.3390/d14070534

Thong, V.D., D.N. Loi, N.T. Luong, H.Q. Huy & H.T. Thanh (2019). New records of bats (Mammalia: Chiroptera) from Cu Lao Cham and Ly Son archipelagos, central Vietnam. *Academia Journal of Biology* 40(4):13–21. https://doi.org/10.15625/2615–9023/v40n4.13529

Thong, V.D., X. Mao, G. Csorba, P. Bates, M. Ruedi, N.V. Viet, D.N. Loi, P.V. Nha, O. Chachula, T.A. Tuan, N.T. Son, D. Fukui, V.T. Tu & U. Saikia (2018). First Records of *Myotis altarium* (Chiroptera:Vespertilionidae) from India and Vietnam. *Mammal Study* 43:1–7. https://doi.org/10.3106/ms2017–0076

Tidemann, C. & D. Woodside (1978). A Collapsible Bat–Trap and a Comparison of Results Obtained with the Trap and with Mist–nets. *Wildlife Research* 5:355. https://doi.org/10.1071/wr9780355

Tolentino, P.J., J.R.L. Navidad, M.D. Angeles, D.A.P. Fernandez, E.L.C. Villanueva, R.D.R. Obeña & I.E. Buot Jr. (2020). Biodiversity of forests over limestone in Southeast Asia with emphasis on the Philippines. *Biodiversitas Journal of Biological Diversity* 21(4): 1597-1613. https://doi.org/10.13057/biodiv/d210441

Tu, V. T., A. Hassanin, T. Görföl, S. Arai, D. Fukui, H.T. Thanh, N.T. Son, N.M. Furey & G. Csorba (2017). Integrative taxonomy of the *Rhinolophus macrotis* complex (Chiroptera, Rhinolophidae) in Vietnam and nearby regions. *Journal of Zoological Systematics and Evolutionary Research* 55:177–198. https://doi.org/10.1111/jzs.12169

Wei, L., N. Han, L. Zhang, K.M. Helgen, S. Parsons, S. Zhou & S. Zhang (2008). Wing morphology, echolocation calls, diet and emergence time of black–bearded tomb bats (*Taphozous melanopogon*, Emballonuridae) from southwest China. *Acta Chiropterologica* 10:51–59. https://doi.org/10.3161/15081100

Wolf, I.D. & D.B. Croft (2012). Observation techniques that minimize impacts on wildlife and maximize visitor satisfaction in night-time tours. *Tourism Management Perspectives* 4: 164–175. https://doi.org/10.1016/j.tmp.2012.08.002

Wilson, D.E. & R.A. Mittermeier (2019). *Handbook of the Mammals of the World – Volume 9 Bats*. Lynx Edicions, Spain, 1008 pp.

Wordley, C.F.R., E.K. Foui, D. Mudappa, M. Sankaran & J.D. Altringham (2014). Acoustic identification of Bats in the Southern Western Ghats, India. *Acta Chiropterologica* 16: 213–222. https://doi.org/10.3161/150811014x683408

Yoon, K.B. & Y.C. Park (2016). Echolocation call structure and intensity of the Malaysian *Myotis muricola* (Chiroptera: Vespertilionidae). *Journal of Forest and Environmental Science* 32: 99–102. https://doi.org/10.7747/jfes.2016.32.1.99

Zhang, L., G. Jones, J. Zhang, G. Zhu, S. Parsons, S.J. Rossiter & S. Zhang (2009). Recent Surveys of Bats (Mammalia: Chiroptera) from China. I. Rhinolophidae and Hipposideridae. *Acta Chiropterologica* 11: 71–88. https://doi.org/10.3161/150811009x465703

Zhang, L., B. Liang, S. Parsons, L. Wei & S. Zhang (2006). Morphology, echolocation and foraging behaviour in two sympatric sibling species of bat (*Tylonycteris pachypus* and *Tylonycteris robustula*) (Chiroptera: Vespertilionidae). *Journal of Zoology* 271: 344–351. https://doi.org/10.1111/j.1469–7998.2006.00210.x

Zhang, L.B., L.R. Lu, S.Y. Zhou, H.H. Zhao, G.H. Lou & S.Y. Zhang (2002). Comparison of the echolocation signals in two species of flat–headed bats at flying. *Zoological Research* 23(4): 296–300.

Author contributions: RAD carried out the fieldwork, data analysis, and drafting and revising the manuscript. APOdG involved in designing the research, data collection, and checking the manuscript and approving its submission. JCD participated in designing and planning the research as well as data collection. PAA designed the research and involved in supervising and revising the manuscript. JCTG conceptualized and designed the research, participated in fieldwork, and approving submission of the manuscript.

Acknowledgements: We acknowledge the support and funding by the DOST Philippines (Department of Science and Technology) through the NICER-CAVES (Center for Cave Ecosystems Research) Program of the UPLB Museum of Natural History, under the research management of the DOST-PCAARRD (Philippine Council for Agriculture, Aquatic, and Natural Resources Research and Development). We would like to thank the DENR (Department of Environment and Natural Resources) Regional Office of CALABARZON for providing the gratuitous permit to collect voucher specimens. We thank our field assistants, Edison A. Cosico, Charlie R. Malizon, Wilson Bulalacao, and Benjie Gurobat, for providing their field expertise. We acknowledge the support of Local Government Units (LGUs) of Cavinti, Tayabas City, Lobo, and Rodriguez, as well as the local guides, cooks, and forest rangers for providing security and logistical support.

The opinions expressed by the authors do not reflect the views of the Journal of Threatened Taxa, Wildlife Information Liaison Development Society, Zoo Outreach Organization, or any of the partners. The journal, the publisher, the host, and the partners are not responsible for the accuracy of the political boundaries shown in the maps by the authors.

Journal of Threatened Taxa is indexed/abstracted in Bibliography of Systematic Mycology, Biological Abstracts, BIOSIS Previews, CAB Abstracts, EBSCO, Google Scholar, Index Copernicus, Index Fungorum, JournalSeek, National Academy of Agricultural Sciences, NewJour, OCLC WorldCat, SCOPUS, Stanford University Libraries, Virtual Library of Biology, Zoological Records.

NAAS rating (India) 5.64

Print copies of the Journal are available at cost. Write to:
The Managing Editor, JoTT,
c/o Wildlife Information Liaison Development Society,
43/2 Varadarajulu Nagar, 5th Street West, Ganapathy, Coimbatore,
Tamil Nadu 641006, India
ravi@threatenedtaxa.org

www.threatenedtaxa.org

OPEN ACCESS

ISSN 0974-7907 (Online) | ISSN 0974-7893 (Print)

October 2023 | Vol. 15 | No. 10 | Pages: 23931–24150
Date of Publication: 26 October 2023 (Online & Print)
DOI: 10.11609/jott.2023.15.10.23931-24150

Articles

Communications

Review

Short Communications

Notes

Publisher & Host

Threatened Taxa