Journal of
Bat Research & Conservation

OPEN ACCESS
www.secemu.org
DOI: 10.14709/BarbJ.14.1.2021.11

ORIGINAL ARTICLE

Towards a regional call library: Classifying calls of a species-rich bat assemblage in a Bornean karst rainforest

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DOI: https://doi.org/10.14709/BarbJ.14.1.2021.11

Keywords: Borneo, call library, Chiroptera, echolocation, karst, tropical rainforest

received: June, 10th 2021
accepted: September, 4th 2021

ABSTRACT

Acoustic monitoring with ultrasonic detectors has emerged, in recent years, as an essential tool to quantify the activity of echolocating, insectivorous bats and identify critical commuting and foraging habitats. Comprehensive reference call libraries are critical for the identification of species from their calls. This is especially important in species diverse areas like Gunung Mulu National Park (Sarawak). This study aims to (1) develop a call library for all known echolocating bat species found in Gunung Mulu National Park, (2) determine if calls of different species can be automatically classified using discriminant function analysis, and (3) examine intraspecific variation in relation to sex and geographical location, for calls in species of the families Rhinolophidae and Hipposideridae. Between 2012 and 2017, insectivorous bats were trapped within and outside the park. Echolocation calls were recorded from a total of 508 individuals, representing 31 species from 8 families. Results from discriminant function analysis indicated that the majority of cave roosting bats, which included *Chaerephon plicatus, Miniopterus australis, Myotis horsfieldii* and 13 species from the families Rhinolophidae, Hipposideridae, and Emballonuridae, could be readily distinguished from their calls, when manually separated into groups according to call structure. However, classification success was much lower for the remaining 15 species that consisted mainly of forest roosting bats from the family Vespertilionidae. This reference call library is expected to contribute to a regional online open-access database. It can be used to survey and monitor selected species in Gunung Mulu National Park as well as highlighting the importance of threatened habitats outside the boundary for these species.

INTRODUCTION

Habitat loss and fragmentation have been identified as the major factors contributing to the decline of bat populations in the tropical forests of Southeast Asia, where peak diversity of threatened bat species is known to occur (Kingston 2013, Meyer et al. 2016, Voigt & Kingston 2016, Frick et al. 2020). In karst landscapes, cave roosting bats are particularly vulnerable to the disturbance caused by limestone quarrying (Clements et al. 2006), uncontrolled mass tourism (Vermeulen & Whitten 1999, Furey & Racey 2016a), swiftlet nest collecting (Hall et al. 2002, Suyanto & Struebig 2007), guano mining (Wiles & Brooke 2010), and hunting (Hall et al. 2002, Wiles & Brooke 2010, Mildenstein et al. 2016). Ongoing conversion of forests to agriculture, in particular large-scale monoculture plantations surrounding karst outcrops that support high densities of cave roosting bats (Clements et al. 2006, Furey & Racey 2016a, Liew et al. 2016), has led to the loss of valuable foraging habitats (Struebig et al. 2009, Furey et al. 2010, Kingston 2013) and reported decline in populations (Hall et al. 2002, Shazali et al. 2017). Therefore, there is an urgent need to improve the efficiency of surveys to document the diversity, distribution, and habitat requirements of bats in both pristine and disturbed areas of the region (Kingston 2010, 2013).

Borneo has a high diversity of bat fauna, with 99 species currently documented (Phillipps & Phillipps 2016, Shazali et al. 2018). Since the late 1980's researchers have conducted numerous surveys to document bat diversity in the Malaysian states of Sabah and Sarawak, with most studies focusing on species inventories, particularly in protected areas (Struebig et al. 2010, Kumaran et al. 2011, Shazali et al. 2018). However, there is still a lack of information on this important group of mammals from many localities (Kumaran et al. 2011, Khan et al. 2019, Yoh et al. 2020).

The majority of studies on insectivorous bats in Borneo have used harp traps and mist-nets to capture, identify, and assess the condition of individual bats (e.g. Struebig et al. 2010, Naharuddin et al. 2015, Shazali et al. 2016, Khan et al. 2019, Yoh et al. 2020). However, capture often causes stress and interferes with the animal's natural behaviour and

therefore, it has limited use for determining activity patterns and the types of habitats used by various bat species for foraging (Hayes et al. 2009). Bats that normally fly in the understory, such as species in the families Rhinolophidae, Hipposideridae, and Vespertilionidae subfamilies Kerivoulinae and Murininae are easily captured in harp traps that are usually set, at ground level, across narrow forest trails or streams (Francis 1989, Kingston et al. 2003a, Struebig et al. 2010). Mist nets are more suitable for use in open or edge space but the species that normally fly in these habitats can often detect and avoid mist nets through long-range echolocation (Francis 1989, Kingston et al. 2003a, Struebig et al. 2010). Therefore, high-flying insectivores are seldom captured and are usually missing from inventories (Francis 1989, Neuweiler 1989, Kingston 2013). However, because these species have less manoeuvrability in flight (Norberg & Rayner 1987), they are occasionally captured in situations where they cannot turn to avoid nets, such as near roosts or when they descend to fly low over rivers to drink or forage (Kingston 2013).

Over the past few decades, acoustic sampling with ultrasonic detectors has been used in numerous studies worldwide to document the occurrence and study the ecology and behaviour of insectivorous bats (Brigham et al. 2004, Britzke et al. 2013). In most temperate areas, many species can be identified from their calls (Fenton & Bell 1981, Waters & Gannon 2004) and extensive call libraries, combined with automatic classifiers, are now available to quantitively and quickly identify species using computer software programs (Adams et al. 2010, Walters et al. 2012, Agranat 2013). As a result, acoustic monitoring programs have been running for several years, particularly in Europe and North America (Walters et al. 2012, Jones et al. 2013, Barlow et al. 2015, Loeb et al. 2015). However, caution is recommended when interpreting results from automatic classification programs as calls may be misclassified (Russo & Voigt 2016, Rydell et al. 2017). Therefore, combining automatic identification with manual validation is considered the best option for a more accurate interpretation of sound files (López-Baucells et al. 2019).

Despite the high diversity of bat species in tropical regions of the world, very few acoustic studies have been conducted in these regions (Walters et al. 2013). One of the biggest obstacles to conducting acoustic monitoring in the tropics is the lack of local and regional call libraries (Furey et al. 2009, Walters et al. 2013, López-Baucells et al. 2019). Although echolocation calls for many species that occur in Southeast Asia have been described (e.g. Kingston et al. 1999, 2000, 2003b, Francis 2008, Furey et al. 2009, Hughes et al. 2010, 2011, Phauk 2013), call recordings are mainly held in the private collections of institutions. Several collections of calls exist for Borneo but few descriptions have been published and recordings are not available in any public database (e.g. Castle et al. 2014, Khan et al. 2020, Mullin et al. 2020, Senawi et al. 2020). Numerous studies have shown that calls, particularly from species in the families Rhinolophidae and Hipposideridae, have substantial geographic variation (Francis 2008, Furey et al. 2009, Hughes et al. 2010, Webala et al. 2019). Published descriptions of species recorded elsewhere in Southeast Asia may therefore have limited application to monitoring the same species in Borneo. Furthermore, to use machine-learning techniques to develop an automatic classifier for species identification a large number of calls must be available and should incorporate intraspecific variation (Hughes et al. 2010, Britzke et al. 2013, López-Baucells et al. 2019, Webala et al. 2019).

In this study, echolocation calls are described for 31 species of insectivorous bats recorded within and outside the boundary of Gunung Mulu National Park (GMNP). The aims of this study were: 1) Build an echolocation call library that can be used to identify insectivorous bats in GMNP; 2) Determine which species of echolocating bats that occur in the park can be reliably identified from their calls, using an automatic classification technique; and 3) Assess intraspecific variation in call structure and frequencies for Rhinolophidae and Hipposideridae, in relation to flight situation, sex and geographical location, which may influence the correct acoustic identification of species.

MATERIALS AND METHODS

Study Sites

The main study area, where bats were sampled to record their echolocation calls, was Gunung Mulu National Park (GMNP) in northern Sarawak, Malaysian Borneo. To compare calls of similar species from a different geographical location, bats were also sampled at Bako National Park (BNP) and Wind Cave Nature Reserve (WCNR) in southwestern Sarawak (Fig. 1A). GMNP (N4.04238° E114.81343°) covers a total area 85,671 hectares and is known for its high mammal diversity (Shazali et al. 2016). The extensive cave systems of the park, caused by its karstic topography, provide numerous roosting opportunities for cave roosting bats (Chapman 1985, Hall 1996). The soils of GMNP are derived from three main rock types: sandstone, limestone and shale; and alluvial clay deposits (Anderson & Chai 1982, Proctor et al. 1983). Altitude starts at 28 metres and extends to 2377 metres above sea level. An estimated 40% of the park is covered in lowland forests of five distinct types: alluvial, mixed dipterocarp, limestone, kerangas, and peat swamp (IUCN 2000). Vegetation at all sampling sites within the park was lowland riverine forest, bounded on one side by limestone scree forest. In contrast, vegetation at locations outside the park consisted of young secondary forest and community gardens.

Between 2012 and 2017, a total of 98 sites within and outside the boundary of GMNP were sampled, over 62 nights, with four-bank harp traps (Francis 1989) and mist nets. The number of harp traps per night varied between one and ten. Inside the park, 80 sites were sampled with harp traps for 57 nights. Traps were set across narrow forest trails, at suitably sized gaps between vegetation along river banks, and at a narrow cave passage in Lagang Cave to capture bats during emergence (Fig. 1). In 2014 and 2015, either one to two combined mist nets (12 m wide and 2.5 m high) or one high pole mist net (12 m wide and 7.5 m high) were used to sample at six sites along a riverbank, across rivers and in open spaces, during 12 nights. Outside the park boundary, two sites were sampled with harp traps for two nights in 2013 and ten sites over three nights in 2014 (Fig.

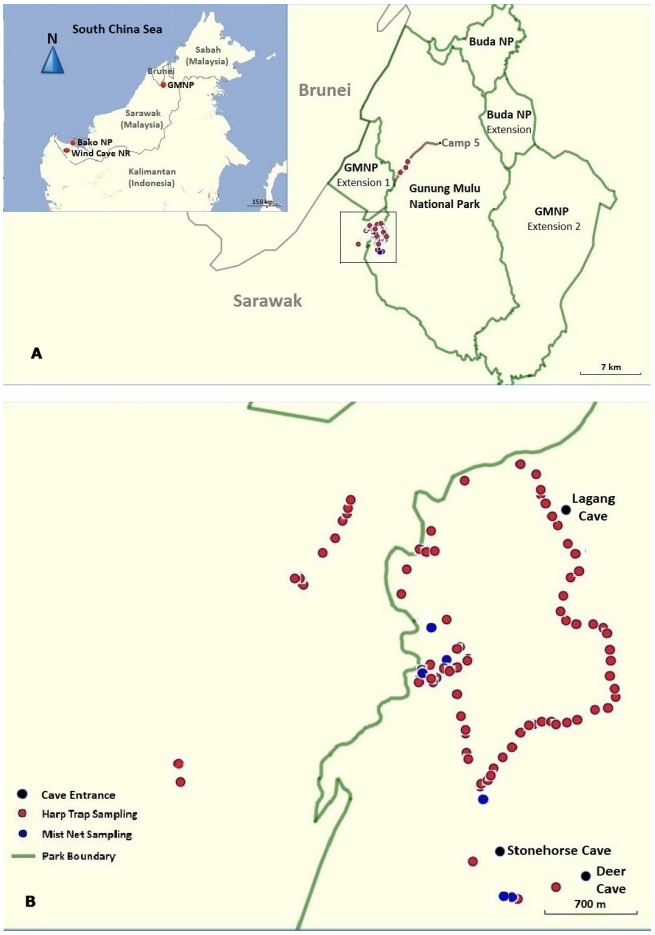

Fig. 1 - A) Map of Gunung Mulu NP with extensions and adjacent protected area. Inset shows locations of Bako NP and Wind Cave NR. **B)** Map of sites sampled outside the park boundary and within the park, between the Park HQ and Deer Cave. Sites that were sampled with harp traps are marked in red and sites sampled with mist nets are in blue.

1). Several individuals of foliage roosting species, *Kerivoula hardwickii* and *Myotis muricola* were opportunistically collected by hand from furled ginger or banana leaves both within and outside the park.

BNP (N1.72023° E110.44673°) is approximately 550 km from GMNP. It covers an area of 2,742 hectares and consists mainly of tropical heath (*kerangas*) forest with smaller areas of mixed dipterocarp, riverine, mangrove, beach forests and open shrubland. Elevation starts at 0 metres and extends to 260 metres above sea level (Hazebroek & Kashim 2000, Khan et al. 2007, Naharuddin et al. 2015). Sampling was conducted along trails and streams in mixed dipterocarp, riverine and tropical heath forest, with three to four harp traps and four to eight mist nets over four nights in 2014 and three nights in 2016. WCNR (N1.41458° E110.13731°) is a 6.16 hectare limestone forest reserve surrounding the Wind Cave (Mohd-Ridwan et al. 2010, Shazali et al. 2017, Morni et al. 2018, Rosli et al. 2018). It is located 48 km from Bako NP and 598 km from GMNP. Sampling with three harp traps was conducted on forest trails just outside the main entrance for two nights in 2016. Georeferenced occurrence data associated with all individuals, recorded in GMNP, BNP and WCNR during this study, has been published to the Global Biodiversity Information Facility (Görföl & Csorba 2020, McArthur & Khan 2020, McArthur et al. 2020).

Echolocation Call Recording

All individuals, except *Hipposideros* cf. *kunzi* and *Emballonura alecto/monticola*, were identified to species following Payne et al. (1985). *H.* cf. *kunzi* was not positively identified to species as there are currently no published records of this species occurring in Borneo (Murray et al. 2018); however, *H. kunzi*, which is common and widespread in Peninsular Malaysia (Murray et al. 2018), was the closest match based on forearm measurement, description of the noseleaf, echolocation call frequency and inspection of photographs to the two individuals captured in our study. *E. alecto/monticola* was only identified to a species pair from a photo of four individuals roosting at a small cave entrance, following the description by Payne et al. (1985) and a description of the unique roosting posture by Kingston et al. (2006). In this study, we assigned individuals of *Kerivoula papillosa* to either the large or small form of the species (Khan et al. 2010, Hasan & Abdullah 2011). We considered individuals with forearm length 43.7 mm and above to be the large form and those with forearm 42.5 mm and below to be the small form.

The majority of bats were recorded at the site of capture, at least 20 m distance from other captured bats to avoid interference from calls emitted by other individuals. Prior to the recording of release calls, individuals were marked on the underside of the wing with a non-toxic white paint marker to avoid re-recording calls from recaptured individuals. Bats were then released either in forest (clutter), along adjacent trails or streams (semi-clutter) or in forest clearings (open space) at or near the site of capture. Several specimens collected were subsequently deposited in either the Universiti Malaysia Sarawak Zoological Museum (Shazali et al. 2016, McArthur & Khan 2020) or the Hungarian Natural History Museum (Görföl & Csorba 2020).

Five different recording devices were used depending on availability. The majority of echolocation calls were recorded using an EM3+ detector (Wildlife Acoustics, USA), set to record at a sampling rate of 380 kHz, in WAC format, with real time expansion. Twenty-eight individuals of various species were recorded with an M500 USB microphone (Pettersson Elektronik AB), while eight individuals were recorded using a Pettersson D1000X detector, with a sampling rate of 500 kHz. *E. alecto/monticola* individuals were recorded with an SM2Bat+ and SMX U1 microphone (Wildlife Acoustics, USA). All recordings from these devices were in real time. One individual of *Rhinolophus luctus* was recorded, in 2012, with a U30 detector (Ultrasound Advice, UK) attached to a H2 digital audio recorder (Zoom, Germany), with a frequency division factor of 10.

Reference calls were collected either in-hand, in a flight tent, in a closed room, or upon release depending on the species. Bats from the families Rhinolophidae and Hipposideridae that produce constant frequency calls were recorded while held stationary, in-hand, at an appropriate distance (30 - 50 cm) from the microphone, in order to record the "resting frequency" of individuals (Neuweiler 1989, Heller & Helversen 1989, Siemers 2004). Such calls would be produced when the bat is perching (Siemers 2004). Rhinolophid and hipposiderid species differ in call intensity,

based on body size, with larger species generally producing lower frequency, higher intensity calls and smaller species higher frequency, lower intensity calls (Heller & Helversen 1989, Jones 1999). Therefore, to record the best quality call signals, larger species were recorded further from the microphone to avoid overloading, which results in "clipping" of the waveform and production of false harmonics (Fenton 2004) and smaller species were held closer to the microphone because their calls experience greater atmospheric attenuation (Griffin 1971). During flight, changes in constant frequency result from a bat moving toward or away from an object, which causes returning echoes to be 1 to 2 kHz higher or lower than the emitted call. To compensate for this effect (termed Doppler shift), the bat will emit a higher or lower call so that the returning echo is the frequency that it is tuned into (Neuweiler 1989, Jones 1999, Schnitzler & Kalko 2001). Variation in frequency that occurs due to the effect of Doppler shift compensation also needs to be included in the analysis of calls, particularly if there are species that overlap in call frequencies (Jones & Holderied 2007). Therefore, most individuals were also recorded after hand release to include the full range of calls produced. *Coelops robinsoni* individuals were also recorded during flight in a flight tent as the very high frequency produced by this species is rapidly attenuated during release (Siemers 2004).

Bats from the genera *Nycteris*, *Kerivoula*, *Murina* and *Glischropus* were recorded in a flight tent and two sizes of tents were used. A larger tent, constructed from two large mosquito nets stitched together and measuring 4 m length, 2 m width, and 2 m height was used up to 2015. From 2016 onwards, a smaller tent measuring 2 m length was considered sufficient to record these species which have slow, manoeuvrable flight and normally fly in cluttered habitats (Kingston et al. 2006, Senawi & Kingston 2019). *Myotis* species were recorded only in the larger sized flight tent. Start frequencies for calls of *K. hardwickii,* and *K. pellucida* were beyond the sampling range of the EM3+ detector, which could only record frequencies up to 190 kHz. Calls for two individuals of *K. hardwickii* calls were recorded with an M500 detector, and the sampling rate (500 kHz) was also too low to capture the start frequency. *K. hardwickii* is reported to produce calls with start frequencies up to 292 kHz, which is possibly the highest echolocation frequency known for bats (Schöner et al. 2015).

Only one individual of *Megaderma spasma* was recorded in a small room (3.9 m length, 3.7 m width and 3 m height). Four individuals of *M. australis* were recorded in the larger flight tent and three individuals were recorded flying in a cave (Lagang Cave) before capture and after release. Two individuals of *Charephon plicatus* were recorded flying in a large room (8.4 m length, 7.7 m width, and 3.8 m height) and 12 individuals upon release at a large open space (a former helipad: 31 m x 33 m) near Deer Cave (Fig. 1B), by two observers, each with a detector stationed at either side of the helipad.

Four individuals of *E. alecto/monticola* and ten of *M. australis* were not captured but recorded as they emerged from cave entrances inside the park. *E. alecto/monticola* were recorded emerging from a small unnamed cave near to Stonehorse Cave and individuals were identified to the species pair prior to emergence (Fig. 1B). No other species were recorded emerging from the cave at the same time as *E. alecto/monticola*. *M. australis* were recorded during emergence from Stonehorse Cave (Fig. 1B). Other species emerging at the same time and identified in recordings were *Rhinolophus creaghi*, *Hipposideros galeritus, H. diadema* and *M. horsfieldii*. *M. australis* is easily separated from these other species by call shape (frequency modulated, ending with a quasi-constant frequency tail). *Rhinolophus* and *Hipposideros* species produce constant frequency calls, while *M. horsfieldii* produces pure frequency modulated calls. No release calls were obtained for *M. australis* due to captured individuals being retained as voucher specimens by other members of the research team. Therefore, recordings of ten individuals which emerged from Stonehorse Cave were later used for analysis instead of release calls.

Differences in calls between the sexes, adults, and juveniles and different sized individuals can occur within a species and is known particularly among several of the Rhinolophidae and Hipposideridae (Jones et al. 1992, Russo et al. 2001, Siemers et al. 2005, Hughes et al. 2010, Puechmaille et al. 2014). Therefore, forearm and weight measurements, sex, and age class were also recorded from all captured individuals. Sex was determined by inspecting the genitalia of individuals (Racey 2009). Late pregnancy in females was determined by gently pressing the abdomen area to detect the presence of a foetus and lactation was determined by the presence of swollen mammary glands and enlarged nipples (Racey 2009). Age class was determined by illuminating the wing with a headlamp to view the closure of the epiphyseal plate in the metacarpal joints of the phalanges (Brunet-Rossinni & Wilkinson 2009).

Call Analysis

Sound files were analysed in Kaleidoscope Call Viewer, version 4.0.2 (Wildlife Acoustics Inc., USA). The following settings were used: FFT size: 256, Window size: 128. Max Cache Size: 256. The files were downloaded from the memory card and converted from WAC to WAV format, using Kaleidoscope convertor.

The calls were classified by call structure into six groups, based on Jones & Teeling (2006) and Huang et al. (2015), which were generally associated with family group, as follows:

Calls dominated by a constant (CF) or quasi-constant frequency (QCF) component, which may be preceded and/or succeeded by a frequency modulated (FM) component:

1. FM-CF-FM calls, family Rhinolophidae.
2. CF-FM calls, family Hipposideridae.
3. QCF Multiharmonic (QCF-MH) calls, family Emballonuridae.

Calls dominated by a FM component, which may also contain a QCF component:

4. FM Multiharmonic (FM-MH) calls, families Megadermatidae and Nycteridae.
5. FM Broadband (FM-B) calls, family Vespertilionidae.

6. FM-QCF calls, families Miniopteridae, Molossidae and some members of the Vespertilionidae subfamilies Myotinae and Vespertilioninae.

Following Furey et al. (2009), the call file was searched for a series of five, clear continuous pulses with a high signal-to-noise ratio. To avoid pseudo-replication (Furey et al. 2009), a single pulse, which in the majority of cases was the third pulse, was selected for measurement. A pulse, which is also referred to as a call or signal, is defined as a single sound produced by an echolocating bat and a continuous series of pulses, calls or signals emitted by a bat is referred to as a pulse or call sequence (Kingston et al. 1999, Loeb et al. 2015). Peak frequency (Fppeak), measured in kilohertz (kHz), was generated automatically in Kaleidoscope by highlighting the selected call in the spectrogram. Start (Fstart) and terminal frequencies (Fend), measured in kHz, were manually measured from the spectrogram. Pulse duration (PD) and interpulse interval (IPI), measured in milliseconds (ms), were measured from the oscillogram. During the process of measuring pulses from several species of Hipposideridae (e.g. *C. robinsoni*, *H. dyacorum*, *H. galeritus*) and FM-QCF pulses of *M. australis*, it was noted that Fppeak was present in the FM component of the pulse rather than the CF or QCF component. Fppeak in Hipposideridae calls is often measured only from the CF component (e.g. Webala et al. 2019) and is also measured by us to manually identify CF-FM and FM-QCF species from acoustic recordings. Therefore, an additional measurement, Fppeak-CF/QCF, was taken for call descriptions of all Hipposideridae and other FM-QCF species where Fppeak occurred in the FM component of the pulse. Harmonics, when present, were also measured. Fppeak for each harmonic was measured for CF calls and additional measurements of Fstart and Fend for were taken for all other calls. Only one call sequence, recorded from one individual, was available for *M. spasma*. Given that Fppeak varied between harmonics in each pulse, two pulses rather than one pulse were selected for measuremente and analysis.

Statistical Analysis

All statistical tests were performed in the PAST, version 3.17 (Hammer et al. 2001). A Linear Discriminant Function Analysis (DFA) was performed on calls from all 31 species and separately on all call groups that did not overlap with other groups: 1. FM-CF-FM calls, 2. CF-FM and QCF-MH calls and 3. FM-B, FM-MH and FM-QCF calls. Call parameters included in the analysis were Fppeak, Fstart, Fend, PD and IPI. To improve the classification success of *M. horsfieldii*, *M. muricola*, *M. australis* and *C. plicatus* calls, additional measurements of the second harmonic (Fppeak, Fstart and Fend) were added to a subsequent DFA conducted on calls for these species. All calls assigned to groups were cross-validated by a leave-one-out cross-validation jackknifing procedure (Hammer 2017). Classification success was defined as the number of calls correctly identified to species divided by the total number of the true species calls. This is the standard interpretation of DFA results presented by most researchers using DFA to classify echolocation calls (e.g. Vaughan et al. 1997, Furey et al. 2009, Hughes et al. 2010, Pham et al. 2021).

A Shapiro-Wilks test was performed on all measurements to test for normal distribution of the data. To assess differences in call parameters between individuals recorded in different flight situations (stationary, enclosure, release in clutter, semi-clutter or open space), a parametric t-test for matched samples was used for normally distributed data, and a non-parametric Wilcoxon signed-rank test was used for data not normally distributed. Parameters examined were Fppeak, Fppeak-CF/QCF, Fstart, Fend, Duration, and IPI. The tests were performed on all individuals for which calls were available for a minimum of three and up to a maximum of 22 individuals per species. In the case of *M. australis*, calls were not available for the same individuals recorded in different situations (i.e. flight tent, flying in a cave and emerging from a cave). Therefore, Analysis of variance (ANOVA) with Tukey Pairwise was used to compare Fppeak, Fppeak-QCF, Fstart and Fend and a Kruskal-Wallis with Mann-Whitney pairwise was used to compare PD and IPI, which were not normally distributed. Only two calls for *C. plicatus*, flying in a large room, were available for comparison to calls recorded in open space and these were insufficient for statistical comparison. However, a T-test for matched samples was performed on alternating calls ("type A and type B"), produced by *C. plicatus* when flying in open space. For analysis, two consecutive pulses representing each call type (A and B) were selected for comparison, from eight individuals released in open space.

T-tests and non-parametric Mann-Whitney U tests (for data that was not normally distributed) were used to compare differences between male and female call frequencies and body size (determined from forearm length) and for geographical variation in Fppeak between several rhinolophid and hipposiderid species that occur in GMNP and the same species which were also captured in BNP and WCNR. Only stationary calls were considered for these analyses and Fppeak was measured from the CF component of all pulses.

RESULTS

Echolocation Calls

Call sequences were recorded from 508 individuals representing 31 species of insectivorous bats. Six of the species captured were not previously recorded in the park, i.e. *Rhinolophus acuminatus, Hipposideros* cf. *kunzi, Kerivoula intermedia, Murina aenea* (Zana et al. 2019), *Murina rozendaali* and *Myotis ridleyi*.

Calls were recorded for five species in the family Rhinolophidae (Fig. 2). Up to four harmonics were measured (Table 1 in Supplementary Materials) and Fppeak was concentrated in the second harmonic (Table 1). Fppeak in stationary calls for this group ranged from *R. philippinensis* (32.8 – 34.8 kHz), *R. luctus* (38.2 – 38.5 kHz), *R. creaghi* (66.0 – 72.1 kHz), *R. borneensis* (78.5 – 83.8 kHz) to *R. acuminatus* (83.7 - 87.5 kHz) and call duration for all individuals varied between 22.4 and 100.6 kHz (Table 1). There was a slight overlap in the lower range of Fppeak recorded for *R. acuminatus* (82.0 – 87.5 kHz) and the upper range for *R. borneensis* (76.6 – 83.8 kHz) when both stationary and release calls were considered.

Eight species in the family Hipposideridae were recorded (Fig. 3). Up to four harmonics were measured (Table 1 in Supplementary Materials) and Fppeak was concentrated in the second harmonic (Table 1). In this group, the lowest Fppeak for stationary calls was recorded for *H. coxi* (44.7 – 51.5 kHz), followed by *H. diadema* (65.1 – 69.4 kHz), *H. galeritus* (99.4 – 115.1 kHz), *H. cervinus* (101.9 – 121.6 kHz), *H. bicolor* (121.5 – 135.5 kHz), *H.* cf. *kunzi* (138.7 – 140.0 kHz) and *H. dyacorum* (135.0 – 163.3 kHz). The highest Fppeak was recorded for *C. robinsoni* (186.2 kHz). There was some overlap in the lower range of Fppeak recorded for *H. cervinus* (111.3 – 121.6 kHz) and the upper range for *H. galeritus* (107.8 – 115.1 kHz), when both stationary and release calls were considered. The bandwidth of the FM component of calls increased as Fppeak increased. The CF component was missing for many *C. robinson*i calls, and the FM component was characterized by a broad bandwidth, starting from a minimum frequency of 190 kHz and ending at 111.0 kHz. Fppeak was concentrated in the FM component in all *C. robinsoni* calls, and for 20 out of 29 stationary calls and 9 out of 17 release calls of *H. dyacorum*. *H. galeritus* also had several calls with Fppeak concentrated in the FM component for 5 out of 39 stationary and 2 out of 22 release calls (Table 1).

E. alecto/monticola was the only species pair recorded in the QCF-MH call group. Up to four harmonics were visible (Fig. 3 and Table 2 in Supplementary Materials), with the second harmonic being the dominant peak frequency (Table 1). Fppeak for calls of four individuals, flying out of a cave entrance, ranged from 45.1 to 46.6 kHz.

Thirteen species were recorded in the FM broadband call group: *Murina aenea, M. peninsularis, M. suilla, M. rozendaali K. hardwickii, K. intermedia, K. minuta, K. papillosa* (separated as two size classes), *K pellucida* (Fig. 4), *Myotis horsfieldii, M. muricola, M. ridleyi* and *Glischropus*

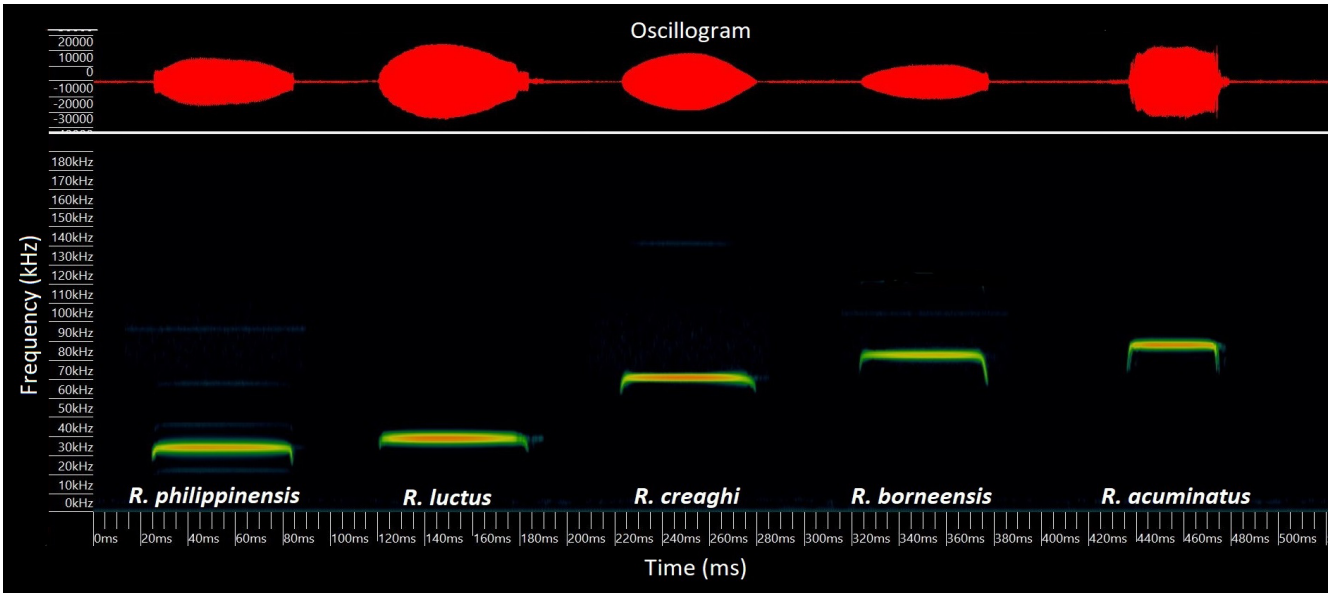

Fig. 2 - Composite spectrogram image of echolocation pulses of five species in the family Rhinolophidae recorded in GMNP. *R. luctus* is represented by a pulse recorded with an M500 detector, while pulses for remaining species were recorded with an EM3+ detector. Time in this spectrogram is scaled differently (500 ms) to the other spectrograms (200 ms) and should not be directly compared.

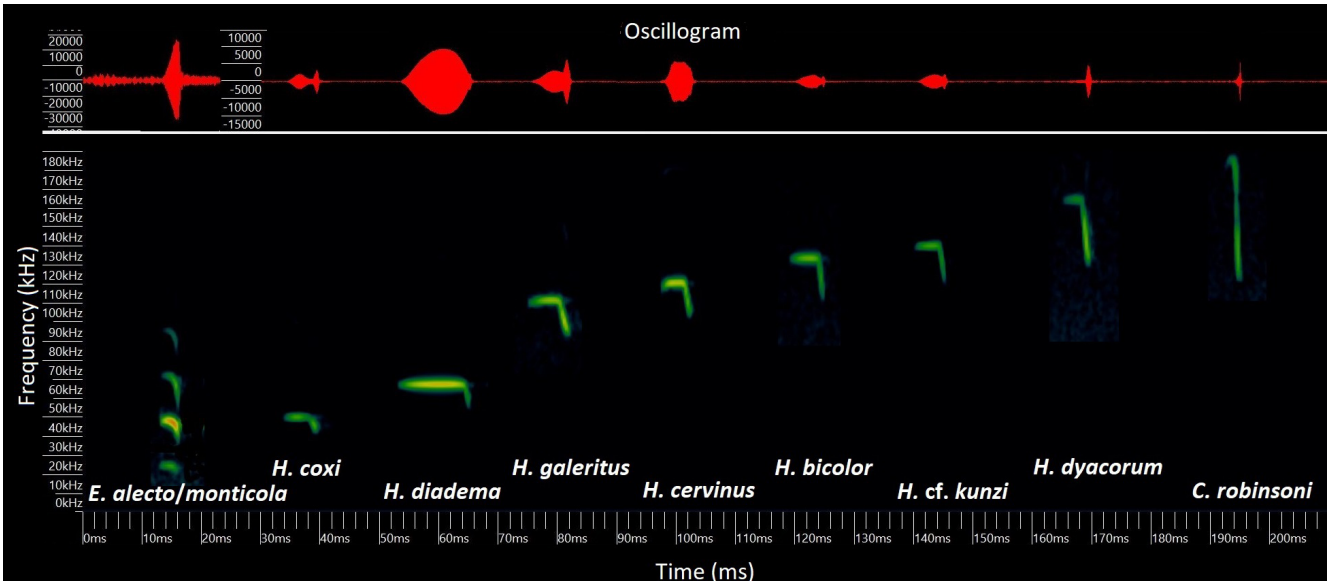

Fig. 3 - Composite spectrogram image of echolocation pulses of *E. alecto/monticola* and seven species in the family Hipposideridae recorded in GMNP. *E. alecto/monticola* is represented by a pulse recorded with an SM2Bat+ detector (emerging from a cave), while pulses for remaining species were recorded with an EM3+ detector.

tylopus (Fig. 5). The highest start frequency measured was for *K. hardwickii* (>250 kHz), which was beyond the range of the M500 microphone. No additional harmonics were present in pulses for *Kerivoula* and *Murina* species. Calls for *M. muricola* changed from FM broadband, when flying in enclosed space to FM broadband with a narrowband QCF tail, when flying in open space and calls for *G. tylopus* reduced in bandwidth with a less distinct narrowband QCF tail in semi-clutter (Fig. 5). Two harmonics were measured for *Myotis* species pulses and up to three harmonics for *G. tylopus* (Table 2 in Supplementary Materials). The first harmonic was dominant in calls for these species (Table 1).

Both *M. spasma* and *N. tragata* produced very low intensity FM multiharmonic calls (Fig. 5). Up to four harmonics were visible in *M. spasma* calls, and Fppeak switched between second, third, and fourth harmonics (Table 2 in Supplementary Materials). *N. tragata* calls had higher starting frequencies, and up to five harmonics were visible. Fppeak also switched between the different harmonics (Table 2 in Supplementary Materials).

Two species were recorded in the FM-QCF group: *M. australis* and *C. plicatus.* Calls differed in both species when flying in enclosed space compared to open space, especially in *C. plicatus*. *M. australis* produced broadband FM pulses ending in a short narrowband QCF tail when flying in the tent (Fig. 6a) and a large cave passage (Fig. 6b). When flying in a narrow cave passage, the FM pulses emitted lacked the narrowband tail (Fig. 6c) and emerging from a cave the pulses changed to more narrowband FM pulses with the QCF component slightly longer in duration (Fig 6d and 6e, Table 1). Second harmonics were present in enclosed space situations (i.e. flying in a tent and flying in a cave) (Table 2 in Supplementary Materials). When flying in a large room, *C. plicatus* produced long duration, broadband FM pulses

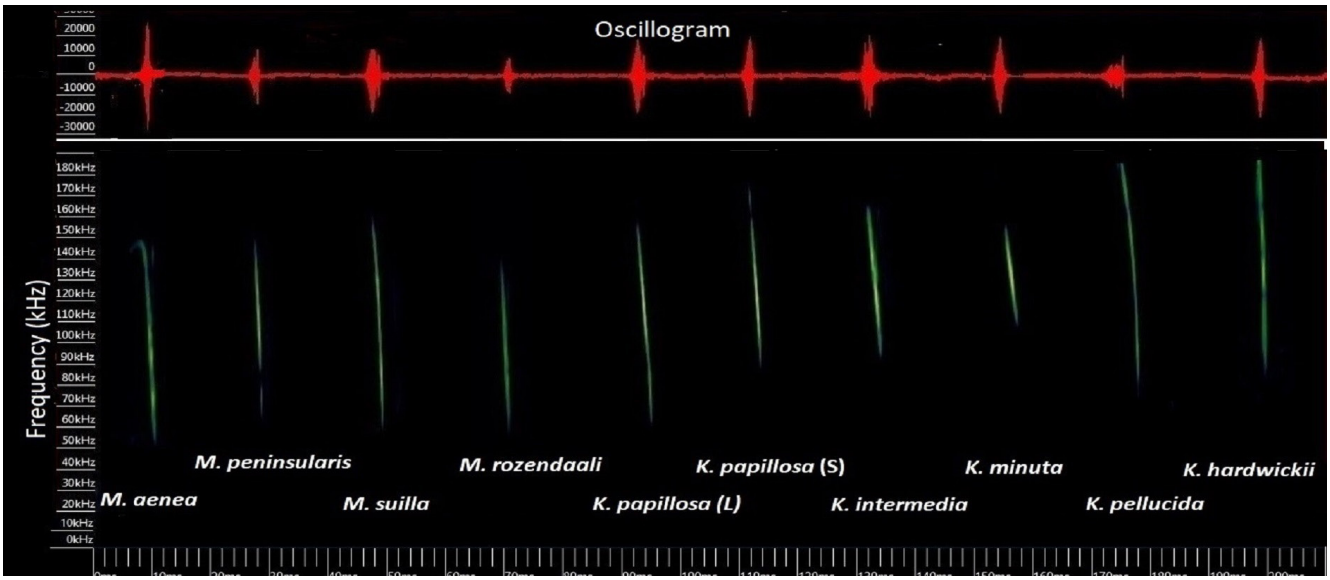

Fig. 4 - Composite spectrogram image of echolocation pulses of *Murina* and *Kerivoula* species recorded in a flight tent at GMNP. *K. papillosa* is separated as two size classes: *K. papillosa* large form (L) and small form (S). *M. aenea* and *M. rozendaali* pulses were recorded with a D1000X detector and M500 microphone respectively, while pulses for remaining species were recorded with EM3+ detector..

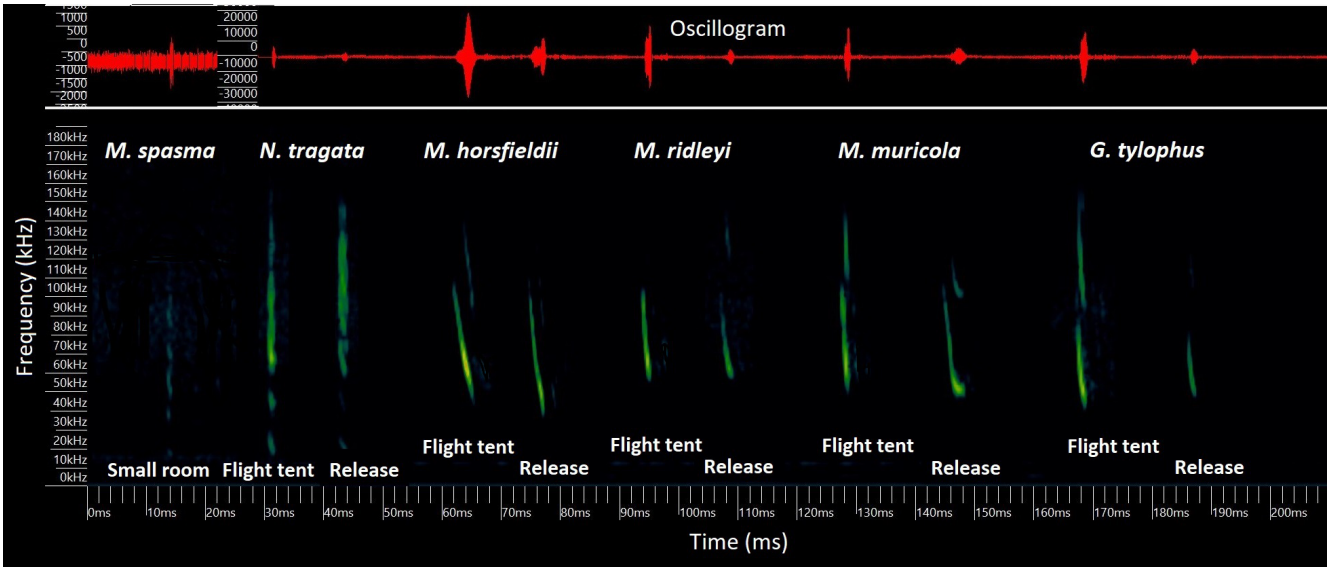

Fig. 5 - Composite spectrogram image of echolocation pulses of *M. spasma* (flying in a small room), *N. tragata*, three *Myotis* species and *G. tylopus* recorded in a flight tent and during release at GMNP. *N. tragata*, *M. ridleyi* and *G. tylopus* were released in semi-clutter on forest trails and *M. horsfieldii* was released at a stream. *M. muricola* produced pulses with a QCF component when released in open spaces.

(Fig. 6f). In open space, this species produced pulses that alternated between a long duration, broadband FM pulse, alternating call type A (Fig. 6g) and a more narrowband QCF pulse, alternating call type B (Fig. 6h). Three harmonics were present, with the first harmonic being dominant when flying in the large room and two harmonics were sometimes present in alternating type A calls but occurred less often in type B calls in open space (Tables 1 and Table 2 in Supplementary Materials).

Discriminant Function Analysis

Analysis was performed on a total of 839 pulses for all species in all recording situations. DFA classified 80.3% of pulses from all species, from the full dataset correctly (Table 3 in Supplementary Materials), which are displayed in the DFA plot according to the six call type groups (Fig. 7). The most important parameters for distinguishing between all calls, according to the eigenvalues, were Fstart, followed by Fppeak and Fend (Table 4 in Supplementary Materials). The FM-CF-FM (family Rhinolophidae) and CF-FM (family Hipposideridae) call groups did not overlap with any of the other call groups. The most important parameter for distinguishing between FM-CF-FM calls was Fppeak, while Fstart was the most important parameter in distinguishing between CF-FM calls. However, there was considerable overlap between the FM-B, FM-MH and FM-QCF groups. The most important parameter in distinguishing species within these call groups was Fstart, followed by Fppeak, Fend and IPI (Table 4 in Supplementary Materials). Although *C. plicatus* pulses were clearly separate from other species and call groups on the DFA plot (Fig. 7), four out of 22 calls were assigned as false positives to *E. alecto/monticola* in the classification matrix (Table 3 in Supplementary Materials).

In a subsequent analysis performed on the FM-CF-FM call group 96.6% of calls were correctly classified. Misclassification in this group was limited to overlap between *R. acuminatus* and *R. borneensis* calls (Fig. 1 and Table 5 in Supplementary Materials). Although *R. luctus* achieved 100% classification success in this analysis, the species was represented by only two calls from two individuals. The QCF-MH call group, which consisted of one species pair (*E. alecto/monticola*), was included in the analysis of the CF-FM call group, because of similarity in measurements of call parameters and 95.6% of calls were correctly classified. Misclassification in these two groups was confined to overlap in calls between *H. cervinus* and *H. galeritus*, while 3 out of 45 *H. dyacorum* calls were incorrectly assigned to *H.* cf. *kunzi* (Fig. 2 and Table 6 in Supplementary Materials).

Within the FM-B, FM-MH and FM-QCF call groups, 68.0% of calls were correctly classified (Fig. 3 and Table 7 in Supplementary Materials). Two distinct clusters of overlapping calls were visible in the DFA plot (Fig. 3 in Supplementary Materials). *Kerivoula*, *Murina* species and *N. tragata* formed one cluster, while *Myotis* species, *M. australis*, *G. tylophus* and *M. spasma* formed another cluster. *C. plicatus* calls achieved 95.5% classification success, with only one call misclassified as *M. muricola*. Within the *Kerivoula*, *Murina* species and *N. tragata* call cluster, the highest classification success was achieved by *M. aenea* (100%) *K. minuta* (85.7%), *N. tragata* (80.0%) and *K. papillosa* large form (76.0%). However, *M. aenea* was only represented by two calls and one call each from *N. tragata*, *M. rozendaali* and *M. australis* were incorrectly assigned to *M. aenea*. All four *Murina* species overlapped mainly with each other and also with *N. tragata. K. hardwickii* calls only overlapped with *K. pellucida*. There was strong overlap between *K. intermedia*, *K. minuta* and *K. papillosa* (small form), while *K. papillosa* (large form) mainly overlapped with *Murina* species. When DFA was conducted on *K. papillosa* (large) and *K. papillosa* (small) exclusively, correct classification was achieved for 93% of calls (Table 7 in Supplementary Materials). Within the *Myotis* species, *M. australis*, *G. tylophus* and *M. spasma* cluster, *M. spasma* calls failed to be classified to species, while *M. ridleyi* achieved 100% classification success. However, *M. ridleyi* was only represented by two calls from one individual and calls from several other species (*M. muricola*, *M. horsfieldii*, *M. peninsularis* and *N. tragata*) were incorrectly classified as

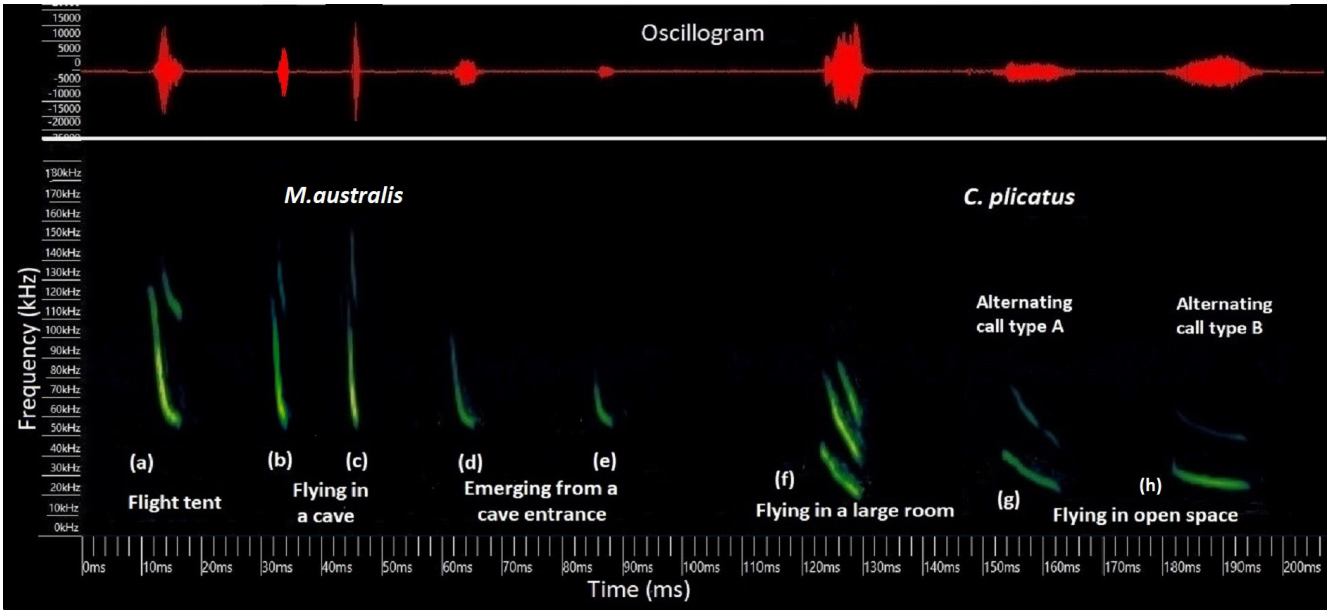

Fig. 6 - Composite spectrogram image of echolocation pulses of *M. australis* (a-e) and *C. plicatus* (f-h) recorded in different flight situations. The echolocation pulse (b) was recorded in a large cave passage before the individual was captured and pulse (c) was recorded in a narrower passage after another individual was released.

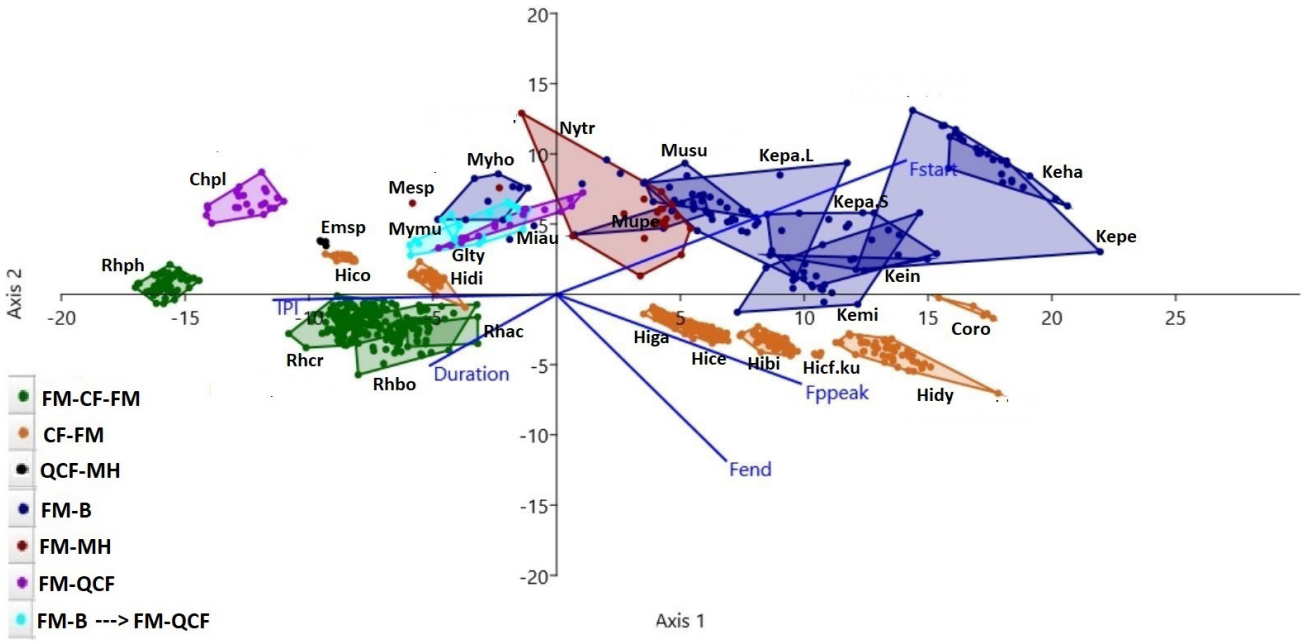

Fig. 7 – Discriminant Function Analysis results plot for all 31 species of insectivorous bats recorded in GMNP. All species are shown in their respective call type groups. Species that change their call type, from FM to FM-QCF in different flight situations (*M. muricola* and *G. tylopus*) are displayed separately. Axis 1 explains 75.5 %, while Axis 2 explains 13.2% of the variation between call parameters. Axis loadings, eigenvalues (which indicate the amount of variation explained by the axes) and percentage variances of the five parameters for all call groups are provided in Table S4.

M. ridleyi. All species in this cluster had overlapping calls. *M. muricola* (47.1%) and *M. australis* (58.8%) calls had strong overlap with each other and also other species in the cluster, while *M. horsfieldii*, with 66.7% classification success, had calls overlapping with three other species. However, when a separate DFA was conducted, with additional measurements of harmonics, for *M. horsfieldii*, *M. muricola*, *M. australis* and *C. plicatus* calls, 100% correct classification success was achieved for all four species (Table 7 in Supplementary Materials). The most important parameters in distinguishing between calls of these species were Fend, followed by Fstart, Fppeak and Fstart of the second harmonic (Table 4 in Supplementary Materials).

Call Situation Comparison

Four species of Rhinolophidae and six species of Hipposideridae were assessed for differences in stationary and release calls: *R. acuminatus, R. borneensis, R. creaghi, R. philippinensis, Hipposideros bicolor, H. dyacorum, H. coxi, H. cervinus, H. galeritus,* and *H. diadema.* Stationary and release calls differed significantly in Fppeak for most individuals, except *H. dyacorum* and *H. coxi*, with one to two kHz lower Fppeak in release calls ($p < 0.001$) (Table 8 in Supplementary Materials). Duration and IPI were shorter in release calls for three species: *R. borneensis*, *R. creaghi* and *H. cervinus* ($p < 0.01$) (Table 8 in Supplementary Materials).

There was no significant difference in all parameters for flight tent and release calls for *N. tragata, K. papillosa, K. pellucida and M. peninsularis*. *K. minuta* differed only in Fppeak, which was higher in release calls ($p < 0.05$). *M. muricola* calls were lower in open space (Fppeak 54.3 - 59.0 kHz, Fstart 64.5 - 107.5 kHz) compared to semi-clutter (Fppeak 52.6 - 74.3 kHz, Fstart 62.0 - 111.5 kHz, $p < 0.05$). For *C. plicatus* calls, measurements of Fppeak (22.8 - 38.9 kHz) and Fstart (27.3 - 49.1 kHz) were lower, Fend (19.6 - 23.7 kHz) was higher and pulse duration (11.1 - 16.0 ms) was longer in open space (n=12), compared to calls from two individuals recorded in a large room (Fppeak 35.8 - 36.2 kHz, Fstart 45.0 - 49.5 kHz, Fend 16.5 - 19.0 kHz, PD 7.4 - 7.5 ms). However, this could not be tested statistically. In open space, alternating call type B for *C. plicatus* was significantly lower in Fppeak (22.8 - 27.2 kHz), Fstart (27.3 - 46.4 kHz) and Fend (17.9 - 23.6 kHz) than call type A (Fppeak 24.2 - 38.9 kHz, Fstart 36.7 - 49.1 kHz, Fend 19.6 - 23.7 kHz, $p < 0.01$), for eight individuals recorded (Table 8 in Supplementary Materials). *M. australis* exhibited lower Fppeak (56.0 - 58.5 kHz) in cave emergence calls compared to the flight tent (60.7 - 70.4 kHz, $p < 0.001$) but there was no significant difference between calls in the flight tent and flying in a cave. There was no significant difference for all other parameters (Table 9 in Supplementary Materials).

Male-Female Comparison

Nine species were assessed for differences in body size (determined by forearm length) and Fppeak stationary calls between sexes: *R. borneensis, R. creaghi, R. philippensis, H. bicolor, H. cervinus, H. coxi, H. diadema, H. dyacorum* and *H galeritus* (Table 10 in Supplementary Materials). Males and females of three species differed significantly in forearm length, with larger females for *H. dyacorum* ($t = 2.62$, $p < 0.05$) and *H. coxi* ($t = 2.39$, $p < 0.05$), and larger males for *R. creaghi* ($t = -3.96$, $p < 0.001$). Of these three species, two showed differences in Fppeak. The smaller males of *H. dyacorum* exhibited higher frequencies (155.5 – 165.4 kHz, $n = 20$) compared to females (148.1 – 156.2 kHz, $n = 5$, $t = -4.58$, $p < 0.001$). The larger males of *R. creaghi* exhibited lower frequencies (66.0 – 69.5 kHz, $n = 31$) compared to females (68.6 – 72.1 kHz, $n = 36$, $z = -6.86$, $p < 0.001$) (Fig. 4 and Table 10 in Supplementary Materials).

Table 1 - Call measurements mean, standard deviation (top) and range of dominant frequency (bottom) for 31 species recorded in Gunung Mulu National Park. Fppeak = peak frequency, Fstart = start frequency, Fend = terminal frequency, PD = pulse duration, IPI = interval between pulses n = number of female ♂ and male ♀ individuals recorded, un = unknown sex.

Species	Fppeak (kHz)	Fppeak CF/QCF (kHz)	Fstart (kHz)	Fend (kHz)	PD (ms)	IPI (ms)	n		
							♂	♀	un
Rhinolophus acuminatus (Stationary)	85.1 ± 2.1 83.7 - 87.5	-	72.6 ± 4.1 68.6 - 76.8	66.8 ± 3.6 63.2 - 70.5	35.1 ± 9.7 25.00 - 44.4	39.8 ± 10.7 27.7 - 48.1	2	1	
Rhinolophus acuminatus (Release)	83.2 ± 1.7 82.0 - 85.1	-	68.2 ± 0.6 67.7 - 68.6	70.2 ± 3.5 67.7 - 72.7	45.9 ± 9.7 36.1 - 55.5	74.9 ± 30.8 39.8 - 97.1	2	1	
Rhinolophus borneensis (Stationary)	81.6 ± 1.2 78.5 – 83.8	-	70.9 ± 4.1 61.1 – 78.2	67.6 ± 4.3 57.9 – 78.2	54.0 ± 13.0 22.4 – 100.6	114.9 ± 37.1 27.7 – 199.2	26	14	
Rhinolophus borneensis (Release)	80.2 ± 1.4 76.6 - 83.6	-	65.9 ± 4.6 57.5 - 77.7	67.9 ± 5.4 54.5 - 79.6	43.1 ± 10.9 17.7 - 62.9	70.9 ± 28.1 18.7 – 164.9	23	7	
Rhinolophus creaghi (Stationary)	69.4 ± 1.7 66.0 - 72.1	-	60.20± 3.5 53.3 - 70.5	58.4 ± 3.8 50.6 – 65.9	53.0 ± 8.2 34.8 - 81.8	127.3 ± 40.9 58.5 - 284.1	43	37	3
Rhinolophus creaghi (Release)	68.1 ± 1.6 63.93- 70.9	-	57.56 ± 3.3 50.7 - 66.4	61.5 ± 3.7 53.6 - 69.6	48.1 ± 9.6 28.1 - 77.9	87.3 ± 20.4 37.4 – 154.4	40	31	1
Rhinolophus luctus (Stationary)	38.3 ± 0.2 38.2 - 38.5	-	32.1 ± 2.2 30.5 - 33.6	27.9 ± 1.3 27.0 - 28.8	64.3 ± 0.4 64.0 - 64.6	91.2 ± 32.8 68.0 - 114.3	1		1
Rhinolophus philippinensis (Stationary)	33.8 ± 0.5 32.8 - 34.8	-	28.2 ± 1.6 24.8 - 31.4	27.1 ± 2.4 22.6 - 30.5	56.2 ± 7.2 43.6 - 68.0	109.1 ± 36.8 51.8 - 257.5	12	20	
Rhinolophus philippinensis (Release)	33.1 ± 0.5 31.7 - 34.1	-	27.8 ± 1.2 25.3 - 30.1	28.9 ± 1.4 24.8 - 31.0	59.1 ± 7.3 46.3 - 75.0	109.8 ± 7.4 89.4 - 123.9	9	18	
Hipposideros bicolor (Stationary)	132.4 ± 2.4 121.5 - 135.5	132.5 ± 1.9 127.0 - 135.5	132.5 ± 1.9 127.0 - 135.5	111.8 ± 3.6 105.0 - 119.1	6.7 ± 0.9 5.0 - 9.0	17.2 ± 3.1 11.7 - 23.2	21	18	
Hipposideros bicolor (Release)	132.1 ± 1.9 126.3 – 135.5	132.1 ± 1.9 126.3 – 135.5	132.1 ± 1.9 126.3 – 135.5	111.3 ± 4.0 103.2 – 118.6	6.5 ± 1.2 3.9 – 9.3	15.7 ± 4.7 8.2 – 29.2	21	18	
Hipposideros cervinus (Stationary)	117.2 ± 2.9 101.9 - 121.6	117.4 ± 2.0 112.8 - 121.6	117.4 ± 2.0 112.8 - 121.6	101.9 ± 3.3 91.8 - 109.6	5.1 ± 0.8 3.9 - 7.1	23.7 ± 7.3 13.7 - 54.3	18	31	2
Hipposideros cervinus (Release)	116.4 ± 2.7 105.0 – 120.4	116.6 ± 2.0 111.3 – 120.4	116.6 ± 2.0 111.3 – 120.4	101.5 ± 3.8 87.7 – 108.6	5.4 ± 0.8 3.4 – 7.1	20.0 ± 6.2 11.20– 40.4	16	24	1
Hipposideros coxi (Stationary)	49.2 ± 2.0 44.7 - 51.5	49.3 ± 1.9 45.3 - 51.5	49.3 ± 1.9 45.3 - 51.5	42.1 ± 1.4 39.6 - 43.6	6.3 ± 0.5 5.0 - 7.1	23.5 ± 3.5 17.6 - 29.1	4	9	
Hipposideros coxi (Release)	50.6 ± 0.8 49.5 – 51.9	50.6 ± 0.8 49.5 – 51.9	50.6 ± 0.8 49.5 – 51.9	42.9 ± 1.3 40.5 – 44.6	6.4 ± 1.1 4.9 – 8.3	23.4 ± 8.0 13.2 – 37.7	2	8	

Table 1- Continuation

Species	Fppeak (kHz)	Fppeak CF/QCF (kHz)	Fstart (kHz)	Fend (kHz)	PD (ms)	IPI (ms)	n		
							♂	♀	un
Hipposideros diadema (Stationary)	67.5 ± 1.2 65.1 - 69.4	67.5 ± 1.0 65.1 - 69.4	67.5 ± 1.0 65.1 - 69.4	56.3 ± 3.1 49.1 - 61.8	10.2 ± 2.6 4.9 - 14.4	29.9 ± 10.2 10.7 - 46.7	16	5	
Hipposideros diadema (Release)	67.0 ± 0.8 65.8 – 68.4	67.0 ± 0.8 65.8 – 68.4	67.0 ± 0.8 65.8 – 68.4	57.2 ± 3.2 54.1 – 64.6	11.1 ± 3.1 7.4 – 16.1	41.8 ± 12.3 28.2 – 64.3	9	2	
Hipposideros dyacorum (Stationary)	146.3 ± 8.8 135.0 - 163.3	158.2 ± 4.6 147.8 - 165.4	158.2 ± 4.6 147.8 - 165.4	128.0 ± 4.0 119.1 - 135.0	5.1 ± 0.7 4.1 - 6.8	16.2 ± 3.0 11.8 - 25.7	6	21	1
Hipposideros dyacorum (Release)	147.5 ± 12.3 129.2 – 172.3	159.2 ± 5.6 147.8 – 172.3	159.2 ± 5.6 147.8 – 172.3	128.1 ± 8.0 116.9 – 151.4	5.3 ± 0.8 4.1 – 7.5	13.7 ± 2.7 10.6 – 20.1	3	13	1
Hipposideros galeritus (Stationary)	111.0 ± 4.3 99.4 - 115.1	112.5 ± 1.6 107.8 - 115.1	112.5 ± 1.6 107.8 - 115.1	94.5 ± 2.7 89.1 - 100.0	6.0 ± 0.9 3.7 - 7.7	25.7 ± 7.6 13.4 - 49.5	13	24	2
Hipposideros galeritus (Release)	111.0 ± 3.6 100.4 – 114.3	112.2 ± 1.3 110.3 – 114.3	112.2 ± 1.3 110.3 – 114.3	94.5 ± 4.1 90.0 – 105.5	5.8 ± 1.0 4.3 – 7.6	21.6 ± 3.6 14.2 – 27.6	10	10	1
Hipposideros cf. *kunzi* (Stationary)	139.3 ± 0.9 138.7 - 140.0	139.3 ± 0.9 138.7 - 140.0	139.3 ± 0.9 138.7 - 140.0	120.2 ± 0.3 120.0 - 120.5	5.5 ± 0.8 5.0 - 6.1	14.6	1	1	
Hipposideros cf. *kunzi* (Release)	139.5 ± 0.7 139.0 – 140.0	139.5 ± 0.7 139.0 – 140.0	139.5 ± 0.7 139.0 – 140.0	120.5 ± 1.3 119.6 – 121.4	6.8 ± 0.5 6.4 – 7.1	19.4 ± 8.8 13.2 – 25.7	1	1	
Coelops robinsoni (Stationary)	186.1 186.1 – 186.2	189.50 ± 0.71 189.0 – 190.0	189.50 ± 0.71 189.0 – 190.0	116.50 ± 2.1 115.0 - 118.0	1.2 ± 0.2 1.1 - 1.3	9.8 ± 4.6 6.5 - 13.1	1	1	
Coelops robinsoni (Flying in tent)	183.7 ± 1.1 183.0 – 184.5	>190.0	>190.0	113.8 ± 3.9 111.0 – 116.5	1.2	14.7 ± 2.0 13.3 – 16.1	1	1	
Coelops robinsoni (Release)	129.0	191.5	191.5	117.5	1.3	12.2	1		
Emballonura alecto/monticola (Emerging from cave)	45.8 ± 0.8 45.1 - 46.6	-	46.9 ± 0.7 46.4 - 47.7	35.2 ± 0.9 34.6 - 36.4	4.4 ± 0.7 3.6 - 5.1	34.0 ± 7.3 26.7 - 42.3			4
Megaderma spasma (Flying in small room 2 calls)	69.0 ± 23.3 52.5 – 85.5	-	93.0 ± 15.6 82.0 – 104.0	31.5	1.0	68.5 ± 56.0 28.9 – 108.1		1	
Nycteris tragata (Flight Tent)	94.9 ± 12.7 67.4 – 116.9	-	141.3 ± 9.4 116.0 – 155.0	61.0 ± 6.4 54.0 – 78.0	1.0 ± 0.2 0.7 – 1.4	20.3 ± 13.8 7.2 – 50.1	8	5	
Nycteris tragata (Release)	82.4 ± 18.5 48.3 – 98.9	-	136.9 ± 11.5 113.5 – 150.0	56.0 ± 19.5 14.0 - 76	1.1 ± 0.3 0.8 – 1.6	16.8 ± 6.1 8.9 – 24.2	5	2	
Murina aenea (Flying in tent)	69.4 ± 9.5 62.7 – 76.1	-	143.3 ± 11.7 135.0 – 151.5	40.75 ± 1.1 40.0 – 41.5	2.81 ± 0.4 2.5 – 3.1	24.15 ± 6.5 19.6 - 28.7	1	1	

Table 1- Continuation

Species	Fppeak (kHz)	Fppeak CF/QCF (kHz)	Fstart (kHz)	Fend (kHz)	PD (ms)	IPI (ms)	n		
							♂	♀	un
Murina peninsularis (Flying in tent)	108.7 ± 13.1 95.8 – 120.0	-	154.4 ± 6.3 148.0 – 163.0	54.8 ± 3.1 51.0 – 57.5	2.4 ± 0.3 2.2 – 2.8	22.5 ± 3.0 19.7 - 25.1	1	3	
Murina peninsularis (Release)	99.7 ± 20.4 73.4 – 123.0	-	136.0 ± 16.4 115.0 – 154.5	60.0 ± 2.9 56.0 – 63.0	1.7 ± 0.6 1.1 – 2.4	18.6 ± 2.7 16.2 – 22.4	1	2	
Murina rozendaali (Flying in tent)	99.5 ± 16.6 87.8 - 111.3	-	150.0 ± 4.2 147.0 – 153.0	42.0 ± 3.5 39.5 – 44.5	1.8 ± 0.4 1.5 - 2.0	27.3 ± 0.5 27.0 - 27.7	1	1	
Murina suilla (Flying in tent)	99.3 ± 21.7 79.5 – 129.0	-	160.6 ± 8.6 151.0 - 170.0	52.0 ± 6.5 47.0 - 63.0	2.2 ± 0.4 1.7 - 2.7	28.1 ± 13.5 18.1 – 49.5	1	4	
Murina suilla (Release)	95.5 ± 3.1 93.0 – 99.0	-	155.3 ± 7.7 146.5 – 160.0	55.5 ± 2.8 52.5 – 58.0	1.8 ± 0.3 1.5 – 2.1	16.0 ± 1.5 14.4 – 17.3	1	2	
Kerivoula hardwickii (Flying in tent)	146.5 ± 23.0 112.4 – 185.9	-	>250.0	73.5 ± 8.6 65.9 – 86.4	2.0 ± 0.3 1.7 – 2.4	13.7 ± 2.8 8.6 – 18.3	8	2	
Kerivoula hardwickii (Release)	148.6 ± 58.3 107.4 – 189.8	-	239.0	82.3 ± 3.9 79.5 – 85.0	1.81	15.4 ± 0.1 15.3 – 15.5	1	1	
Kerivoula intermedia (Flying in tent)	113.2 ± 15.9 102.0 – 124.5	-	169.8 ± 13.2 160.5 - 179.1	94.1 ± 9.0 87.7 - 100.5	1.9 ± 0.1 1.8 - 2.0	13.6 ± 2.4 11.9 - 15.3	2		
Kerivoula intermedia (Release)	132.78 ± 3.15 130.6 – 135.0	-	177.5 - >190.0	97.3 ± 8.8 91.00 – 103.50	1.8 ± 0.2 1.65 – 1.92	14.3 ± 0.0	2		
Kerivoula minuta (Flying in tent)	121.0 ± 4.9 112.5 – 127.5	-	166.8 ± 18.0 153.0 - 214.4	95.3 ± 6.8 85.5 – 103.6	2.0 ± 0.1 1.8 - 2.2	14.3 ± 1.4 12.6 – 16.8	1	9	
Kerivoula minuta (Release)	130.5 ± 5.6 124.5 – 138.0	-	153.3 ± 16.8 128.6 – 164.5	101.0 ± 6.8 95.5 – 108.0	1.8 ± 0.3 1.5 – 2.2	14.2 ± 1.2 12.8 – 15.6	1	3	
Kerivoula papillosa (L) (Flying in tent)	109.8 ± 14.1 93.0 – 136.5	-	164.7 ± 14.6 150.5 – 212.5	62.7 ± 9.8 43.0 – 94.5	2.6 ± 0.5 1.8 - 3.2	15.5 ± 2.6 10.9 – 19.9	9	9	
Kerivoula papillosa (L) (Release)	118.1 ± 19.0 87.0 – 138.0	-	159.6 ± 5.7 149.0 – 166.0	63.6 ± 4.1 59.0 – 69.5	2.3 ± 0.3 1.8 – 2.7	17.2 ± 6.0 11.2 – 28.8	4	3	
Kerivoula papillosa (S) (Flying in tent)	126.0 ± 10.0 109.4 – 139.5	-	176.4 ± 15.0 157.5 – 194.0	84.6 ± 10.9 65.5 – 99.0	2.3 ± 0.6 1.4 - 3.4	15.3 ± 3.2 9.7 - 21.5	4	5	2
Kerivoula papillosa (S) (Release)	131.7 ± 19.3 106.5 – 172.5	-	178.9 ± 14.2 158.5 – >190.0	86.4 ± 5.9 74.5 – 96.0	2.2 ± 0.5 1.4 – 2.6	14.2 ± 3.1 10.4 – 19.7	5	4	
Kerivoula pellucida (Flying in tent)	136.3 ± 8.1 126.0 – 153.0	-	>190.0	65.9 ± 11.0 53.5 – 87.0	2.3 ± 0.2 2.0 – 2.6	12.9 ± 1.8 10.9 - 16.6	6	4	

Table 1- Continuation

Species	Fppeak (kHz)	Fppeak CF/QCF (kHz)	Fstart (kHz)	Fend (kHz)	PD (ms)	IPI (ms)	n		
							♂	♀	un
Kerivoula pellucida (Release)	130.7 ± 28.2 97.5 – 178.5	-	>190.0	80.8 ± 28.0 55.0 – 123.5	2.0 ± 0.4 1.4 – 2.4	12.2 ± 2.8 8.6 – 15.5	4	2	
Myotis horsfieldii (Flying in tent)	58.0 ± 6.0 48.4 – 63.1	-	106.5 ± 11.7 85.9 – 117.3	39.4 ± 5.1 32.3 – 47.5	4.1 ± 1.3 2.4 – 5.7	34.1 ± 22.9 17.4 – 79.2	4	1	
Myotis horsfieldii (Release: semi-clutter - trail)	73.4	-	119.6	36.8	5.7	56.3	1		
Myotis horsfieldii (Release: semi-clutter - stream)	48.6	-	118.6	33.9	3.5	25.0	1		
Myotis horsfieldii (Release: open space)	66.0	-	90.0	42.0	2.4	45.5	1		1
Myotis muricola (Flying in tent)	66.4 ± 2.6 63.1 – 69.1	-	86.3 ± 3.1 81.8 – 89.1	51.4 ± 2.1 48.6 – 53.6	2.9 ± 0.4 2.6 – 3.5	42.5 ± 33.7 19.4 – 92.3	3	1	
Myotis muricola (Release: semi-clutter)	58.1 ± 6.5 52.6 – 74.3	-	93.1 ± 19.8 62.0 – 111.5	49.6 ± 2.1 46.0 – 52.5	4.1 ± 0.8 3.2 – 5.9	74.8 ± 28.7 33.7 – 113.2	8	2	
Myotis muricola (Release: open space)	56.1 ± 2.5 54.3 – 59.0	-	90.8 ± 23.1 64.5 – 107.5	49.8 ± 1.6 48.0 – 51.0	4.1 ± 0.2 3.9 – 4.3	102.4 ± 27.9 73.4 – 129.0	2	1	
Myotis ridleyi (Flying in tent)	63.1	-	109.1	54.1	2.6	17.0	1		
Myotis ridleyi (Release: semi-clutter)	68.9	-	96.4	54.1	2.1	22.5	1		
Glischropus tylopus (Flying in tent)	55.6 ± 0.1 55.5 – 55.7	-	87.5 ± 3.5 85.0 – 90.0	40.5 ± 0.7 40.0 – 41.0	1.7 ± 0.7 1.3 – 2.2	20.3 ± 0.2 20.1 - 20.4	2		
Glischropus tylopus (Release: semi-clutter)	64.5 ± 2.2 62.9 – 66.0	-	82.0 ± 4.2 79.0 – 85.0	47.0 ± 1.4 46.0 – 48.0	1.7 ± 1.1 0.9 – 2.4	57.1 ± 32.2 34.3 – 79.9	2		
Miniopterus australis (Flying in tent)	65.5 ± 4.8 60.7 – 70.4	62.0 ± 1.0 60.5 – 62.7	119.9 ± 11.8 102.7 – 128.6	52.6 ± 1.2 50.9 – 53.6	4.6 ± 1.5 3.5 – 6.8	48.1 ± 26.0 29.2 – 86.3	1	1	2
Miniopterus australis (Flying in cave)	61.5 ± 3.4 57.8 – 64.5	59.5 ± 2.4 57.8 – 62.3	107.6 ± 31.4 72.4 – 132.7	51.5 ± 1.5 49.8 – 52.4	2.5 ± 1.4 1.6 – 4.1	48.6 ± 16.3 32.0 – 64.7	1	2	
Miniopterus australis (Emerging from cave entrance)	57.4 ± 0.9 56.0 – 58.5	57.4 ± 0.9 56.0 – 58.5	95.2 ± 12.8 78.6 – 112.4	51.8 ± 1.1 50.0 – 53.2	4.0 ± 0.4 3.7 – 4.8	57.7 ± 4.7 52.2 – 67.1	10		10
Chaerephon plicatus (Flying in large room)	36.0 ± 0.3 35.8 - 36.2	24.2 ± 0.1 24.1 - 24.2	47.3 ± 3.2 45.0 - 49.5	17.8 ± 1.8 16.5 - 19.0	7.5 ± 0.1 7.4 - 7.5	222.4 ± 142.6 121.6 - 323.3	2	2	
Chaerephon plicatus (Release: open space) Alternating call type A	29.4 ± 5.1 24.2 - 38.9	29.4 ± 5.1 24.2 - 38.9	43.5 ± 4.3 36.7 - 49.1	22.0 ± 1.5 19.6 - 23.7	13.3 ± 1.4 11.1 - 15.4	224.7 ± 66.2 95.4 – 324.5	2	10	
Chaerephon plicatus (Release: open Space) Alternating call type B)	24.3 ± 1.5 22.8 – 27.2	24.3 ± 1.5 22.8 – 27.2	34.7 ± 7.2 27.3 – 46.4	20.8 ± 1.7 17.9 - 23.6	13.9 ± 1.3 11.8 – 16.0	158.5 ± 57.2 93.1 – 258.8	1	7	

Geographical Comparison

Fppeak from stationary calls was compared for two species of Rhinolophidae and five Hipposideridae recorded at BNP and WCNR, to those in GMNP: *R. borneensis* (GMNP n = 40, BNP/WCNR n = 6), *R. luctus* (GMNP n = 2, BNP/WCNR n = 3), *H. bicolor* (GMNP n = 39, BNP/WCNR n = 4), *H. cervinus* (GMNP n = 51, BNP n = 32), *H. coxi* (GMNP n = 13, BNP n = 5), *H. dyacorum* (GMNP n = 28, BNP/WCNR n =6) and *H. galeritus* (GMNP n = 39, BNP/WCNR n = 21). There was no significant difference in Fppeak for *R. borneensis, R. luctus, H. bicolor* and *H. galeritus* between localities (Table 11 in Supplementary Materials). Fppeak for *H. coxi* in BNP/WCNR(45.4 ± 0.8, range 44.5-46.4 kHz) was significantly lower (t = 4.39, p <0.01) compared to GMNP (49.3 ± 1.9, range 45.3 – 51.5 kHz). *H. cervinus* calls at BNP (124.2 ± 1.7, range: 121.1-126.9 kHz) were significantly higher in Fppeak (t = 16.01, p < 0.001) compared to GMNP (117 ± 2.0, range: 112.8 – 121.6 kHz). Fppeak for *H. dyacorum* at BNP (153.5 ± 4.0, range 148.0 – 157.2 kHz) was significantly lower (t = 2.32, p < 0.05) compared to GMNP (158.2 ± 4.6, range 147.8 – 165.4 kHz) when sexual dimorphism in call frequency was not considered. However, five *H. dyacorum*, captured at BNP were females (148.0 – 157.2 kHz) and when compared to five females from GMNP (148.1 – 156.2 kHz), and there was no significant difference in Fppeak (t = 0.06, p = 0.96) (Table 11 in Supplementary Materials). In addition to these species, we also captured and recorded stationary calls for *Rhinolophus affinis* at WCNR (Fppeak: 69.0 – 69.1 kHz, n=3) and *R. trifoliatus* at BNP (Fppeak: 48.7 – 49.5 kHz, n = 3). Both species have previously been reported for GMNP at locations outside our sampling area (Medway 1977, Azhar et al. 2013).

All the reference calls associated with this study have contributed to the Asian Bat Call Database, currently being developed by the Hungarian Natural History Museum (HNHM), Southeast Asian Bat Conservation Research Unit (SEABCRU) and associated project partners and are available for download from the Chirovox website (http://chirovox.elte.hu/).

DISCUSSION

In this study, we described the echolocation call characteristics of 31 species of insectivorous bats, in different flight situations that relate to the habitats the species normally fly in at GMNP. To test how accurately calls could be automatically assigned to species, we performed a DFA, using five call parameters (Fppeak, Ftart, Fend, PD and IPI) and achieved an overall classification score of 80.3%. When species were subsequently separated into groups according to call structure, nine species *(R. creaghi*, *R. luctus*, *R. philippinensis*, *H. cerinus*, *H. coxi*, *H. diadema*, *H*. cf. *kunzi*, *C. robinsoni* and *E. alecto/monticola*) were classified with 100% accuracy, four species (*H. cervinus*, *H. dyacorum*, *H. galeritus* and *C. plicatus*) with >90% accuracy and two species (*R. acuminatus* and *R. borneensis*) with >80% accuracy. When additional measurements of harmonics (Fppeak, Fstart and Fend) for another three species (*M. horsfieldii*, *M. muricola* and *M. australis*) were added to the DFA, these species could be classified with 100% accuracy. We also examined males and females in the families Rhinolophidae (*R. borneensis*, *R. creaghi* and *R. philippinensis*) and Hipposideridae (*H. bicolor*, *H. dyacorum*, *H. coxi*, *H. cervinus*, *H. galeritus* and *H. diadema*) for differences in Fppeak for the CF component of their calls and found that female *R. creaghi* generally produced higher frequency signals compared to males and male *H. dyacorum* produced higher frequencies compared to females. Finally, when we compared calls from two species of Rhinolophidae (*R. borneensis* and *R. luctus*) and five species of Hipposideridae (*H. bicolor*, *H. cervinus*, *H. coxi*, *H. galeritus* and *H. dyacorum*) from GMNP to the same species that occur in southwestern Sarawak (BNP and WCNR), we found differences in the range of Fppeak for *H. cervinus* and *H. coxi*, between the two localities.

Among the bats recorded in our study at GMNP, all species in the families Rhinolophidae and Hipposideridae, (except *R. acuminatus*), *Emballonura* species, *M. horsfieldii*, *M. australis* and *C. plicatus* are known to predominantly roost in caves (Payne et al. 1985, Struebig et al. 2010, Phillipps & Phillipps 2016). Once calls were separated by structure and additional harmonics were considered, all of the calls achieved high classification success. Therefore, the majority of cave roosting bats in GMNP can be identified acoustically to species level and are most suitable for future acoustic monitoring in our study area.

H. coxi is a rare cave roosting species that is currently classified as endangered by the IUCN Red List (MacArthur 2016, Rajasegaran 2019). The peak frequency of the call, ranging from 45 to 52 kHz, is the lowest frequency recorded among the Hipposideridae in GMNP and so far, does not overlap with any other Hipposiderid species in Borneo. Therefore, this species is an ideal candidate for acoustic monitoring in GMNP. However, in southwestern Sarawak, where we recorded the range in peak frequency of *H. coxi* between 44.5 and 46.4 kHz, there may be overlap in peak frequency with both *E. monticola* and *E. alecto*, which have been recorded with a range between 45.2 and 46.5 kHz in the same region (F.A.A. Khan unpublished data). Although *Emballonura* species can be manually distinguished from *H. coxi* by call shape, shorter pulse duration and longer interval between pulses, there is potential for misclassification using automatic call measurement or classification techniques, depending on which call parameter is prioritised during classification (Russo & Voigt 2016).

Calls from the forest roosting specialists (*Kerivoula* and *Murina* species) had much lower classification success, as in other studies in Southeast Asia (Hughes et al. 2011) and are best identified to the group level. As previously reported by Kingston et al. (1999), call parameters of all four *Murina* species strongly overlapped but could be distinguished from most *Kerivoula* species. There was some overlap between *Murina* species and K. papillosa (large). However, call sequences of Murina species are typically produced as single pulses or in groups of two, while call sequences of *Kerivoula* species are typically produced in groups of more than two pulses (Kingston et al. 1999). In this study, we only considered single pulses. Therefore, further analysis of the number of pulses per group within the call sequences of these species may improve classification results. *K. hardwickii* and *K. pellucida* calls were separated from other *Kerivoula* species by higher start frequencies. *K. intermedia* and *K. minuta*

had strong overlap in call parameters. However, *K. papillosa* (both large and small form) had higher classification success (86% and 82% respectively). The small form, with forearm length <44 mm, is generally accepted as the true *K. papillosa*, while the larger form, with forearm length >44 mm, may represent an undescribed species endemic to Borneo (Khan et al. 2010, Hasan & Abdullah 2011). In this study, there was only 7% overlap in call parameters between the two forms, which supports the hypothesis that these are two separate species. Both large and small forms of *K. papillosa* are generally associated with tall, closed canopy forest and therefore may be good indicators of forest quality (Kingston et al. 2006, Struebig et al. 2013). The study of this group may continue to be dependent more on capture techniques to confirm their identity, as their high frequency calls attenuate quickly and are often missed in acoustic surveys (Furey et al. 2009, Kingston 2013). However, acoustic sampling may still prove to be an additional asset to surveys, particularly when species can be recorded in situations where they fly close to the microphone, such as emerging from roosts and flying along narrow trails. Although there is strong overlap between the calls of species in this group, collectively they can potentially be used as an indicators of habitat quality (Huang et al. 2019). Therefore, species level identification is not essential to make conservation decisions for forest-dependent bats as a whole (Yoh et al. 2020).

Our study supports previous studies highlighting the need to consider intraspecific variation when designing call libraries, as we found differences in call parameters dependant on recording situation, sex and geographical location for several species (Barclay 1999, Russo et al. 2017). Several species in this study showed the ability to alter their calls (e.g. *C. plicatus, M. australis, M. muricola*) when flying in enclosed space and open space. This ability suggests that they are not confined to foraging in either the edge or open space and probably use both habitat types and adjust calls accordingly (Schnitzler & Kalko 2001). Both *C. plicatus* and *M. muricola* have been detected flying in a variety of edge and open habitat types (e.g. paddy fields, water bodies and forest canopy, in a study from Thailand (Suksai & Bumrungsri 2020). *C. plicatus* is generally categorized as an open space forager (Utthammachai et al. 2008, Phillipps & Phillipps 2016). However, all the *C. plicatus* individuals examined in this study were captured while foraging beneath the canopy over a river 18 m wide, which we consider to be a confined edge space (McArthur & Khan 2020).

We observed a difference in the range of Fppeak between stationary calls among Rhinolophids and Hipposiderids, with four species (*H. bicolor*, *H. cervinus*, *H. galeritus* and *H. dyacorum*) exhibiting a large range (>7.5 kHz, with a variation of 17.6 kHz recorded for *H. dyacorum*) compared to remaining species that exhibited little variation (<6.5 kHz). The presence or absence of sexual dimorphism does not seem to account for this variation between all species (Table 9 in Supplementary Materials). Therefore, it is unclear why certain species exhibit more stable Fppeak than others (Chen et al. 2009, Hughes et al. 2010, Jiang et al. 2010). In the family Rhinolophidae, female bats are usually larger than males (Wu et al. 2014). However, *R. creaghi*, showed the reverse, with slightly larger males (Fig. 9 in Supplementary Materials). *R. creaghi* is a common species at GMNP that can be easily captured and produces a high-intensity call at a relatively low frequency. To our knowledge, there are no published studies regarding *R. creaghi* mating systems. Therefore, this species would be an ideal candidate for future studies on the factors that drive the evolution of sexual dimorphism in some species of Rhinolophidae and Hipposideridae.

The range of Fppeak that we measured for *R. acuminatus*, *R. borneensis* and *R. luctus* in GMNP is ~2 kHz lower than the range reported for Sabah (Francis 2008, Mullin et al. 2020, Senawi et al. 2020), while the range of Fppeak for *R. creaghi* at GMNP is 2-3 kHz higher than the range reported by Senawi et al. (2020). Fppeak measured for *R. trifoliatus* calls recorded at BNP and WCNR is within the same range as individuals from Sabah (Francis 2008, Mullin et al. 2020). Fppeak for *H. galeritus* at GMNP is within the same range as frequencies reported by Mullin et al. (2020), however Francis (2008) reported frequencies up to 3 kHz higher for this species in Sabah. Fppeak for *H. diadema* calls at GMNP are up to 3 kHz higher than the range reported in Sabah by Francis (2008). The range of Fppeak that we measured for *H. cervinus* calls (112.8 – 121.6 kHz) in GMNP is lower than the range (115 – 126 kHz) reported from Sabah (Francis 2008, Mullin et al. 2020, Senawi et al. 2020). The range of Fstart, Fend and Fppeak measured for *K. minuta*, *K. papillosa* and *K. pellucida* flight tent calls in our study is generally within the same range of frequencies reported by Senawi et al. (2020). However, we measured higher Fstart, lower Fend and Fppeak for *M. horsfieldii* flight tent calls in GMNP compared to Senawi et al. (2020). Lower Fstart was measured for *M. muricola* flight tent calls in GMNP, while Fend and Fppeak were within a similar range to frequencies reported by Senawi et al. (2020). It is important to note that different researchers and software used to extract call parameters may produce different results (Clement et al. 2014, Kraker-Castañeda et al. 2020) and this is one of the main reasons why it is important for call files to be made publicly available for comparison.

The advantage of acoustic sampling is that it provides a non-invasive sampling method and does not interfere with the bat's normal activity pattern (Hayes et al. 2009). Therefore, it is a useful method to investigate habitat use and activity patterns in an area once echolocation calls can be identified (Britzke et al. 2013). Once bats have been captured in an area and the composition of species is known, the activity of identifiable species can be monitored between different habitats or over time within the same habitats (Hayes 1997, Britzke et al. 2013). However, the technique is also biased due to the different intensities of bats' calls, where some of the low intensity calls may not be picked up by the detector (Jones & Teeling, 2006). Also, not all calls can be reliably identified to species due to overlapping characteristics in calls produced by several species, particularly those occurring in species-rich habitats (Kingston et al. 2000, Jones & Holderied 2007, Hughes et al. 2011). Another disadvantage is that the method cannot be used alone to estimate species abundance (Hayes et al. 2009, Frick 2013). However, recent research indicates that acoustic sampling alone may be used to estimate population density of single species at cave entrances during emergence, in situations where the majority of individuals pass within

the detection range of a microphone (Kloepper et al. 2016, Revilla-Martín et al. 2021). Such methods have yet to be tested for caves hosting multiple species (Revilla-Martín et al. 2021). As we found that the majority of cave bats could be identified acoustically to species level at GMNP, this site could provide the opportunity to test the suitability of these methods further. An additional challenge in Southeast Asia has been the high cost of recording equipment. However, the recent introduction of much cheaper recording technology, such as the Audiomoth (Hill et al. 2018), has increased the accessibility and capacity for bioacoustics research, including species monitoring using these devices.

There are several limitations in this study to consider that may impact the quality of the call library and therefore, the successful classification of calls to species level from acoustic recordings. Fourteen species were represented by six or less individuals and of these, *R. luctus*, *H*. cf. *kunzi*, *C. robinsoni*, *M. aenea*, *M. rozendaali, K. intermedia* and *G. tylopus* were each represented by two individuals, and *M. spasma* and *M. ridleyi* by only one individual. Release calls, particularly for species that fly in uncluttered habitats, may not be fully representative of the calls of free-flying bats (Clement et al. 2014, Russo & Voigt 2016). Harmonics, used in this study to separate several species, may not be present in the calls of free-flying bats. There are an additional seven species of insectivorous bats known from previous surveys at GMNP, two of which (*Cheiromeles torquatus* and *Myotis gomantongensis*) were reported from our study area but we failed to capture or obtain reference calls for (Chapman 1985, Millen & Lim 2018). The remaining five species (*Rhinolophus trifoliatus*, *Philetor brachypterus, Kerivoula whiteheadi, Rhinolophus affinis* and *Arielulus cuprosus*) were reported from outside our study area (Medway 1977, Azhar et al. 2013, Millen & Lim 2018). Therefore, further capture surveys and the inclusion of reference calls from free-flying bats of known species identity will be important to address these limitations.

We included measurements of five parameters in the DFA that have also been used for similar analyses in previous studies within the region (e.g. Furey et al. 2009, Phauk et al. 2013). Several studies have only included Fppeak and PD for rhinolophid and hipposiderid species in their DFA (e.g. Hughes et al. 2010, Phauk et al. 2013). Generally, these species concentrate Fppeak in the CF component of their calls (Kingston et al. 2000) and PD is a useful parameter to distinguish between calls of the two families (Heller & Helversen 1989). For the family Rhinolophidae, we found that Fppeak was the most important parameter to distinguish between species. However, in Hipposideridae which had a number of individuals producing calls with Fppeak concentrated in the FM component of the pulse, we found that Fstart followed by Fppeak and Fend (Table 4 in Supplementary Materials) was the most important parameter for distinguishing between species. Therefore, exclusion of this parameter from the analysis would likely lead to lower classification success within in this group. On the other hand, the addition of other pulse measurements that were not included in this study may improve classification success, particularly for species in the FM-QCF group. There is now a range of sound analysis software used in recent studies, e.g. Sonobat (Sonobat, USA), Anabat Insight (Titley Scientific, UK) and Avisoft SasLab Pro (Avisoft Bioacoustics, Berlin, Germany) that automatically extract a range of pulse measurements (Mullin et al. 2020, Yoh et al. 2020, Pham et al. 2021). It is possible that parameters, additional to those that we selected for pulse measurement (e.g. frequency of the knee, time from the start of the call to the knee etc.) may potentially be useful to improve classification success of calls examined in our study.

Currently, in Borneo and Southeast Asia, one of the drawbacks to acoustic monitoring of bats is the time taken to manually process sound recordings and classify calls to species. Therefore, the availability of automatic classification methods would be a great advantage to acoustic studies in the region. Our study shows that development of automatic classifiers is possible for bat calls in Borneo. However, no current classifiers used in other regions have achieved 100% accuracy in identifying calls to species (Russo & Voigt 2016). In the species rich tropics misclassification of calls is likely to be common and total reliance on results generated through these methods could potentially lead to management decisions that negatively affect populations of vulnerable species (Rojas et al. 2019). For example, a rare and threatened species such as *H. coxi* could potentially be misclassified as a common *Emballonura* species and a false negative such as this would mean that *H. coxi* is missed in surveys and threatened roosts or habitats that the species depends on are left unprotected. On the other hand, a false positive result, where *Emballonura* sp. is misclassified as *H. coxi*, could give the impression that the species is more abundant than in truth and not accurately reflect changes in populations. It is therefore imperative that the current limitations of automatic classifiers are considered and results are manually verified (López-Baucells et al. 2019)

The limestone karst area of GMNP encompasses over 500 km of cave passages that continue to be surveyed annually (Waltham 2019). However, surveys have focused on measuring the physical dimensions of the caves and less is known about the biological diversity that inhabits these extensive subterranean ecosystems (Moulds et al. 2013). In the absence of light, guano from bats and swiftlets is a major source of nutrients that supports unique cave fauna, including many troglobitic species that are restricted to cave environments (Chapman 1983, 1984, Moulds et al. 2013, Deharveng & Bedos 2019). Chapman (1985) and Hall (1996) conducted surveys of cave roosting bats in GMNP and estimated populations of several species in a few selected caves, but apart from a study that includes the roosting ecology of *H. coxi* in Lagang Cave (Rajasegaran 2019), no further surveys have been undertaken since then. Although these caves are now relatively well protected from human disturbance, with only a few select caves open to visitors (Moulds et al. 2013, IUCN 2017), a legacy of illegal swiftlet nest collecting may have impacted both swiftlet and bat populations in targeted caves (Waltham 2019). Roosting ecology and population counts of bats in Wind Cave (Fig. 1) and nearby Fairy Cave (Bau Limestone Area) have been well studied and the use of acoustic recording devices has been a useful aid to identify species in roost surveys (Morni et al. 2018, Rajasegaran et al. 2018, Rosli et al. 2018). Acoustic monitoring will be a particularly useful tool to aid in the identification of insectivorous bat species that inhabit

various caves at GMNP. This will allow the management team to assess the vulnerability of sensitive caves that host high diversity and presence of rare bat species and help identify caves in need of additional protection from illegal activities or increased tourism in the future (Tanalgo et al. 2018).

While threats to bats roosting inside the protected area of GMNP may be considered minimal (IUCN 2017), forested areas outside the boundary are currently threatened by the development of large scale oil palm (*Elaeis guineensis*) plantations (Abdullah 2019). Research shows that forest clearing and the establishment of oil palm plantations has severe negative impacts on biodiversity (Fitzherbert et al. 2008, Foster et al. 2011). Results from several trapping studies in Southeast Asia have indicated that bat species richness and abundance declines drastically in oil palm and other monoculture plantations compared to nearby intact forests, with the virtual absence of understory insectivores (Danielsen & Heegaard 1995, Fukuda et al. 2009, Lobite 2017, Yoh et al. 2020).

Many species of insectivorous bats are known to travel long distances from cave roosts to foraging sites (Norberg & Rayner 1987). For example, in Thailand, acoustic surveys detected *C. plicatus* up to 25 Km from cave roosts (Utthammachai et al. 2008). Recapture surveys conducted in Peninsular Malaysia indicated that at least two cave roosting *Rhinolophus* species that forage in forest understorey dominated bats assemblages up to 11 km away from karst (Struebig et al. 2009). Considering the proximity of caves and karst to the boundary of GMNP, particularly the western section (Fig. 1), it is highly likely that many bat species forage beyond the boundary. Bat surveys conducted in the Sungai Ingei Protection Forest (Brunei), located next to the Sarawak border, suggest that a number of cave roosting species use these forests. Large numbers of Creagh's Horseshoe Bat (*R. creaghi*) were captured at this site, which is approximately 10 km from GMNP's Karst (Struebig et al. 2012). *R. creaghi* is known to roost in large colonies in caves and Sungai Ingei is the only site in Brunei where this species has been captured. *R. creaghi* was also the most abundant forest understory bat captured during our study at GMNP (McArthur & Khan 2020). This species and a number of other cave roosting species were also captured near the area designated for oil palm and it is highly likely that these species regularly commute and forage in this area. Large-scale forest clearing and the development of oil palm plantations so close to the park boundary, and to caves which host large populations of bats, will very likely form a barrier to nightly dispersal. This is likely to particularly impact forest understory species that use short-range echolocation and wing designs adapted for navigation/foraging in cluttered environments. This means they are poorly adapted to foraging or commuting in more open habitats (Kingston 2013, Furey & Racey 2016b, Huang et al. 2019).

CONCLUSION

The results of this study show that the majority of cave roosting, insectivorous bats in GMNP can be readily distinguished from their calls and are suitable candidates for acoustic monitoring. However, we confirm that intraspecific differences in call frequencies are present between geographical locations, through sexual dimorphism, and between different recording situations. Therefore, these variables need to be considered when attempting to identify species from their calls. With the development of our call library, acoustic sampling methods will provide better information and further evidence on the foraging ecology of karst dependent bats in the surrounding landscapes of GMNP, that can potentially lead to better protection of their commuting and foraging habitats. In view of the recent introduction of cheaper recording devices and increased bioacoustics research, the use of acoustic monitoring is likely to increase in the Southeast Asian region in the near future. To facilitate this, it is important to target aerial insectivores that remain under-represented in call libraries and ensure recordings are conducted in suitable conditions. Without adequate call libraries and knowledge of call diversity within specific localities, accurate interpretation of acoustic sampling results will not be feasible.

ACKNOWLEDGEMENTS

We are very grateful to Joe Chun-Chia Huang who contributed ideas and commented on an earlier draft of this paper. We extend our gratitude to colleagues who contributed to the field work, including Mohd Isham Azhar, Syafiqah Shazali, Nurul Farah Diyana Ahmad Tahir, Nur Mukminah Naharuddin, Mohd Amsyari Morni, Qhairil Shyamri Rosli, Julius William Dee, Nurfarhana Mazlan, Michael and Caroline Schoner, Rebbeca Ermisch, Linda Dombrowski, Oisin Jangin Bagly, Robyn Wilson, Gábor Csorba, Tamás Garfol, Benjamin Lee, Matthew Struebig, Stephen Rossiter, Juliana Senawi, Tigga Kingston and other SEABCO 2015 post conference trip participants and UNIMAS undergraduate students who assisted during 2015 and 2017 fieldtrips. We particularly thank MT Abdullah for guidance. We are grateful to Sarawak Forest Department for providing permit Nos. NCCD.907.4.4 (JLD. 12)-3, NPW.907.4.4(JLD.14)-121 and Park Permits WL11/2015, WL62/2017, to conduct field sampling. Financial support for this research was provided to F.A.A.K through the : Ministry of Higher Education Grant FRGS/1/2019/WAB13/UNIMAS/03/2 and Newton-Ungku Omar Fuad Mobility Grants GL/F07/ NUOF/03/2017/ NI160114. Support and equipment was provided to E.M.A by Borsarmulu Park Management Sdn. Bhd. We are also very grateful for financial support provided by the Asian Soundscape Network, Academia Sinica, Taiwan and BIFA: Biodiversity Information Fund for Asia under project BIFA04_24. Finally we thank two anonymous reviewers for their valuable comments that helped to improve the quality of this paper.

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