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The role of ultrasonic bat detectors in improving inventory and monitoring surveys in Vietnamese karst bat assemblages

Neil M. FUREY*, Iain J. MACKIE, Paul A. RACEY

School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, U K

Abstract Bats account for 30% of mammal diversity in SE Asia and are potential bioindicators of wider biodiversity impacts resulting from habitat loss and climate change. As existing sampling techniques in the region typically fail to record bats that habitually fly in open areas and at higher altitudes, current inventory efforts are less than comprehensive. Acoustic sampling with bat detectors may help to overcome these limitations for insectivorous bats, but has yet to be tested in mainland SE Asia. To do so, we sampled bats while simultaneously recording the echolocation calls of insectivorous species commuting and foraging in a variety of karst habitats in north Vietnam. Monitoring of cave-dwelling bats was also undertaken. Discriminant function analysis of 367 echolocation calls produced by 30 insectivorous species showed that acoustic identification was feasible by correctly classifying 89.1% of calls. In all habitats, acoustic sampling and capture methods recorded significantly more species each night than capture methods alone. Capture methods consequently failed to record 29% (ten spp. of aerial insectivores) of the bat fauna in commuting and foraging habitats and 11% (two spp.) of that in our cave sample. Only four of these species were subsequently captured following significantly greater sampling effort. This strongly suggests that acoustic methods are indispensable for maximizing bat inventory completeness in SE Asia. As accurate inventories and monitoring are essential for effective species conservation, we recommend the inclusion of acoustic sampling in future studies of bat assemblages across the region [*Current Zoology* 55 (5): 327 – 341, 2009].

Key words Bats, Echolocation, Inventory completeness, Karst, Vietnam

Southeast (SE) Asia harbors one of the highest levels of species richness and endemism in the world (Mittermeier et al., 1999) and represents a global priority for biodiversity conservation (Myers et al., 2000). With the highest relative rate of deforestation for any major tropical region, as much as 42% of its biodiversity may be lost by 2100 if current rates continue (Sodhi et al., 2004). Bats account for a major proportion of mammal diversity within the region (ca. 30%, Corbet and Hill, 1992) and possess a variety of traits which recommend their use as bioindicators reflecting wider biodiversity impacts as a result of habitat loss and climate change (reviewed by Jones et al., 2009). Like much of the region's fauna however, the conservation status of many SE Asian bats poses a major concern (Lane et al., 2006; Kingston, 2008).

Development of effective methods for inventorying and monitoring bat populations is essential if their conservation needs are to be accurately determined and their potential as bioindicators realized. While the nocturnal and volant nature of bats hinders such assessments, two sampling devices are ubiquitously employed in SE Asian bat research: mist nets and harp traps. Mist nets are regarded by some as less effective in the Asian tropics, due to the prevalence of forest-dwelling species which can detect and avoid them (Francis, 1989; Kingston et al., 2003). Although such bats appear more susceptible to capture with harp traps (Francis, 1989; Kingston et al., 2003), both capture methods are rarely employed more than a few metres above ground level in Asian surveys (with some notable exceptions involving canopy mist nets: Francis, 1994; Hodgkison et al., 2004). The result is that species which habitually fly in open areas and/or above the forest canopy are invariably under represented, even in the most intensive studies (e.g. Kingston et al., 2003). These constraints limit the comprehensiveness of existing inventory and monitoring efforts, an essential requirement for effective conservation planning and management.

Acoustic sampling with ultrasound (bat) detectors is extensively used in temperate regions (see Brigham et al., 2004) and is increasingly recognized as an important alternative or complement to conventional capture methods for bat species inventories (O'Farrell and Gannon, 1999; MacSwiney et al., 2008). Bat detectors are particularly useful for detecting the presence of insectivorous bats which habitually fly in open spaces outside the range of ground-based traps because such species tend to produce high intensity echolocation calls (Fenton, 1990; Neuweiler, 1990). For instance, MacSwiney et al. (2008) found that simultaneous acoustic sampling in the neotropics increased the number of bat species by 30% above that recorded by direct capture. However, due to fundamental differences in the taxonomic composition of

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* Corresponding author. E-mail: n.furey@abdn.ac.uk

the neotropical bat fauna compared to that of the Palaeotropics (Hutson et al., 2001; Proches, 2005), it remains unclear whether acoustic sampling is similarly applicable in SE Asia. Despite its potential, acoustic sampling is rarely employed in bat inventory and monitoring surveys in continental SE Asia, and has yet to be utilized for this purpose in Indochina (Vietnam, Laos, Cambodia). As a result, detailed descriptions of the echolocation calls produced by most bat species in the wider region are lacking and most importantly, the utility of acoustic sampling in overcoming the limitations of traditional sampling methods remains untested.

This study addresses this issue by comparing simultaneous acoustic sampling with conventional capture methods in a variety of natural and modified karst landscapes in north Vietnam. With at least 73 species (Corbet and Hill, 1992; Hendrichsen et al., 2001; Borrisenko and Kruskop, 2003; Furey, 2009), the country's northern region (> 20° N) supports high bat diversity representing two-thirds of the national bat fauna (Can et al., 2008) and one-fifth of that in SE Asia (Simmons, 2005; Kingston, 2008). Since nearly three-quarters of the known bat species frequently or occasionally roost in caves and/or rock crevices, forested karsts within the area support a substantial proportion of the Vietnamese bat fauna (Furey, 2009). As Vietnamese caves harbor high bat diversity (Furey, 2009) and are therefore of conservation interest, we additionally assess the efficacy of bat detectors for monitoring cave-dwelling bat assemblages.

The study was conducted as part of longer-term sampling at Kim Hy Nature Reserve which relied upon the two most commonly adopted capture methods (mist nets and harp traps) in SE Asia (Furey, 2009). We consequently (1) provide the first description of time-expanded echolocation calls from Vietnamese bat populations; (2) determine the extent to which in-country bat species can be identified by their echolocation calls; and, (3) assess the utility of acoustic sampling in improving the completeness of species inventories in a range of above-ground habitat types and in monitoring cave-dwelling bat assemblages.

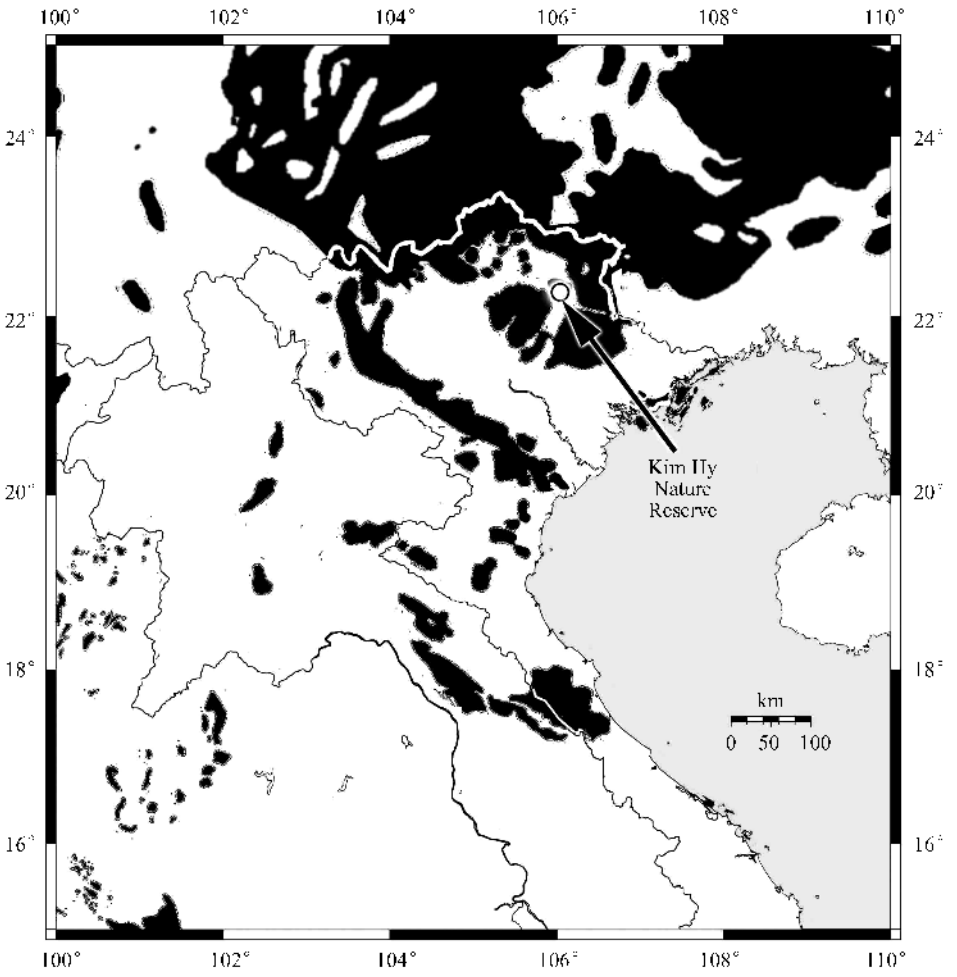

Fig.1 Distribution of karst (black) and location of Kim Hy Nature Reserve in north Vietnam
The map was created by Ricardo Insua-Cao using online map creation (http://www.aquarius.ifm-geomar.de/) and data from Hamilton-Smith and Ackroyd (2001).

1 Materials and Methods

1.1 Study area

Kim Hy Nature Reserve (22°11′ – 22°18′N, 105°54′ – 106°08′E) is located in Bac Kan province, north-east Vietnam and covers an area of 15, 461 ha (Tordoff et al., 2004) (Fig.1). The site was designated as a nature reserve in 1998 and its core conservation area comprises an uplifted and forested karst massif with elevations spanning 250 – 1000 metres above sea level (m a.s.l.). This is surrounded on all sides by generally lower elevation areas, which include areas of permanent agriculture, remnant forest patches and human settlements. These collectively form the reserve's buffer zone, which encompasses an area of 20, 528 ha (Tordoff et al., 2004). Surface water is absent from the core conservation area. Local terrain is steep and highly dissected and comprises a mosaic of semi- to fully discrete valleys separated by steep to sheer karst ridges. Forests at Kim Hy are classified as seasonal broadleaved evergreen forests over limestone (Trung, 1978). Forests within the southern and central portions of the reserve are essentially primary, while valley floors on the northern flank are largely used for agriculture with remnant forest persisting mostly on hillsides and ridgetops. Local climate is monsoonal with an average annual rainfall of 1593 mm, an average annual humidity of 81% and an average monthly temperature range of 12.3℃ in January to 25.7℃ in July (35 year average from the Ngan Son station in Van et al., 2000). The wet season lasts from May to September and the dry season from October to April, with April typically representing a transition between the two seasons.

1.2 Sampling sites and capture methods

1.2.1 Species inventory A total of 42 nights of sampling were conducted in 2007 at sites representative of three above-ground habitats at Kim Hy Nature Reserve: primary forest (22°11′N, 106°02′E), disturbed forest (22°14′N, 105°58′E) and agriculture/degraded forest (22°16′N, 106°02′E). Sampling sites were located > 8 km apart and situated centrally within larger areas (≥3 km^2) which were homogenous in terms of geology, landform and vegetation condition. Each site was sampled for seven nights during both the dry and wet season. Sampling was avoided on consecutive nights at the same location and during full moon periods.

Detailed descriptions for forest and non-forest vegetation at Kim Hy Nature Reserve are provided by Hardiman et al. (2002). For indicative purposes however, primary forests at Kim Hy are dominated by the canopy and emergent tree species *Burretiodendron tonkinense* (Tiliaceae), while the middle storey is dominated by shade-tolerant members of the Euphorbiaceae (*Mallotus*, *Antidema* and *Glochidion* spp.), Fagaceae (*Lithocarpus* spp.), and more locally, Moraceae (*Streblus* spp.) (Hardiman et al., 2002). The primary forest understorey is relatively clear due to the predominantly rock/scree substrate and density of the forest canopy. Disturbed forests at Kim Hy include the aforementioned species and generally lack an emergent tree layer. They possess much reduced canopy cover with blurred distinctions between remaining forest strata, and a densely vegetated understorey which includes an abundance of wild banana (*Musa* spp.) on valley floors. Forests on hillsides and ridgetops in disturbed areas typically retain greater canopy cover relative to those on valley floors. Agriculture/degraded forests comprise a mixture of permanent rice cultivation on valley floors, which are encircled by heavily degraded forests on surrounding hillsides and ridgetops. Being unsuitable for cultivation, karst hillsides and ridgetops in settled areas at Kim Hy typically support corridors of forest vegetation (Hardiman et al., 2002; Furey, 2009).

Mist nets and harp traps were used for sampling. Two sizes of mist net (10×3 m^2 & 12×2.5 m^2) were used depending on local topography, both being equal in area and 70 denier nets with a mesh size of 16×16 mm^2. Harp traps consisted of four frames and had a capture surface of 2.4 m^2. Sampling points in each habitat were located in inter-valley passes on ridgetops and in a variety of microhabitats on valley floors. Due to logistical constraints, harp traps were solely employed on valley floors while mist nets and harp traps were employed on ridgetops. Traps on ridgetops were opened at sunset, operated for 5 hours each night and attended constantly, while harp traps on valley floors were operated overnight. The latter were opened at sunset, checked hourly until midnight and again the following morning. We carefully standardized trapping methods to ensure equal sampling effort between the three habitats and between the dry and wet seasons. Sampling effort for mist nets was calculated as m^2 of net multiplied by the number of hours for which they were set (m^2mnh), while harp trap effort was similarly calculated as $metres^2$ of harp trap multiplied by the number of hours of use (m^2hth).

1.2.2 Cave monitoring A total of eight nights of sampling were conducted at An Tinh Cave # 1 (22°11.799′N, 106°02.130′E; entrance altitude: 660 m a.s.l.) in 2006 and 2007. An Tinh Cave # 1 (ATC # 1) is located in an area of primary forest within the southern interior of Kim Hy Nature Reserve and possesses a single large entrance (42 m wide, 10 m high). In simplified terms, the cave consists of an enormous passageway (> 500 m long, 20 – 76 m wide, 10 – 58 m high) which initially descends at > 40° for 95 m and then levels off for approximately 50 m, before ascending to a large plateau and subsequently descending until its end. The main roost area within the cave (in terms of numbers of bats) overlies the plateau where temperatures and humidity remain at 16 – 17℃ and ≈90% throughout the

year. Habitats within the cave include a subterranean lake approximately midway along its length. Cave dimensions were measured using a laser measurement unit (Disto Lite 5, Leica Geosystems) and clinometer, while microclimate data was recorded throughout 2006/7 with data loggers (Tinytag Plus TGP-1500, Gemini Data Loggers). Four nights of sampling were undertaken each year at ATC # 1 at approximately forty day intervals between April and September, which represents the beginning to the end of the wet season for the region. Sampling was avoided during full moon periods and standardized. Two mist nets (10×3 m^2 & 7×3 m^2) and one harp trap were employed on each occasion at the cave entrance, all of which were opened at sunset, operated for five hours and attended constantly.

1.3 Acoustic sampling

1.3.1 Species inventory Simultaneous recordings were made each night using a D980 bat detector (Pettersson Elecktronic AB, Uppsala, Sweden) at a sampling rate of 350 kHz and stored on audio tapes using a Sony Professional Walkman recorder (Model WM-D6C, Sony, Tokyo). Continuous recordings were made for three ten minute periods, the first beginning 30 minutes after sunset, and the second and third at subsequent half hour intervals. During these periods, the bat detector was set to repeatedly record three seconds of real time and time-expand ($\times 10$) the recordings, which were stored on Channel 1 of the Walkman. This method allows only 9% of real time to be recorded in a given period (Jones et al., 2000), but was standardized in all habitats, in order to facilitate their comparison. To minimize call variability and changes in detection due to habitat structure, we attempted to record calls in the most open space available in all three habitats. However, due to their different structural complexity, our sample undoubtedly includes calls affected by clutter as well as those produced in less cluttered and open spaces. As species within the Murininae and Kerivoulinae subfamilies produce calls of very low intensity (Kingston et al., 1999) and are thus difficult to sample with bat detectors, we relied upon capture methods alone to sample members of these groups. In all habitats, the microphone was directed towards natural or manmade gaps in the vegetation, with the bat detector maintained at an angle of 45° approximately 1.3 m above the ground.

1.3.2 Cave monitoring To minimize potential avoidance behavior and changes in echolocation calls due to bats perceiving traps and personnel at the entrance of ATC # 1, acoustic sampling was conducted one night prior to each trapping session. Each night, continuous time-expanded recordings ($\times 10$) were made using a D980 detector and Sony Professional Walkman for six ten minute periods, the first beginning at sunset, with subsequent recording periods at half hour intervals. Due to the large size (ca. 400 m^2) and complicated terrain surrounding the cave entrance, sampling points away from the cave entrance were inadequate to ensure recordings were exclusively of emerging bats. Sampling was therefore undertaken from a central point at the entrance, within a clump of boulders which screened the recorder from detection by emerging bats. The microphone was orientated directly into the cave with the bat detector maintained at an angle of 0° (due to the > 40° passageway descent) approximately 1.3 m above the ground.

1.4 Species identification and call description

Bats captured were measured, photographed and identified in the field using Borrisenko and Kruskop (2003), Hendrichsen et al. (2001) and unpublished field keys developed by N. Furey. All were marked on their toe claws with non-toxic paint and released as near as possible to their capture site. Recaptured bats were excluded from the study. Where required to confirm species identifications, a minimum number of specimens were retained as vouchers. Skulls and bacula (where taxonomically important) were subsequently prepared for measurement and examination. Museum accession numbers for voucher specimens are available from the first author. Taxonomy follows Simmons (2005).

We constructed a reference collection of calls from captured bats (identified to species) which were hand-released in the same areas where we acoustically sampled. Since the present study formed a subset of a longer term study undertaken at the same sampling sites between 2005 – 2007 (Furey, 2009), reference collections included recordings made throughout this period. Call recordings were made as long after release as possible to maximize their resemblance to calls made during normal flight. The initial calls in each recording were avoided and one call was selected per bat for statistical description of call parameters and subsequent analysis. For species with less than five captures however, two calls per individual were analyzed. As five species of aerial insectivore (*Hypsugo cadornae*, *H. pulveratus*, *Pipistrellus javanicus*, *Myotis ater* and *M. muricola*) presently require laboratory examination for reliable identification and were represented by few captures ($\leqslant 5$), a tethered zipline (Sweczak, 2000) was employed to record calls of these species in flight. We are aware that ziplines can produce aberrant behavior, however at present there appears to be no other method of obtaining representative flight recordings for such species in the field, while retaining voucher specimens for laboratory identification. The reference collection of echolocation calls was subsequently employed for identification of bat species recorded in the acoustic sampling.

All recordings were digitized for analysis using Bat Sound software (ver. 3.31, Pettersson Elecktronic AB) at a sampling rate of 44.1 kHz, with 16 bits/sample. Spectrograms were examined using a 512-size Fast Fourier

Transformation and a Hanning window. Following MacSwiney et al. (2008), spectrogram parameters initially used to analyze recordings from the acoustic sampling were standardized (2000 ms per plot; threshold = 15; amplitude contrast = 1). Only search phase calls of sufficient intensity for measurement and identification were considered for analysis. Within each 10 minute file, a sequence of five calls for each species identified was selected for measurement. One call in each sequence was used in statistical descriptions of call parameters and analysis. To avoid pseudoreplication, call data from the acoustic sampling at ATC # 1 was confined to recordings made on a single night for each species. An exception to this was made for one species: *Rousettus leschenaultii*, a cave-dwelling pteropodid whose echolocation calls were detected only within the confines of ATC # 1. To improve sample sizes for this species, recordings from two nights in 2006 and two in 2007 were analyzed. Since ATC # 1 supports a colony of > 1000 *R. leschenaultii* all year round (N. Furey, unpublished data) and a maximum of one call from each ten minute recording was analyzed, the risk of pseudoreplication was minimized.

For each call, six parameters were measured: call duration (D), inter-pulse interval (IPI, time from the start of one call to the onset of the next), start frequency (SF, frequency value at the start of the call), middle frequency (MF, frequency value at half the calls duration), end frequency (EF, frequency value at the end of the call) and peak frequency (FmaxE, frequency of maximum energy for the whole call). D and IPI (ms) were obtained from oscillograms, FmaxE (kHz) from power spectra, and all other parameters from spectrograms (kHz). All measurements were taken from the call harmonic containing the greatest energy. In addition, the position of the harmonic containing the most energy and number of harmonics present in each call was noted for the purposes of describing the echolocation calls produced by each species.

1.5 Statistical procedures

To test the efficacy of acoustic data in correctly identifying bat species, a discriminant function analysis was performed. As Box's M test indicated that covariance matrices were not homogenous ($F = 6.929$, $P < 0.001$), quadratic discriminant function analysis was applied. Cross-validation was employed in the analysis. Multivariate analysis of variance (MANOVA) was employed to examine the statistical significance of the discriminant function analysis models and Wilk's λ values were used to assess the discrimination power of each variable. The non-parametric Wilcoxon signed rank test was employed to compare species richness per night determined by capture methods against that produced by capture methods plus acoustic sampling. All tests were performed with MINITAB 15.1.1, with the exception of Box's M test which was performed using SPSS Statistics 17.0. In all tests, values of $P < 0.05$ were considered significant.

2 Results

2.1 Description of echolocation calls

A total of 1740 minutes of time-expanded calls from free flying bats were analyzed (1260 minutes from the three above-ground habitats and 480 minutes from ATC # 1) from the acoustic sampling. In combination with data from captured bats, 382 echolocation calls of 31 species belonging to the Pteropodidae (1 species), Megadermatidae (1), Rhinolophidae (8), Hipposideridae (5), Vespertilionidae (10) and six distinct phonic types (the acoustic equivalent of morpho-species) were analyzed.

2.1.1 Pteropodidae, genus *Rousettus* As large numbers of *R. leschenaultii* emerged from ATC # 1 during each sampling session, it could not be ensured that call sequences recorded were produced by single individuals. Inter-pulse interval measurements were therefore excluded from the analyses. The echolocation signals of *Rousettus* species consist of brief clicks which are produced by tongue movements in the mouth (as opposed to tonal signals produced in the larynx). In our sample for *R. leschenaultii* ($n = 15$), these clicks ranged from 42.7 ± 3.9 (mean ± *SD*) kHz to 13.2 ± 1.1 kHz, and had a peak frequency of 20.4 ± 5.1 kHz and a call duration of 0.08 ± 0.02 ms (Fig.2a). As these broadband clicks sound very different to the tonal signals produced by insectivorous bats when time-expanded, the echolocation calls of *R. leschenaultii* cannot be confused with any other bat species at Kim Hy.

2.1.2 Megadermatidae, genus *Megaderma* The Megadermatidae was represented by a single species, *Megaderma lyra*, which produced relatively brief (2.6 ± 0.9 ms), multi-harmonic and frequency-modulated calls (Table 1a, Fig.2a). Calls typically contained three to four harmonics and the second harmonic invariably contained the greatest energy. This second harmonic ranged from 56.4 ± 2.4 kHz to 32.9 ± 1.2 kHz, with an FmaxE of 42.5 ± 1.5 kHz. As harmonics represent integer multiples of the fundamental signal, the four typically produced by *M. lyra* considerably increase the bandwidth of its calls.

2.1.3 Rhinolophidae, genus *Rhinolophus* The eight species of rhinolophid in our sample produced stereotypical calls characterized by a long constant-frequency component which was preceded and terminated by a brief frequency-modulated component (Table 1a, Fig.2b). The second call harmonic contained the most energy and all eight species operated at high duty cycles, with values ranging from 41.1 ± 6.9% in *Rhinolophus sinicus* to 59.5 ± 16.6% in *R. macrotis*. Peak frequency (FmaxE) and middle frequency (MF) values ranged from 27.5 – 29.5 kHz in *R. paradoxolophus* to 102.3 – 106.1 kHz

Table 1a Descriptive statistics of call parameters for 1 megadermatid, 8 rhinolophid and 5 hipposiderid bat species at Kim Hy Nature Reserve, Vietnam

Species	Call structure	SF (kHz)	EF (kHz)	FmaxE (kHz)	MF (kHz)	D (ms)	IPI (ms)	*n*
MEGADERMATIDAE								
Megaderma lyra	FM	56.4 ± 2.4 (52.4 – 59.6)	32.9 ± 1.2 (31.4 – 34.7)	42.5 ± 1.5 (39.5 – 44.5)	42.1 ± 1.2 (40.2 – 43.2)	2.6 ± 0.9 (1.2 – 3.7)	105.6 ± 27.4 (66.6 – 140.7)	8
RHINOLOPHIDAE								
Rhinolophus paradoxolophus	FM/CF/FM	23.7 ± 1.0 (21.7 – 25.4)	22.7 ± 1.3 (20.0 – 26.3)	28.5 ± 0.4 (27.5 – 29.5)	28.4 ± 0.5 (27.5 – 29.5)	60.5 ± 12.4 (23.6 – 83.8)	108.1 ± 21.5 (32.1 – 143.7)	44
Rhinolophus macrotis	FM/CF/FM	59.4 ± 1.2 (57.6 – 61.7)	53.1 ± 2.4 (50.5 – 57.7)	66.4 ± 0.9 (65.2 – 67.7)	66.4 ± 0.9 (65.2 – 67.5)	30.4 ± 7.5 (17.5 – 42.5)	56.3 ± 22.8 (24.7 – 81.8)	11
Rhinolophus pearsoni	FM/CF/FM	42.9 ± 2.3 (40.0 – 47.6)	40.9 ± 2.4 (35.8 – 45.5)	53.0 ± 1.5 (51.1 – 55.4)	53.0 ± 1.5 (51.1 – 55.4)	41.5 ± 9.7 (26.7 – 59.7)	96.5 ± 25.1 (39.6 – 125.5)	18
Rhinolophus yunanensis	FM/CF/FM	42.8 ± 1.5 (40.8 – 45.0)	40.2 ± 2.2 (37.8 – 45.1)	53.8 ± 1.8 (51.1 – 55.9)	53.8 ± 1.8 (51.1 – 55.9)	40.5 ± 2.9 (36.0 – 45.0)	92.5 ± 17.8 (54.9 – 111.9)	8
Rhinolophus pusillus	FM/CF/FM	90.2 ± 1.7 (87.9 – 94.0)	86.8 ± 6.2 (80.7 – 101.0)	105.0 ± 1.2 (102.3 – 106.1)	105.0 ± 1.0 (102.7 – 106.1)	31.6 ± 8.9 (20.5 – 47.6)	66.9 ± 28.4 (27.5 – 66.9)	10
Rhinolophus stheno *	FM/CF/FM	72.2 ± 6.5 (65.3 – 80.7)	69.9 ± 5.5 (64.9 – 79.7)	91.1 ± 1.0 (89.8 – 92.0)	90.9 ± 0.9 (89.8 – 91.6)	30.5 ± 11.5 (14.9 – 50.6)	66.2 ± 27.0 (35.8 – 103.0)	6
Rhinolophus sinicus	FM/CF/FM	61.5 ± 2.4 (58.2 – 64.8)	58.6 ± 3.0 (54.2 – 63.4)	76.8 ± 2.1 (74.3 – 79.1)	76.8 ± 2.1 (74.3 – 79.3)	33.8 ± 4.0 (28.7 – 38.1)	84.9 ± 2.3 (69.2 – 131.1)	7
Rhinolophus affinis	FM/CF/FM	56.9 ± 4.5 (51.8 – 69.3)	56.6 ± 3.3 (50.3 – 62.8)	71.1 ± 0.9 (69.5 – 73.4)	71.1 ± 1.0 (69.3 – 73.4)	43.2 ± 10.4 (17.6 – 55.4)	89.4 ± 13.7 (52.7 – 105.2)	18
HIPPOSIDERIDAE								
Hipposideros pomona	CF/FM	125.0 ± 2.5 (122.0 – 128.2)	104.1 ± 6.3 (95.9 – 112.2)	125.1 ± 2.3 (122.0 – 127.7)	125.2 ± 2.3 (122.2 – 127.5)	7.0 ± 2.3 (3.7 – 9.3)	20.9 ± 4.5 (12.5 – 26.3)	7
Hipposideros lylei	CF/FM	69.5 ± 1.4 (67.1 – 70.6)	59.1 ± 4.0 (55.4 – 65.9)	70.0 ± 0.8 (69.1 – 71.3)	69.8 ± 0.5 (69.1 – 70.4)	8.4 ± 2.1 (6.3 – 11.1)	28.7 ± 13.3 (10.3 – 42.0)	5
Hipposideros armiger	CF/FM	64.6 ± 1.2 (61.8 – 66.4)	55.7 ± 1.8 (53.0 – 58.9)	65.0 ± 1.1 (63.2 – 66.8)	64.9 ± 1.1 (62.7 – 67.0)	11.1 ± 2.2 (6.0 – 14.8)	45.7 ± 15.3 (26.4 – 95.9)	29
Hipposideros larvatus	CF/FM	86.3 ± 2.1 (81.1 – 89.7)	75.2 ± 3.1 (68.5 – 82.3)	86.5 ± 1.8 (83.8 – 89.3)	86.4 ± 1.7 (83.5 – 89.3)	7.8 ± 1.4 (5.2 – 11.2)	35.5 ± 6.6 (25.0 – 56.2)	32
Aselliscus stoliczkanus	CF/FM	127.9 ± 2.6 (124.6 – 130.5)	110.8 ± 4.6 (102.9 – 114.1)	127.5 ± 2.6 (124.3 – 130.8)	127.4 ± 2.9 (124.1 – 131.3)	4.7 ± 0.6 (4.0 – 5.6)	21.5 ± 5.4 (14.4 – 28.5)	5

* One call per bat was analyzed except for *R. stheno*, for which 2 calls per individual were included. CF = constant-frequency; FM = frequency-modulated; SF = start frequency; EF = end frequency; FmaxE = frequency of maximum energy; MF = middle frequency; D = duration; IPI = inter-pulse interval. Values are given as mean, ± SD (min-max).

in *R. pusillus*. With the exception of two species, *R. pearsoni* and *R. yunanensis*, values for FmaxE and MF did not overlap between species, indicating that these parameters may be employed for acoustic identification of all but the latter two rhinolophids in our sample.

2.1.4 Hipposideridae, genera *Hipposideros* and *Aselliscus* The five species of hipposiderid analyzed produced calls beginning with a relatively long and almost constant-frequency component which terminated in a comparatively brief and downward frequency-modulated component (Table 1a, Fig.2a). All species produced calls with the greatest energy contained in the second harmonic and operated at lower duty cycles (ranging from 22.5 ± 3.7% for *Aselliscus stoliczkanus* to 34.3 ± 16.1% for *Hipposideros lylei*) compared to rhinolophids, due to their shorter and non-overlapping call durations. The structure of hipposiderid calls facilitates their unequivocal separation from all rhinolophid species in our sample. FmaxE and MF values ranged from 62.7 – 67.0 kHz in *H. armiger* to 124.1 – 131.3 kHz in *A. stoliczkanus*. With the exception of the latter species and *H. pomona*, FmaxE and MF ranges did not overlap between species, indicating that these variables may be used for acoustic identification of *H. lylei*, *H. armiger* and *H. larvatus*.

2.1.5 Vespertilionidae, genera *Myotis*, *Scotomanes*, *Ia*, *Pipistrellus* and *Hypsugo* The ten species of vespertilionid bat in our sample produced steep, downward frequency-modulated calls dominated by the fundamental harmonic, which ended for some species in a quasi constant-frequency or narrowband component (Table 1b, Fig.2c).

Species within the genus *Myotis* produced relatively brief (mostly < 5 ms) and exclusively frequency-modulated calls of relatively large bandwidth (overall species mean 45.1 kHz), with the exception of *M. siligorensis*. Calls of this species ended in a short

distinctive narrowband portion which contained the most energy in the call at 78.3 ± 2.4 kHz, rendering it easily distinguishable from all other bat taxa known at Kim Hy. Extensive overlap occurred in all parameters for the previously undescribed calls of the small-bodied *M. ater* and *M. muricola*, although sample sizes for both species were small. Call parameters similarly overlapped between the large-bodied *M. chinensis* and *M. ricketti*, with the exception of start frequency (SF) which was consistently higher in *M. chinensis* at 83.6 ± 4.3 kHz.

Table 1b Descriptive statistics of call parameters for 10 vespertilionid species and 6 unidentified phonic types at Kim Hy Nature Reserve, Vietnam

Species	Call structure	SF (kHz)	EF (kHz)	FmaxE (kHz)	MF (kHz)	D (ms)	IPI (ms)	*n*
VESPERTILIONIDAE								
Myotis chinensis *	FM	83.6 ± 4.3 (78.0 – 90.9)	25.2 ± 3.5 (19.9 – 30.1)	49.0 ± 5.6 (40.7 – 55.7)	41.2 ± 6.4 (33.2 – 50.7)	3.6 ± 0.9 (2.7 – 5.2)	81.0 ± 15.3 (62.8 – 114.9)	8
Myotis siligorensis	FM/QCF	112.4 ± 14.3 (85.0 – 129.4)	72.8 ± 2.6 (69.0 – 78.0)	78.3 ± 2.4 (75.7 – 83.4)	76.2 ± 2.7 (70.7 – 81.6)	3.5 ± 0.9 (2.3 – 5.2)	67.3 ± 27.4 (37.6 – 149.6)	16
Myotis ater *	FM	104.7 (95.4 – 110.0)	57.5 (53.7 – 60.1)	66.7 (64.3 – 71.3)	62.5 (60.4 – 64.1)	1.4 (1.0 – 1.7)	69.6 (47.7 – 86.6)	4
Myotis muricola *	FM	97.8 (75.3 – 114.1)	54.5 (51.5 – 59.2)	66.2 (62.0 – 73.6)	59.7 (57.0 – 63.6)	1.9 (1.0 – 2.4)	58.2 (21.4 – 118.7)	4
Myotis ricketti	FM	65.9 ± 5.3 (58.5 – 73.4)	28.8 ± 2.2 (25.3 – 31.2)	45.3 ± 3.7 (40.7 – 49.7)	39.2 ± 3.1 (35.0 – 42.1)	4.0 ± 1.2 (2.3 – 5.5)	94.7 ± 18.7 (78.3 – 116.0)	5
Scotomanes rnatus	FM	54.1 ± 7.0 (43.0 – 62.0)	21.0 ± 1.9 (18.6 – 23.1)	31.7 ± 2.5 (29.7 – 35.9)	28.8 ± 1.8 (26.6 – 31.3)	3.4 ± 0.8 (2.4 – 4.4)	91.0 ± 26.6 (50.9 – 122.4)	6
Ia io	FM	41.1 ± 5.5 (27.7 – 48.0)	16.1 ± 2.2 (13.2 – 20.4)	25.8 ± 2.5 (21.3 – 30.4)	21.9 ± 3.1 (15.9 – 28.3)	4.4 ± 1.6 (2.5 – 7.7)	114.6 ± 64.5 (25.1 – 294.5)	18
Pipistrellus javanicus	FM/QCF	79.9 ± 28.7 (54.8 – 116.0)	47.3 ± 5.5 (41.6 – 49.5)	51.3 ± 3.3 (47.9 – 53.2)	50.3 ± 2.9 (46.8 – 52.7)	3.5 ± 2.5 (1.3 – 7.1)	59.5 ± 12.2 (49.1 – 70.9)	6
Hypsugo pulveratus	FM/QCF	75.9 ± 7.2 (65.2 – 82.9)	34.1 ± 1.0 (32.6 – 35.1)	42.4 ± 2.5 (39.1 – 45.9)	39.4 ± 2.2 (37.0 – 42.9)	2.1 ± 1.6 (0.9 – 4.8)	58.3 ± 10.5 (44.1 – 71.7)	5
Hypsugo cadornae	FM	65.8 ± 12.6 (47.3 – 82.5)	27.6 ± 2.2 (24.2 – 30.1)	37.5 ± 1.6 (35.2 – 40.0)	36.6 ± 1.8 (33.5 – 39.4)	2.8 ± 2.0 (1.0 – 6.8)	72.8 ± 30.5 (41.3 – 129.4)	9
UNIDENTIFIED PHONIC TYPES								
Phonic type 1 (16.7 kHz)	FM/QCF	22.5 ± 3.2 (19.2 – 27.6)	14.4 ± 1.1 (12.3 – 16.0)	16.7 ± 1.0 (15.0 – 18.4)	16.8 ± 1.0 (15.2 – 18.4)	17.8 ± 9.1 (7.7 – 31.8)	423. 8 ± 185.0 (190.3 – 721.0)	9
Phonic type 2 (21.7 kHz)	FM/QCF	30.2 ± 2.9 (23.5 – 34.2)	19.1 ± 1.5 (15.9 – 20.8)	21.7 ± 1.1 (20.0 – 23.4)	22.0 ± 1.2 (19.7 – 24.2)	14.2 ± 4.0 (9.0 – 22.2)	322.7 ± 115.7 (168.1 – 496.0)	12
Phonic type 3 (27.4 kHz)	FM/QCF	33.2 ± 5.6 (27.5 – 49.2)	24.6 ± 1.8 (20.8 – 27.9)	27.4 ± 1.4 (25.0 – 29.5)	27.3 ± 1.5 (23.4 – 31.3)	12.6 ± 3.5 (7.0 – 18.4)	266.6 ± 99.7 (101.4 – 501.0)	22
Phonic type 4 (36.7 kHz)	QCF	38.5 ± 2.0 (35.7 – 42.8)	34.5 ± 0.9 (33.1 – 35.7)	36.7 ± 1.2 (35.2 – 39.5)	36.2 ± 1.2 (34.6 – 38.9)	14.2 ± 4.4 (8.2 – 22.1)	153.2 ± 40.5 (96.3 – 210.0)	12
Phonic type 5 (45.3 kHz)	FM/QCF	49.7 ± 3.7 (44.3 – 55.9)	42.9 ± 1.9 (40.6 – 46.5)	45.3 ± 2.0 (42.9 – 48.8)	44.9 ± 2.0 (42.1 – 48.4)	7.6 ± 1.6 (3.4 – 9.6)	128.6 ± 68.3 (65.2 – 298.4)	17
Phonic type 6 (62.0 kHz)	FM/QCF	77.8 ± 11.9 (64.1 – 92.4)	59.1 ± 2.1 (55.9 – 61.1)	62.0 ± 1.8 (59.5 – 64.1)	61.2 ± 1.9 (58.1 – 63.3)	4.5 ± 1.3 (3.0 – 5.9)	75.9 ± 28.6 (58.6 – 133.1)	6

* One call per bat was analyzed except for species marked with an asterisk, for which 2 calls per individual were analyzed. Abbreviations are as given in table 1a. QCF = quasi constant-frequency. Values are given as mean, ± SD (for n≥5) (min-max).

P. javanicus and *H. pulveratus* produced frequency-modulated calls with a respective FmaxE of 51.3 ± 3.3 kHz and 42.4 ± 2.5 kHz. The calls of both species ended in narrowband tails at 47.3 ± 5.5 kHz and 34.1 ± 1.0 kHz, respectively. In contrast, the previously undescribed calls of *H. cadornae* frequently lacked a narrowband portion and had an FmaxE of 37.5 ± 1.6 kHz and an EF of 27.6 ± 2.2. Call durations (D) and inter-pulse intervals (IPI) overlapped extensively between these species, but with little or no overlap in EF, FmaxE and MF, all three are readily distinguished acoustically. Compared to these three species, the significantly larger-bodied *Ia io* produced lower frequency-modulated calls with an SF of 41.1 ± 5.5 kHz, an FmaxE of 25.8 ± 2.5 kHz and an EF of 16.1 ± 2.2 kHz. The remaining species in our vespertilionid sample, *Scotomanes ornatus*, produced calls which were structurally similar to those of *I. io*, but which were intermediate in all frequency parameters (SF, EF, FmaxE and MF) between the latter species and *H. cadornae*, with relatively little overlap

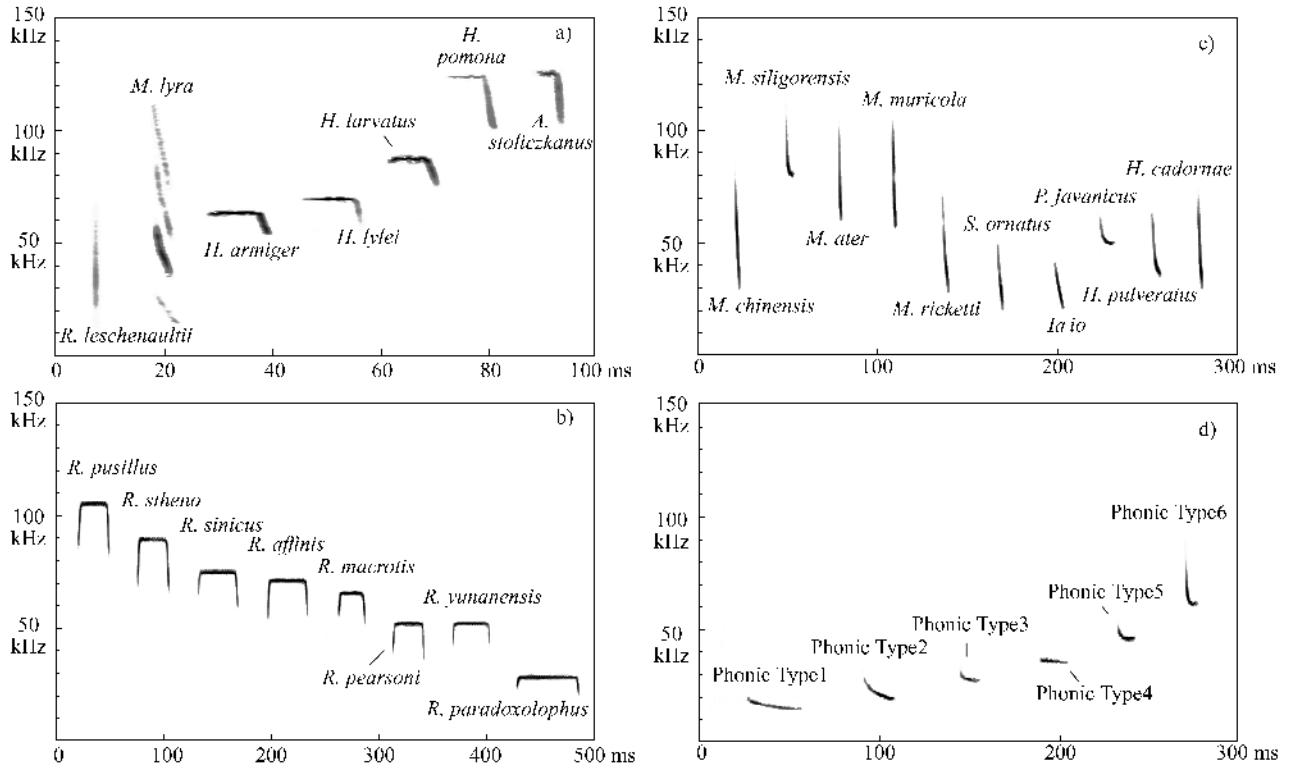

Fig.2 Echolocation calls of 31 species of bats at Kim Hy Nature Reserve: a) Pteropodidae, Megadermatidae and Hipposideridae; b) Rhinolophidae; c) Vespertilionidae; and, d) six unidentified phonic types.

occurring in the EF, FmaxE and MF values for the three species.

2.1.6 Unidentified phonic types In addition to the ten vespertilionid species above, calls of six distinct phonic types were recorded. All are believed to represent aerial insectivores within the Vespertilionidae, Molossidae or the recently-erected Miniopteridae and emitted a mixture of broadband and/or narrowband signals dominated by the fundamental harmonic (Table 1b, Fig.2d).

Phonic type 1 produced shallow broadband calls which comprised a long quasi constant-frequency signal and possessed the longest mean call duration (17.8 ± 9.1 ms) of all species in our sample. Call frequencies spanned 22.5 ± 3.2 to 14.4 ± 1.1 kHz, with a FmaxE of 16.7 ± 1.0 kHz. In contrast, phonic type 2 produced calls which were similar in duration (14.2 ± 4.0 ms), but higher in frequency (FmaxE = 21.7 ± 1.1 kHz) with virtually no overlap in several parameters (EF, FmaxE, MF). The third phonic type produced calls which were again higher in frequency (FmaxE = 27.4 ± 1.4 kHz), exhibited little or no overlap in several parameters (EF, FmaxE, MF) with phonic types 1 and 2, and possessed a slightly shorter mean call duration (12.6 ± 3.5 ms). Compared to the other species in our study, phonic types 1 – 3 were most similar in frequency values to those produced by *I. io*.

Phonic type 4 was distinct from all other species in our study in producing narrowband (4.1 ± 1.5 kHz) calls of long duration (14.2 ± 4.4 ms) with an FmaxE of 36.7 ± 1.2 kHz. The fifth phonic type produced search phase calls which typically consisted of a short frequency-modulated portion followed by a comparatively long quasi constant-frequency portion and contained the greatest call energy at 45.3 ± 2.0 kHz. This type exhibited several frequency parameters which overlapped with those of *H. pulveratus* and *P. javanicus* (EF, FmaxE, MF). As such, it is possible that some calls representing the lower and upper ranges of phonic type 5 could represent these species respectively (but see discriminant function analysis results below). The remaining phonic type, phonic type 6, produced calls which resembled those of *M. siligorensis* in comprising a steep frequency-modulated portion followed by a short narrowband portion, but were at rather lower frequencies (with an FmaxE of 62.0 ± 1.8 kHz).

2.2 Discriminant function analysis

Thirty-one bat species were assessed in the analysis. As all species could be unequivocally separated into two groups by their call structures, quadratic discriminant analysis was undertaken for i) species whose calls contained a constant-frequency portion terminating in a frequency-modulated portion (eight rhinolophids and five hipposiderids); and, ii) species whose calls comprised a frequency-modulated signal (with or without a narrowband portion) or a quasi-constant frequency signal

(*R. leschenaultii*, *M. lyra*, ten vespertilionids and six unidentified phonic types).

2.2.1 Constant-frequency species (genera *Rhinolophus*, *Hipposideros* and *Aselliscus*) Quadratic discriminant function analysis resulted in a 97.0% correct classification rate (194 calls correctly classified out of 200), and 92.0% (184 calls correctly classified) when cross-validated (Table 2a). As several call parameters were correlated, these were excluded from analyses and the best model relied upon three variables (EF, FmaxE and D), which a MANOVA showed was significant (Wilk's $\lambda = 0.00036$, $F = 206.459$, $P < 0.001$). Calls of six species were correctly classified 100% of the time (*R. paradoxolophus*, *R. macrotis*, *R. pusillus*, *H. pomona*, *H. armiger* and *H. larvatus*), while correct classification rates of > 80% were achieved for a further three species (*R. stheno*, *R. sinicus* and *R. affinis*). Approximately one-quarter of calls for *R. pearsoni* and *R. yunanensis* were incorrectly classified as the other species, while > 50% of those for *A. stoliczkanus* were misclassified as *H. pomona*. Correct classification rates for the remaining species, *H. lylei*, were similarly low at 40%, due to misclassification as *R. affinis* and *H. armiger*. Wilk's λ values demonstrated that the discrimination power of the three variables in decreasing order was: FmaxE (0.0023), EF (0.01605) and D (0.13065).

Table 2a Classification matrix for species emitting CF calls (genera *Rhinolophus*, *Hipposideros*, *Aselliscus*)

Classified as	True groups												
	R. par.	R. mac.	R. pea.	R. yun.	R. pus.	R. sth.	R. sin.	R. aff.	H. pom.	H. lyl.	H. arm.	H. lar.	A. sto.
R. par.	44	0	0	0	0	0	0	0	0	0	0	0	0
R. mac.	0	11	0	0	0	0	0	0	0	0	0	0	0
R. pea.	0	0	13	2	0	0	0	0	0	0	0	0	0
R. yun.	0	0	5	6	0	0	0	0	0	0	0	0	0
R. pus.	0	0	0	0	10	0	0	0	0	0	0	0	0
R. sth.	0	0	0	0	0	5	0	0	0	0	0	0	0
R. sin.	0	0	0	0	0	1	6	1	0	0	0	0	0
R. aff.	0	0	0	0	0	0	1	17	0	2	0	0	0
H. pom.	0	0	0	0	0	0	0	0	7	0	0	0	3
H. lyl.	0	0	0	0	0	0	0	0	0	2	0	0	0
H. arm.	0	0	0	0	0	0	0	0	0	1	29	0	0
H. lar.	0	0	0	0	0	0	0	0	0	0	0	32	0
A. sto.	0	0	0	0	0	0	0	0	0	0	0	0	2
Total *n*	44	11	18	8	10	6	7	18	7	5	29	32	5
n correct	44	11	13	6	10	5	6	17	7	2	29	32	2
% correct	100	100	72	75	100	83	86	94	100	40	100	100	40

The discriminant function analysis model relied on three parameters (EF, FmaxE, D) and provided an overall correct classification rate of 92.0% when cross-validated. R. par. = *R. paradoxolophus*; R. mac. = *R. macrotis*; R. pea. = *R. pearsoni*; R. yun. = *R. yunanensis*; R. pus. = *R. pusillus*; R. sth. = *R. stheno*; R. sin. = *R. sinicus*; R. aff. = *R. affinis*; H. pom. = *H. pomona*; H. lyl. = *H. lylei*; H. arm. = *H. armiger*; H. lar. = *H. larvatus*; A. sto. = *A. stoliczkanus*.

2.2.2 Frequency-modulated species (genera *Rousettus*, *Megaderma*, *Myotis*, *Scotomanes*, *Ia*, *Pipistrellus*, *Hypsugo* and six unidentified phonic types)

Due to correlations between several call parameters, the best model relied upon only two frequency parameters (EF and FmaxE), which nonetheless produced an overall classification rate of 90.7% (165 calls correctly classified out of 182) and 81.3% (148 calls correctly classified) when cross-validated. MANOVA demonstrated that the model was significant (Wilk's $\lambda = 0.00200$, $F = 204.648$, $P < 0.001$). As the call parameters we used were unlikely to adequately differentiate the broadband clicks of *R. leschenaultii* from the tonal signals emitted by insectivorous bats (which differ greatly to the ear when time-expanded), a second analysis was conducted excluding *R. leschenaultii*. This model gave an overall classification rate of 96.4% (161 calls correctly classified out of 167), a cross-validated rate of 86.2% (144 calls correctly classified) and was also significant (Wilk's $\lambda = 0.00150$, $F = 230.835$, $P < 0.001$) (Table 2b). In this second analysis, two species, *M. chinensis* and *M. siligorensis*, were correctly classified 100% of the time, while correct classification rates of 83% – 89% were achieved for a further three vespertilionid species (*I. io*, *P. javanicus* and *H. cadornae*). Classification rates for the six phonic types ranged from 83% – 96%. Classification rates for *M. ater* and *M. muricola* ranged from 50% – 75%, due to misclassification as each other. The remaining vespertilionid species in our sample

Table 2b Classification matrix for species emitting FM calls (genera *Megaderma*, *Myotis*, *Scotomanes*, *Ia*, *Pipistrellus*, *Hypsugo* and six unidentified phonic types)

Classified as	True groups																
	M. lyr.	M. chi.	M. sil.	M. ate.	M. mur.	M. ric.	S. orn.	I. io	P. jav.	H. pul.	H. cad.	PT 1	PT 2	PT 3	PT 4	PT 5	PT 6
M. lyr.	4	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
M. chi.	0	8	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
M. sil.	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M. ate.	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	1
M. mur.	0	0	0	2	3	0	0	0	1	0	0	0	0	0	0	0	0
M. ric.	1	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
S. orn.	0	0	0	0	0	0	4	2	0	0	1	0	0	0	0	0	0
I. io	0	0	0	0	0	0	1	16	0	0	0	0	1	1	0	0	0
P. jav.	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	1	0
H. pul.	2	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0
H. cad.	1	0	0	0	0	1	1	0	0	0	8	0	0	0	0	0	0
PT1	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0
PT2	0	0	0	0	0	0	0	0	0	0	0	1	11	0	0	0	0
PT3	0	0	0	0	0	0	0	0	0	0	0	0	0	21	0	0	0
PT4	0	0	0	0	0	0	0	0	0	1	0	0	0	0	11	0	0
PT5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0
PT6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Total *n*	8	8	16	4	4	5	6	18	6	5	9	9	12	22	12	17	6
n correct	4	8	16	2	3	3	4	16	5	3	8	8	11	21	11	16	5
% correct	50	100	100	50	75	60	67	89	83	60	89	89	92	96	92	94	83

The discriminant function analysis model relied on two parameters (EF, FmaxE) and provided a overall cross-validated classification rate of 86.2%. M. lyr. = *M. lyra*; M. chi. = *M. chinensis*; M. sil. = *M. siligorensis*; M. ate. = *M. ater*; M. mur. = *M. muricola*; M. ric. = *M. ricketti*; S. orn. = *S. ornatus*; P. jav. = *P. javanicus*; H. pul. = *H. pulveratus*; H. cad. = *H. cadornae*; PT1-6 = phonic types 1-6.

(*M. ricketti*, *S. ornatus* and *H. pulveratus*) were correctly classified 60% – 67% of the time, while *M. lyra* was correctly classified 50% of the time. Wilk's λ values indicated that the discrimination power of the two variables in our sample was: EF (0.01301) and FmaxE (0.01644).

2.3 Species inventory and cave monitoring

2.3.1 Species inventory A total of 133 bats of 25 species and five families were captured in the three above-ground habitats (Tables 3 and 4). The Vespertilionidae was best represented in terms of species richness with eight species, although it accounted for fewer captures (24.8% of the total) relative to the Hipposideridae (34.6%) with six species. Comparable levels of species richness and abundance were recorded in the Rhinolophidae with seven species representing 21.8% of captures, whereas pteropodids were less well represented with three species and 15.8% of captures. Megadermatidae comprised a single species, *M. lyra*, and accounted for the lowest proportion of captures (3.0%). The single most abundant species, *H. larvatus*, accounted for 17.3% of total captures and was the commonest species in primary forest, while the most abundant species in disturbed forest and agriculture/degraded forest were *M. cyclotis* and *R. leschenaultii*, respectively. Sixty percent of all bats captured were caught in ground mist nets and the remainder in harp traps (Table 3). Of the 25 species recorded, eight were captured in both mist nets and harp traps, ten exclusively in mist nets and seven exclusively in harp traps.

Table 3 Sampling effort for capture methods at Kim Hy Nature Reserve

Habitat	Ground mist net			Harp trap		
	m^2 mnh	*n*	S	m^2 hth	*n*	S
Primary forest	2430	37	10	162	24	11
Disturbed forest	2436	24	11	163	22	8
Agriculture/degraded forest	2430	19	7	165	7	3
subtotal		80	18		53	14
ATC # 1 2006	1020	223	9	48	26	13
ATC # 1 2007	1020	135	8	48	24	9
subtotal		358	11		50	15

n = number of individuals captured; S = number of species; m^2 mnh = metre^2 mist net hour; m^2 hth = metre^2 harp trap hour.

Analysis of recordings of free-flying bats from the acoustic sampling revealed the presence of ten insectivorous bat species which were not captured by mist nets or harp traps in any of the three above-ground habitats (Table 4). Our acoustic sampling thus raised the total number of species recorded from 25 to 35 species, an overall increase of 29%. The average number of species recorded per night with capture methods and capture methods plus acoustic sampling was 2.4 and 3.4, 2.1 and 3.9 and 1.3 and 4.9 in primary forest, disturbed forest and agriculture/degraded forest, respectively. As a

consequence, the number of species recorded per night with acoustic sampling in combination with capture methods was significantly higher than that recorded by capture methods alone in all three habitats (primary forest: Wilcoxon's $t = 45.0$, $n = 14$, $P = 0.009$; disturbed forest: $t = 55.0$, $n = 14$, $P = 0.006$; agriculture/degraded forest: $t = 105.0$, $n = 14$, $P = 0.001$). The proportion of additional species detected by the acoustic sampling alone was greatest in agriculture/degraded forest (47%), followed by disturbed forest (36%) and primary forest (22%) (Table 4).

Table 4 Bat species recorded in three above-ground habitats and at An Tinh Cave # 1 at Kim Hy Nature Reserve, by capture methods (C) and acoustic methods (A)

Species	Primary forest	Disturbed forest	Agriculture/ degraded forest	An Tinh Cave # 1	
				2006	2007
Pteropodidae					
Rousettus leschenaultii	C		C	C, A	C, A
Cynopterus sphinx			C		
Eonycteris spelaea	C	C		C	C
Megadermatidae					
Megaderma lyra	C		C		
Rhinolophidae					
Rhinolophus paradoxolophus	C, A			C, A	C, A
Rhinolophus macrotis	C			C	C
Rhinolophus pearsoni	C, A[a]	C, A[a]	C, A[a]	C, A[a]	C, A[a]
Rhinolophus yunanensis	A[a]	C, A[a]	A[a]	A[a]	C, A[a]
Rhinolophus pusillus	C	C, A	C	C, A	C
Rhinolophus sinicus	C			C	
Rhinolophus affinis	A	C, A	C, A		
Hipposideridae					
Hipposideros pomona	A[b]	C, A[b]	C, A[b]	C, A[b]	C
Hipposideros lylei		A			
Hipposideros armiger	C, A	C, A	A	C, A	C, A
Hipposideros larvatus	C, A	A	C, A	C	
Aselliscus stoliczkanus	C, A[b]	A[b]	C, A[b]	C, A[b]	C
Coelops frithii	C			C	
Vespertilionidae					
Myotis chinensis		C			
Myotis siligorensis	A	A		C, A	C, A
Myotis ricketti				A	A
Scotomanes ornatus	C				
Ia io				C, A	C, A
Pipistrellus javanicus	A		A		
Hypsugo pulveratus	C				
Hypsugo cadornae		A	A		
Murina tubinaris	C	C			
Murina cyclotis	C	C	C	C	C
Murina tiensa	C				
Murina sp. nov.	C	C			
Harpiocephalus harpia	C	C			
Kerivoula titania		C			
Unidentified phonic types					
Phonic type 1 (16.7 kHz)	A		A		
Phonic type 2 (21.7 kHz)		A	A		
Phonic type 3 (27.4 kHz)	A	A	A		
Phonic type 4 (36.7 kHz)			A		
Phonic type 5 (45.3 kHz)		A	A		
Phonic type 6 (62.0 kHz)		A	A	A	
No. of species captured	18	14	10	15	13
Species recorded acoustically†	10	13	13	10	7
Total no. of species†	23	22	19	17	14
Percentage of additional species recorded in acoustic sampling	22	36	47	12	7

Superscript annotations refer to a) *R. pearsoni*/*R. yunanensis* and b) *H. pomona*/*A. stoliczkanus*, which cannot be unequivocally separated by acoustic data at Kim Hy and are thus treated as single taxa in the relevant species totals (†).

2.3.2 Cave monitoring A total of 408 bats of 16 species and four families were captured in ATC # 1 in 2006 – 2007 (Tables 3 and 4). Rhinolophidae and Hipposideridae were best represented in terms of species richness with six and five species respectively and accounted for 18.6% and 5.9% of total captures, respectively. Pteropodidae comprised two species, *Eonycteris spelaea* and *R. leschenaultii*, which accounted for the majority of bats caught at the site in both years (69.1% collectively), followed by the rhinolophid *R. paradoxolophus* (14.0% collectively). The Vespertilionidae was represented by three species in both years and accounted for 6.4% of total captures. Eighty-eight percent of bats were captured in ground mist nets and the remainder in harp traps (Table 3). Of the 16 species recorded, ten species were captured in both mist nets and harp traps and six species exclusively in harp traps.

Analysis of recordings from the acoustic sampling revealed the presence of two additional insectivorous bat species that were not captured by mist nets or harp traps, which raised the site total from 16 to 18 species (Table 4), an overall increase of 11%. The average number of species recorded per night with capture methods and capture methods plus acoustic sampling was 8.8 and 10.0 respectively in 2006 and 6.8 and 9.0 in 2007. Consequently, the number of species recorded per night with acoustic sampling in combination with capture methods was significantly higher than that recorded by capture methods alone (Wilcoxon's $t = 21.0$, $n = 8$, $P = 0.036$).

3 Discussion

Ours is the first study to describe the echolocation calls produced by Vietnamese bat populations and the first in continental SE Asia to compare species inventories based on conventional capture methods with those derived from simultaneous acoustic sampling. Of the 31 bat species described, all were unequivocally assigned into one of two groups by their echolocation call structure (CF or FM bats). Discriminant function analysis demonstrated that acoustic identification of insectivorous species (30 species) in both groups is feasible by providing high levels of correct classification, with cross-validated rates of 92.0% and 86.2%, respectively (89.1% overall). Twenty bat species representing at least four families were identified in acoustic sampling and the number of bat species recorded by acoustic sampling and capture methods each night at all sampling sites was significantly greater than that recorded by capture methods alone. As a result, our capture methods, which comprised the two most commonly utilized sampling devices in SE Asian bat surveys, failed to record ten species (or 29% of the bat fauna) in the three above-ground habitats and two species (or 11% of the bat fauna) in our cave sample, all of which were detected by acoustic sampling only.

3.1 Species identification

Our results demonstrate that correct acoustic identification of SE Asian bat species is feasible using the echolocation call parameters we analyzed. Although this study provides the first published information on the echolocation calls of several bat species (e. g. *H. lylei*, *M. chinensis*, *M. ater*, *M. muricola*, *S. ornatus*, *P. javanicus*, *H. pulveratus* and *H. cadornae*), our call parameter data is generally consistent with that for species for which published and unpublished information exists from neighboring Laos and China (Francis and Habersetzer, 1998; Ma et al., 2003; Zhao et al., 2003; Li et al., 2006; Thabah et al., 2006; 2007; Jones and Zhang, 2008; Sun et al., 2008). Furthermore, rates of correct classification in discriminant function analysis were comparable to those of other studies around the world (see reviews in Jones et al., 2000; Russo and Jones, 2002; Fukui et al., 2004; MacSwiney et al., 2008). For instance, Parsons and Jones (2000) obtained a correct classification rate of 79% for 12 species in the U. K., Russo and Jones (2002) a rate of 82% for 18 species in Italy, while MacSwiney et al. (2008) achieved a correct classification rate of 84% for 26 species in Mexico. As such, our study suggests that correct acoustic identification of free-flying bat species is an equally viable goal in SE Asia.

As only one call from each of the phonic types was classified as belonging to one of the ten vespertilionid species in our analysis (Table 2b), this further suggests that each type represents a previously unrecorded bat species at Kim Hy. The calls of phonic types 1 – 3 were set apart from species such as *I. io* by their shallow broadband structure and notably longer call durations and most likely represent other large-bodied molossid (e. g. *Tadarida* spp.) or vespertilionid (e. g. *Nyctalus* spp.) taxa. Emballonurids (e. g. *Taphozous* spp.) are an unlikely possibility, as these typically emit calls characterized by a multi-harmonic structure (Jones and Teeling, 2006). As dominant call frequencies scale negatively with body mass in vespertilionids (Jones, 1999), phonic type 4 may represent a relatively large-bodied aerial insectivore such as *Scotophilus* spp., two species of which are widespread in north Vietnam (Corbet and Hill, 1992). The remaining phonic type, type no. 6, likely represents a medium-sized and previously unrecorded vespertilionid (e. g. *Pipistrellus* spp.), or miniopterid (*Miniopterus* spp.) bat species at Kim Hy.

As the taxonomy of many SE Asian bat taxa remains uncertain (Francis et al., 1999), acoustic analyses are likely to prove an increasingly valuable means of field identification for species which are morphologically similar but acoustically divergent (Jones and Barlow, 2001). For example, Sun et al. (2008) recently revealed the existence of two distinct species (one large, one small) within the taxon *R. macrotis*, with dominant call

frequencies of 49 kHz and 65 kHz, respectively. As our sample of *R. macrotis* had an FmaxE of 66.4 ± 0.9 kHz (and forearm lengths of 40.3 ± 1.0 mm, n = 39), the species at Kim Hy evidently represents the smaller of the two forms, the correct name for which may be *R. siamensis* (Francis et al., 1999; Hendrichsen et al., 2001). More rarely, a lack of acoustic divergence may signal the possible presence of conspecifics. For instance, our data indicates that call parameters for *R. pearsoni* and *R. yunanensis*, two morphologically similar species (Csorba et al., 2003), overlap extensively in north Vietnam. As Jones and Zhang (2008) encountered the same situation in China and found no clear divergence in mtDNA haplotypes between the two species, this possibility warrants further investigation.

The existence of intra-specific variation in echolocation calls due to geographical location (Thomas et al., 1987) means that reference recordings from each site under investigation are required to reliably identify species whose call parameters may overlap with those of others in certain parts of their range. For instance, whereas Jones and Zhang (2008) recorded extensive overlap in FmaxE values between *R. affinis* and *R. sinicus* in China, no such overlap occurred in our similarly-sized sample, permitting confident acoustic identification of both species. Conversely, while overlap occurred in call parameters for *A. stoliczkanus* and *H. pomona* in our study, it appears that overlap in FmaxE values for these species may be absent at some Vietnamese sites (pers. comm. Vu Dinh Thong). Since habitat structure also induces variability in echolocation calls (Schnitzler et al., 2003), recordings from a variety of environments are required to elucidate the full range of calls produced by different species. Given the current lack of detailed call descriptions for most SE Asian bats however, assemblage studies utilizing acoustic methods are likely to require the continued use of phonic types in the immediate future. As a consequence, further research to expand knowledge of the echolocation calls produced by bat species (and aerial insectivores in particular) in the region is clearly desirable.

3.2 Sampling methods and inventory completeness

We employed a time-expansion system for recording and analyzing bat echolocation calls. Time-expansion systems are ideal where in-depth signal analysis and species identification are required (Parsons et al., 2000), whereas frequency-division and heterodyne systems may be more applicable in situations where less detailed or continuous recordings are required and are frequently employed with automated recorders in remote monitoring studies (Limpens and McCracken, 2004). Direct sampling of ultrasound to computer hard disk provides a high-quality, real-time output suitable for detailed sound analysis, although the need for a laptop in the field could constrain its use in the humid tropics. Extensive advice on the most appropriate system and sampling approach in different situations is given by Brigham et al. (2004).

In the present study, simultaneous acoustic sampling resulted in a significant increase in the overall number of bat species recorded in a variety of foraging and commuting habitats (29%) and in a cave sample (11%). Furthermore, while four of the ten bat species exclusively recorded by acoustic methods in the three above-ground habitats were subsequently captured in longer-term sampling at Kim Hy (Furey, 2009), the remaining six were not. As this longer-term sampling was undertaken at the same sites (with effort similarly partitioned between habitats, seasons and trap types) and represented a four-fold increase in mist net sampling (7296 vs. 35829 m^2 mnh) and a nine-fold increase in harp trap sampling (490 vs. 4, 165 m^2hth), this strongly suggests that acoustic methods are indispensable to maximize inventory completeness. This applies particularly to aerial insectivores which habitually fly in open areas and/or above the forest canopy beyond the range of conventional capture devices. A similar conclusion was reached by MacSwiney et al. (2008), who found that simultaneous acoustic sampling increased the number of species by 30% over that of capture methods in the neotropics. Thus, in spite of major differences in the taxonomic composition of bat assemblages between the New and Old world, our study indicates that acoustic sampling is equally useful in improving inventory completeness in the Palaeotropics.

Notwithstanding the above, our results also indicate that acoustic sampling should not be considered as a replacement for conventional capture methods in bat species inventories in SE Asia. This is demonstrated by the fact that 13 insectivorous species were exclusively recorded by capture methods in our above-ground habitat sample and five at ATC # 1 (Table 4). As numerous bat species echolocate at very low intensities (e. g. species within the Murininae and Kerivoulinae subfamilies and *Coelops frithii*), acoustic methods are unlikely to improve upon the results provided by harp traps for such species. For example, although *M. cyclotis* was the most abundant bat captured in disturbed forest in our study (79% of which were caught in harp traps), acoustic sampling consistently failed to detect the species. Nonetheless, in situations where inventory completeness is important, the present study demonstrates that acoustic sampling is essential to overcome the inherent limitations of conventional capture methods. As accurate species inventories and monitoring are vital for effective conservation of SE Asian bat diversity, we therefore recommend the inclusion of acoustic sampling in future studies of bat assemblages across the region.

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