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Original paper

Bats (Chiroptera) of Bidoup Nui Ba National Park, Dalat Plateau, Vietnam

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Abstract. We determined species diversity, seasonal reproduction, and echolocation patterns in the bat community of Bidoup Nui Ba National Park (BNBNP), Lam Dong Province, on the Dalat Plateau of the Central Highlands of Vietnam. We documented 27 species with 211 individuals captured in 26 994 m^2 mist-net-hours and 3015 m^2 harp-trap-hours of effort. We found five species of pteropodids and 22 species of insectivorous bats in four families, including regional records and species seldom captured in Vietnam. Bat species richness at BNBNP is now known to be 33 species, including six found in a prior study. Based on the inverse Simpson Index of Diversity, evenness of captures was low, reflecting the high abundance of a few species with many species documented by just one or two individuals. Insectivorous bats were pregnant in the late dry season, but not during the wet season when lactation occurred and volant juveniles were captured. Echolocation call characteristics were determined for 19 species of insectivorous bats. Call patterns were consistent with some but not all reports in the literature from elsewhere in southeast Asia. This suggests the existence of cryptic species or geographic and habitat variability in echolocation calls of southeast Asian bats that requires further study.

Key words: echolocation, reproduction, species diversity, Vietnam.

National parks and other protected areas are integral to the conservation of biodiversity in tropical Asia (Squires 2014; Francis 2019). Bats are very important components of mammalian diversity in this region, including Vietnam, but many land management units lack intensive knowledge of the bat communities that inhabit them (Furey et al. 2010; Kingston 2010). Bidoup Nui Ba National Park (BNBNP) was established in 2004 as a high priority conservation area within Vietnam, is the fifth largest (66 000 ha) of the 33 national parks in the country, and spans a wide range of elevations from about 650 to 2300 m above sea level (Bidoup Nui Ba National Park 2019). One survey of small mammals at BNBNP conducted intermittently during 2002 to 2009 included

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preliminary efforts to document bats but noted that their inventory was "far from complete" (Abramov et al. 2009: 71). The objectives of our study were to more intensively determine the species diversity, reproductive phenology, and echolocation characteristics in the bat community of BNBNP. Studies of the bat communities of other national parks and nature reserves in Vietnam have been limited in number but have increased over the past 20 years (e.g., Hendrichsen et al. 2001; Furey et al. 2009, 2010, 2011; Kruskop and Shchinov 2010; Minh et al. 2011; Thong 2015; Son et al. 2016; Tu et al. 2016).

Materials and methods

Study area and forest categories

BNBNP is an isolated mountainous reserve located in Lam Dong Province on the Dalat Plateau, in the southernmost Central Highlands of south-central Vietnam (Fig. 1). Established in 2004, BNBNP has 90% forest cover composed primarily of montane evergreen (broadleaf) forest, with patches of coniferous forest and mixed broadleaf-coniferous forest (Tran 2011; Joshi et al. 2015). The area is influenced by a dry, cool season from November through March, and a warm, wet season from April

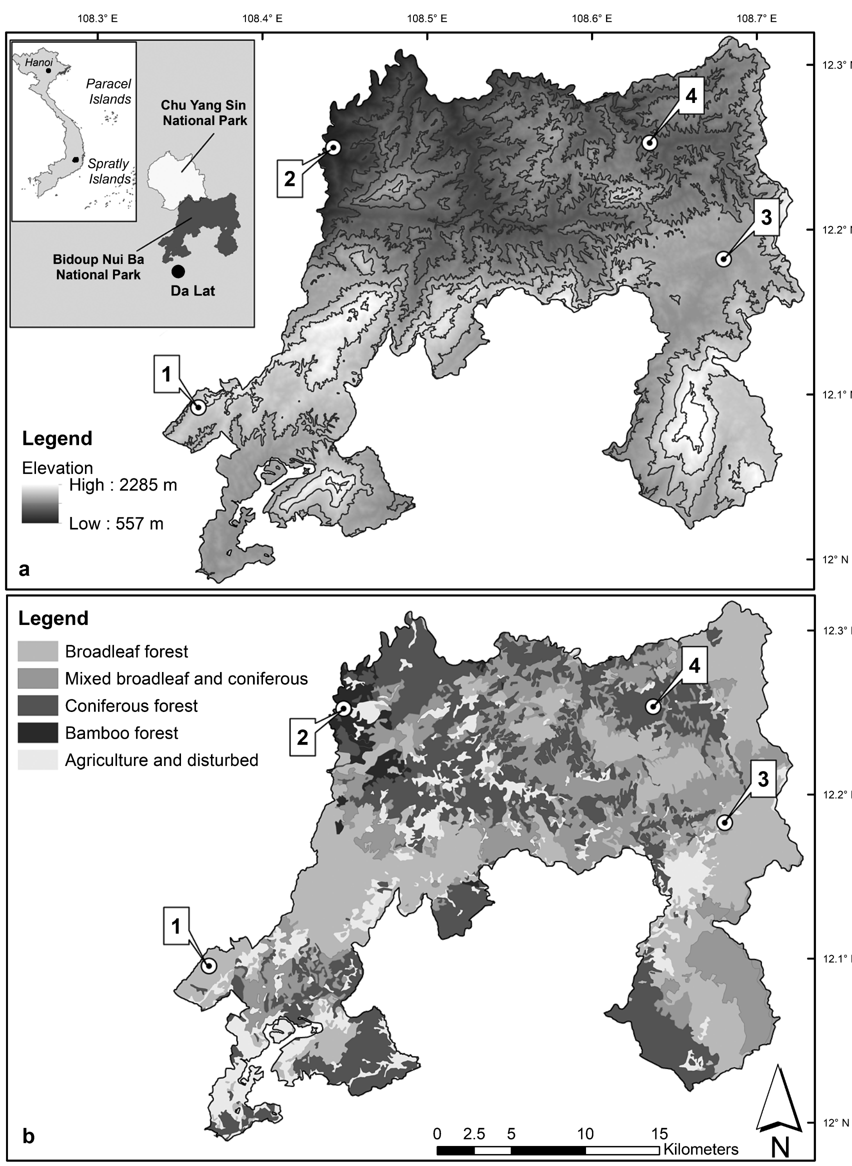

Fig. 1. Location of four field camps for sampling bats in Bidoup Nui Ba National Park, Vietnam, 2014–2016 relative to elevation (a) and forest cover classes (b). Elevation data at a scale of 1:50 000 courtesy of the Vietnam Publishing House of Natural Resources, Environment, and Cartography, Hanoi, and forest cover data at the same scale from the Vietnam Forest Inventory and Planning Institute, Hanoi.

through October (Pham-Thanh et al. 2019) with a mean annual rainfall of approximately 1870 mm, minimum temperatures of –0.1°C, and maximum of 31.5°C (Brodribb and Feild 2008; Tran 2011).

We tabulated descriptive forest categories at capture sites for each species of bat captured. We used five categories compiled from unpublished 2010 forest cover classes provided by the Vietnam Forest Inventory and Planning Institute, Hanoi with a scale of 1:50 000. We characterized forest within a 50 m circular radius around each bat capture site as agricultural and disturbed, broadleaf forest, coniferous forest, mixed broadleaf and coniferous forest (MBC), bamboo and mixed forest (BMF), or some combination of categories. Within tables we listed, in descending order of abundance, the forest categories present at all capture sites for each species of bat. We limited our forest cover results to descriptive totals within categories because most species of bats were seldom captured, forest cover was measured remotely and imprecisely, and vegetation analyses are lacking in most studies of southeast Asian bat communities for comparison. For analysis we provided a comparison of the proportions and 95% confidence intervals (*CI*s) of bats sampled that fell under the most frequent forest category (broadleaf forest) by families and most frequently captured species. We then examined for overlap of these *CI*s for proportions with the proportional availability of the most frequent category among all sites where netting and trapping occurred. We calculated proportions and *CI*s following the method of Newcombe (1998) using a correction for continuity.

We sampled bats at BNBNP near four field camps established during 2014–2016 in the dry (March) and early wet (May and June) seasons (Fig. 1). Camp 1 was located in the interior of the BNBNP on a foot trail 1.2 km from the nearest road at 12.09662°N 108.35684°E, elevation 1609 m, in broadleaf forest that was previously selectively logged in about 1980. Bats were captured at 23 of 32 geo-referenced sampling locations, all within 2.7 km of the camp and in the broadleaf forest remote sensing category (see below), at elevations ranging from 1541 m to 1786 m ($\bar{X} = 1556 \pm 359$ m). We sampled at the Camp 1 area from 3 to 11 June in 2014, and from 21 to 26 March 2015. Camp 2 was in mixed agriculture-secondary forest habitat at 12.249424°N 108.436981°E, elevation 644 m on trails accessible from paved roads by motorbike. Bats were sampled at four locations in coniferous forest and in bamboo and mixed forest habitats at Camp 2, all within 0.3 km of the camp at elevations ranging from 650 m to 675 m ($\bar{X} = 664 \pm 11$ m). We sampled at the Camp 2 area from 17 to 19 March 2015. Camp 3 was along a paved roadway in forested habitat near Giang Ly Forest Guard Station, 12.18241°N 108.67995°E, elevation 1454 m. We captured bats at 13 of 17 geo-referenced sampling locations at Camp 3 on 11 nights from 11–21 May 2015 and 16–23 March 2016; 14 locations were within 3.7 km of the camp, with one location 8.0 km north of the camp. Sampling elevations at Camp 3 ranged from 1094 m to 1656 m ($\bar{X} = 1486 \pm 136$ m). Forest categories at netting sites around Camp 3 were primarily in broadleaf forest (11 sites), with other categories including agricultural and disturbed lands (two sites), mixed agricultural and broadleaf forest (two sites), broadleaf and conifer (one site), or bamboo and mixed forest (one site). A permanent plot of forest structure and tree biodiversity is located near Camp 3 (Hoa et al. 2018). Camp 4 was in mixed coniferous and broadleaf evergreen forest at 12.25294°N 108.63507°E, elevation 1057 m. The camp was accessible by foot trails into the park interior about 9.2 km (straight line distance) from the nearest road. Bats were captured on 14–17 March 2016 at 12 of 19 geo-referenced locations within 1.9 km of Camp 4 at elevations ranging between 1050 and 1108 m ($\bar{X} = 1073 \pm 20$ m). Forest categories at sampling sites around Camp 4 were broadleaf forest (six sites), coniferous forest (three sites), combinations of coniferous with mixed broadleaf and coniferous forest (nine sites), or agricultural and disturbed land (one site).

Bat sampling

We captured bats using mist nets and harp traps set at ground level across trails, over small ponds and streams, or near edges of forest. Mist nets ranged from 3.0 to 18.0 m in length and were about 2.6 m in height, whereas harp traps ranged from 1.0 to 2.1 m^2 in area. Mist nets were set from two to 12 h nightly, whereas harp traps were left open all night. In June 2014 we sampled on eight nights for 458 m^2 harp trap h (m^2 hth; three traps per night) and 2724 m^2 mist net h (m^2 nh; 1–5 nets per night of three sizes ranging 6–12 m in length). In March 2015 we sampled on nine nights for 329 m^2 hth (0–3 traps per night) and 7903 m^2 nh (2–12 nets per night of six sizes ranging 3.0–18.0 m in length). In May 2015 we sampled on 11 nights, for 1233 m^2 hth (1–2 different traps per night) and 3750 m^2 nh (1–5 nets per night of four sizes ranging 6–13 m in length). In March 2016 we sampled for bats on 10 nights, deploying 995 m^2 hth (1–6 different traps per night) and 12 617 m^2 nh (6–14 nets per night of four sizes ranging 6–18 m in length). Total effort was 26 994 m^2 nh and 3015 m^2 hth, respectively.

We preserved voucher specimens in ~95% ethanol in the field for 12 hours and then reduced the ethanol concentration to 70%. We retained most bats as voucher specimens but released 53 on site (36 of these were *Rhinolophus affinis*). We categorized adult females as pregnant, lactating, post-lactating, or non-reproductive following standard field techniques for bats (Racey 2009). In cases where pregnancy was detected in voucher specimens we recorded numbers of visible embryos. Age was categorized as volant juvenile or adult based on fusion of the phalangeal epiphyses (Brunet-Rossinni and Wilkinson 2009). We verified species identifications on voucher specimens using external and cranial morphology. We relied on echolocation characteristics of three species of small *Rhinolophus* bats for confirmation of morphological identifications because identifications of vouchers from GenBank may be uncertain. Frequency of maximum energy (FMAXE) measurements of *R. stheno* at BNBNP were consistent with those from multiple areas in southeast Asia, but did not overlap with those recorded for *R. microglobosus* from the same regions (Francis 2008, 2019; Hughes et al. 2010; Phauk et al. 2013). *Rhinolophus pusillus* and *R. lepidus* are difficult to distinguish morphologically and available DNA information is limited. Therefore we tentatively grouped morphologically similar bats with non-overlapping ranges of FMAXE averaging 93.7 ± 1.3 kHz as *R. lepidus* following several sources (e.g., Shi et al. 2009; Li et al. 2014; Raghuram et al. 2014), and bats averaging 100.1 ± 0.9 kHz as *R. pusillus* following others (e.g., Francis and Habersetzer 1998; Shi et al. 2009; Zhang et al. 2009).

We also took samples of liver or wing tissue in ethanol for DNA analysis for species verification. We verified identifications of eight species from nine samples using DNA analysis (Supplemental Table S1). A 685 bp fragment of the COI mitochondrial cytochrome c oxidase gene (DNA barcode) was amplified by using primers VF1d-VR1d (Ivanova et al. 2006). Tissue samples were extracted using DNeasy blood and tissue kit, Qiagen (Hilden, Germany). Extracted DNA from the fresh tissue was amplified by DreamTaq PCR mastermix, Thermo Fisher Scientific (Vilnius, Lithuania). The PCR volume consisted of 21 µl (10 µl of mastermix, 5 µl of water, 2 µl of each primer at 10 pmol/µl, and 2 µl of DNA or higher depending on the quantity of DNA in the final extraction solution). PCR condition was: 95°C for 5 minutes to activate the taq; with 40 cycles at 95°C for 30 s, 50°C for 45 s, 72°C for 60 s; and the final extension at 72°C for 6 minutes. PCR products were subjected to electrophoresis through a 1% agarose gel, 1st BASE (Selangor, Malaysia). Gels were stained for 10 minutes in 1× TBE buffer at 2 pg/ml of ethidium-bromide, and visualized under UV light. Successful amplifications were purified to eliminate PCR components using GeneJET™ PCR Purification Kit, Thermo Fisher Scientific (Vilnius, Lithuania). Purified PCR products were sent to Macrogen Inc. (Seoul, South Korea) for sequencing. Sequences generated in this study were aligned with one another using De Novo Assemble function in the program Geneious v.7.1.8 (Kearse et al. 2012). They were then compared with other sequences using the Basic Local Alignment Search Tool (BLAST) in GenBank.

All samples and voucher specimens were deposited in collections at the Department of Vertebrate Zoology, Institute for Ecological and Biological Resources at the Vietnam Academy of Sciences and Technology, Hanoi. Collecting methods, euthanasia, and specimen preparation followed guidelines for obtaining mammal specimens as approved by the Mammal Society of Japan (http://www.mammalogy.jp/en/guideline.pdf) and the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016). Field work was carried out with the permission of the Ministry of Agriculture and Rural Development, Hanoi, Vietnam.

Analysis of species diversity

We measured species richness of bats at BNBNP as the total number of species captured (*n*). We calculated predicted species richness using the Solow and Polasky (1999) computation method in program Spade (Chao et al. 2016b) and a hypothetical increase in sampling effort that was double the total number of bats captured during 2014–2016. We estimated inventory completeness as the ratio of observed species richness to predicted species richness × 100%. We used program SpadeR (Chao et al. 2016a) to quantify species diversity as the maximum likelihood estimator for the inverse Simpson Index of Diversity (1/D) and expressed evenness of distribution of individuals among species as (1/D)/*n* (Magurran 1988).

Echolocation recording and analysis

We recorded echolocation calls of bats, including individuals that were prepared as voucher specimens, to compare results with the literature on echolocation of bats recorded elsewhere in Asia. Such comparisons may be useful aids to species identification, particularly for cryptic taxa that may be members of species complexes that are not yet well understood (Kruskop 2013; Francis 2019; Wilson and Mittermeier 2019), and can also indicate geographic variation in call structure within species (Ith et al. 2015, 2016). Bats were recorded primarily as they were followed in flight in an enclosure made with mosquito netting (2 m high × 2.5 m wide × 6 m long), but also when hanging freely on the sides of the enclosure or while held in hand if flight did not occur. Recordings of bats in flight in enclosures or in hand are commonly employed for bat surveys in Asia (Kingston et al. 1999; Hughes et al. 2010, 2011; Kingsada et al. 2011), but measurements can be biased compared to recordings of free-flying bats. However, given low capture success for most species and the need for voucher specimens we did not release bats for recordings in the open.

We recorded and analyzed echolocation calls as WAV files using an Echometer EM3 digital ultrasonic recorder (Wildlife Acoustics 2016). The EM3 allows recording at sampling rates of 256 and 384 kHz (providing analysis of calls up to frequencies of about 192 kHz). We analyzed properties of recorded calls in Hanning windows using spectrograms, oscilloscope tracings, and power spectra features of Call Viewer software (Skowronski and Fenton 2008). We analyzed time and frequency characteristics for 12 calls per individual, selecting calls that provided the greatest amount of information. For bats with predominantly frequency modulated (FM), including FM/quasi-constant frequency (FM/Q-CF) calls, we measured (all in kHz) start frequency, end frequency, frequency of maximum energy (FMAXE), midpoint frequency, bandwidth, and duration (ms). For bats with predominantly CF calls (including CF/FM and FM/CF/FM calls) we measured (in kHz) FMAXE, the frequency range of the preceding upsweep (FM rise) if present, and the frequency range of the terminal downsweep (FM tail), as well as the sound duration (ms). We did not measure interpulse intervals because of the confined recording context. We were interested in variation among calls within the species rather than variation among individual bats: for each measure, we provide mean ± 1 standard deviation (*SD*), 95% confidence limits (*CI*) for means, coefficients of variation (*CV*) as percent values (*SD*/Mean × 100), and ranges of calls. We compared consistency of our measurements with published values in the literature for the same species reported from elsewhere in Asia. Values in the literature are reported in a wide variety of ways, sometimes as single values or ranges with no other summary statistics, making such comparisons somewhat qualitative. We emphasized overlap of FMAXE measurements for each species reported elsewhere with those from BNBNP, but provide a detailed summary of previously published call measurements, references, and full summary statistics from our study as Supplementary Tables S2 and S3 to allow readers to make independent judgements. Dissimilar values may indicate possible geographic or habitat variation in echolocation frequencies within species, species identification issues, or evolutionary and taxonomic differentiation requiring future study.

Results

Species richness, diversity, evenness, and general distribution

We captured 211 bats of 27 species in five families (Table 1). Thirteen species were considered rare: nine documented by single captures and four by two captures (Table 1). Eight species provided noteworthy distribution records (provincial or wider): *Sphaerias blanfordi*, *Rhinolophus* cf. *marshalli*, *Hipposideros* cf. *swinhoei*, *Eptesicus pachyomus*, *Kerivoula dongduongana*, *Kerivoula titania*, *Nyctalus* cf. *plancyi*, and *Phoniscus jagorii*; most of these also were rare and represented by just one or two bats captured (Table 1). Among the rare species, six (*R.* cf. *marshalli*, *H.* cf. *swinhoei*, *E. pachyomus*, *K. titania*, *N.* cf. *plancyi*, and *P. jagorii*) have seldom been reported in surveys anywhere within Vietnam (Table 1). Our molecular analyses confirmed identification of eight species with a high level of confidence (≥ 97.9% similarity with sequences published on GenBank) (Supplemental Table S1). One other sample (BNB030) was morphologically similar to *R. lepidus* (Supplemental Table S1), but additional confirmation is required because the *R. lepidus* and *R. pusillus* sequences within GenBank are assigned to specimens that may have uncertainties in their morphological identifications. Future DNA verification also would be useful to confirm our tentative morphological identifications of *R.* cf. *marshalli*, *H.* cf. *swinhoei*, *E. pachyomus*, and *N.* cf. *plancyi*.

Simpson's inverse index of diversity was 7.689 (*CI* 5.973, 9.402) and evenness was 0.285 (*CI* 0.221, 0.348). A hypothetical doubling of numbers of bats captured would result in an additional 8.4 (*CI* 0.0, 18.9) added species, suggesting an inventory completeness of 75.8%. The index of evenness reflected the finding that relatively few species of bats were taken in abundance whereas many species were rarely captured. The six most abun-

Table 1. Families and species of bats documented, number of individuals captured (M = male, F = female, E = escaped), general locations (based on field camps nearest to collection sites; Fig. 1), elevations (mean ± *SD*, 95% *CI*, range) of capture locations, information about geographic distributions within Vietnam, and forest cover categories within 50 m radius of capture sites for each species of bat captured at Bidoup Nui Ba National Park, 2014–2016

Families and species	*n* (M, F)	Camps	Elevation (m)	Published distribution	Forest cover [1]
Pteropodidae					
Cynopterus sphinx [2]	13 (9, 4)	2, 3, 4	1009 ± 324 *CI* 813, 1205 (650–1477)	Includes Lam Dong Province (Kruskop 2013; Kruskop and Abramov 2011)	A (4) B (1) BMF (1) B/C (2) BMF/C (4) MBC/C (1)
Eonycteris spelaea	4 (3, 1)	2	660 ± 6.5 *CI* 650, 670 (650–663)	Includes Lam Dong Province (Kruskop 2013)	BMF (1) BMF/C (3)
Macroglossus sobrinus	3 (1, 2)	2	663 ± 0	Includes Lam Dong Province (Kruskop 2013)	BMF (3)
Megaerops niphanae	2 (0, 2)	4	(1050–1068)	Includes Lam Dong Province (Kruskop 2013)	C/MBC (1) MBC/C (1)
Sphaerias blanfordi	8 (4, 4)	3	1447 ± 5.6 *CI* 1442, 1452 (1444–1456)	New to southern Vietnam and Lam Dong Province (Kruskop 2013)	A (6) B/C (2)
Megadermatidae					
Lyroderma lyra	1 (1, 0)	1	1609	Includes Lam Dong Province (Kruskop 2013; Francis 2019)	B (1)
Rhinolophidae					
Rhinolophus affinis [2]	64 (35, 29)	1, 3, 4	1527 ± 184 *CI* 1481, 1573 (1063–1786)	Includes Lam Dong Province and Bidoup Nui Ba National Park (Kruskop and Abramov 2011; Kruskop 2013; Abramov et al. 2009)	A (7) A/B (1) B (42) C (2) MBC (5) C/MBC (2) MBC/C (2) NR (3)
Rhinolophus lepidus [2]	21 (3, 18)	2, 3	1485 ± 211 *CI* 1389, 1581 (675–1648)	Includes Lam Dong Province and Bidoup Nui Ba National Park (Abramov et al. 2009; Kruskop and Abramov 2011; Kruskop 2013)	A (5) B (15) C (1)
Rhinolophus pusillus	14 (6, 8)	1, 3, 4	1492 ± 131 *CI* 1417, 1567 (1444–1629)	Includes Lam Dong Province (Kruskop 2013)	A (3) B (9) C/MBC (1) NR (1)
Rhinolophus cf. *marshalli*	1 (1)	2	650	*R. marshalli* (*sensu stricto*) new to Lam Dong Province and southern Vietnam (Kruskop 2013; Thong 2012)	BMF (1)
Rhinolophus stheno	6 (3, 3)	3	1639 ± 20 *CI* 1618, 1660 (1600–1656)	Includes Lam Dong Province (Kruskop 2013)	B (6)
Hipposideridae					
Hipposideros galeritus	13 (7, 6)	1, 2, 3	1170 ± 482 *CI* 879, 1652 (670–1648)	Includes Lam Dong Province (Kruskop 2013)	B (7) C (6)
Hipposideros gentilis	1 (0, 1)	1	1589	Includes Lam Dong Province (Kruskop and Abramov 2011; Kruskop 2013)	B (1)
Hipposideros cf. *swinhoei*	1 (0, 1)	3	1444	New to Lam Dong Province (Kruskop 2013). Only one other record in southern Vietnam (Cat Tien National Park; Kruskop and Vasenkov 2016)	A (1)
Vespertilionidae					
Arielulus circumdatus [2]	5 (5, 0)	1,3	1569 ± 72 *CI* 1479, 1659 (1444–1615)	Includes Lam Dong Province and Bidoup Nui Ba National Park (Abramov et al. 2009; Kruskop and Abramov 2011; Kruskop 2013)	A (1) B (3) NR (1)
Eptesicus pachyomus	1 (1, 0)	1	1569	Previously known only from Son La Province, far northern Vietnam (as *E. pachyomus andersoni*; Ruedi et al. 2018; Tu et al. 2017)	B (1)
Kerivoula dongduongana [2]	2 (1, 1)	3, 4	(1058–1444)	New to Lam Dong Province (Tu et al. 2018)	A (1) C/MBC (1)
Kerivoula titania	1 (1, 0)	3	1453	New to Lam Dong Province. Southernmost record in Vietnam (Kruskop 2013, Kuo et al. 2017, Tu et al. 2018)	A/B (1)
Murina cyclotis	1 (1, 0)	2	670	Includes Lam Dong Province (Kruskop 2013)	C (1)
Murina harpioloides	2 (1, 1)	1, 3	(1569–1600)	Includes Lam Dong Province and Bidoup Nui Ba National Park (Abramov et al. 2009; Kruskop and Abramov 2011; Kruskop 2013) Type locality Dalat Plateau (Kruskop and Eger 2008)	B (2)

Table 1. Continued

Families and species	*n* (M, F)	Camps	Elevation (m)	Published distribution	Forest cover[1]
Murina huttoni	11 (6, 5)	1, 3, 4	1472 ± 203 *CI* 1336, 1608 (1077–1656)	Includes Lam Dong Province (Son et al. 2015)	B (6) C (1) B/C (3) C/MBC (1)
Myotis ater	6 (3, 3)	2, 3	1342 ± 329 *CI* 996, 1688 (670–1477)	Includes Lam Dong Province (Kruskop 2013)	B (5) C (1)
Myotis horsfieldii[2]	8 (3, 4, 1E)	3, 4	1379 ± 178 *CI* 1230, 1528 (1077–1506)	Includes Lam Dong Province and BNBNP (Abramov et al. 2009; Kruskop and Abramov 2011; Kruskop 2013)	A (1) B (5) C/MBC (1) MBC/C (1)
Nyctalus cf. *plancyi*	1 (1, 0)	4	1052	New to Lam Dong Province. Very few records elsewhere in Vietnam (Kruskop 2013)	C/A (1)
Phoniscus jagorii[2]	1 (0, 1)	1	1570	New to Lam Dong Province. Very few records elsewhere in Vietnam (Thong et al. 2006; Kruskop 2013)	B (1)
Pipistrellus coromandra[2]	18 (11, 7)	1, 3	1577 ± 85 *CI* 1535, 1619 (1444–1786)	Includes Lam Dong Province and Bidoup Nui Ba National Park (Abramov et al. 2009; Kruskop 2013)	A (1) B (15) MBC (2)
Scotomanes ornatus	2 (1, 1)	3, 4	(1072–1491)	Includes Lam Dong Province and Bidoup Nui Ba National Park; also southernmost locations in Vietnam (Abramov et al. 2009; Kruskop and Abramov 2011; Kruskop 2013)	MBC (1) C/MBC (1)

[1] We characterized vegetation for a 50 m circular radius around each bat capture site as agricultural and disturbed (A), broadleaf forest (B), coniferous forest (C), mixed broadleaf and coniferous forest (MBC), and bamboo and mixed forest (BMF). Where more than one forest category was present at a site, both categories are listed in descending order of abundance and separated by a slash (/), with numbers of individuals captured in each category in parentheses. NR = no coordinates recorded at the capture site.
[2] Identification confirmed by DNA analysis (Supplemental Table S1).

dant species (Table 1) and numbers captured in descending order of abundance were *Rhinolophus affinis* (64), *R. lepidus* (21), *Pipistrellus coromandra* (18), *R. pusillus* (14), *Hipposideros galeritus* (13), and *Cynopterus sphinx* (13). *Cynopterus sphinx*, *H. galeritus*, and *R. lepidus* were documented over a wide range of elevations (Table 1). Most of the sites where 21 of the 27 species were taken included elevations > 1400 m a.s.l. (Table 1). Two of the five species of pteropodids were taken only above 1000 m a.s.l. (Table 1).

Most species of bats were captured at sites in forest cover categories that reflected the intensity of sampling within those categories. Remotely sensed forest categories at 74 sites (including sites where nets or traps were set but no bats were captured) at BNBNP were primarily in broadleaf forest (51; 68.9%, *CI* 57.0%, 78.9%), followed by coniferous with mixed broadleaf and coniferous (8), coniferous (5), agricultural and disturbed (3), agriculture and broadleaf forest (2), and one each in five other categories or combined categories. Except for pteropodids, the proportion of all bats captured were also mostly in broadleaf forest and within the 95% *CI* of the proportion of sites trapped or netted that fell into the broadleaf forest category (Table 2). This was true for bats in all families and for each of the eight species of bats captured most frequently (eight or more captures per species; Tables 1 and 2). The low proportion of pteropodids in this category corresponded to the greater proportions of captures of two species in the agricultural and disturbed cover category: *Sphaerias blandfordi* (6 of 8 or 75.0%, *CI* 35.6%, 95.6%) and *Cynopterus sphinx* (4 of 13 or 30.8%, *CI* 10.4%, 61.1%). The captures of most species of bats including pteropodids were sparsely distributed among a variety of categories and combined categories (Table 1).

Female reproduction: litter size and seasonality of birthing

We examined 94 females of 20 species for evidence of reproduction (Table 3). Pregnancies ($n = 59$) were observed in 14 species, all in March prior to the seasonal rains. Single embryos were recorded in all females examined except for twin embryos in three of four pregnant *Pipistrellus coromandra* and one *Murina huttoni*. Lactating females or volant juveniles were found in eight species during the rainy season (May, June), when no pregnant females were noted (Table 3). Capture of one volant juvenile pteropodid (*Cynopterus sphinx*) provided the only evidence for bat reproduction during the dry season.

Table 2. Proportion of bats captured in the most frequently sampled site category (broadleaf forest). The proportional availability of broadleaf forest among all sites was highest among all categories (68.9%, *CI* 57.0%, 78.9%)

Group or species	*n* bats	*n* captured in broadleaf forest	% in broadleaf forest (95% *CI*)
All bats	206	120	58.2% (*CI* 51.2%, 65.0%)
Pteropodidae	30	1	3.3% (*CI* 0.2%, 19.1%)
Rhinolophidae	106	72	67.9% (*CI* 51.2%, 65.0%)
Rhinolophus affinis	64	42	65.6% (*CI* 52.6%, 76.8%)
Rhinolophus lepidus	21	15	71.4% (*CI* 47.7%, 87.8%)
Rhinolophus pusillus	14	9	64.2% (*CI* 35.6%, 86.0%)
Hipposideridae	15	8	53.3% (*CI* 27.4%, 77.7%)
Hipposideros galeritus	13	7	53.8% (*CI* 26.1%, 79.6%)
Vespertilionidae	58	38	65.5% (*CI* 51.8%, 77.2%)
Murina huttoni	11	6	54.5% (*CI* 24.6%, 81.9%)
Pipistrellus coromandra	18	15	83.3% (*CI* 57.7%, 95.6%)

Table 3. Reproduction information for adult female bats captured in March prior to the rainy season and during the rainy season in May and June at Bidoup Nui Ba National Park, Vietnam

Bat families and species	*n*	March 2015, 2016	May 2015, June 2014
Pteropodidae			
Cynopterus sphinx	4	3 NR, 1 VJM	1 NR
Eonycteris spelaea	1	1 P (rel)	
Macroglossus sobrinus	1	1 P (1 emb)	
Megaerops niphanae	2	2 P (1 emb, 1 ND)	
Sphaerias blanfordi	4	1 P (rel)	3 NR
Rhinolophidae			
Rhinolophus affinis	23	22 P (5-1 emb, 17 rel)	1 L
Rhinolophus lepidus	18	10 P (1 emb each), 1 NR	7 L
Rhinolophus pusillus	8	4 P (1 emb each), 1 NR	3 ND
Rhinolophus stheno	3	3 P (1 emb each)	
Hipposideridae			
Hipposideros galeritus	6	4 P (1 emb each), 1 NR	1 L
Hipposideros pomona	1	0	1 NR
Hipposideros cf. *swinhoei*	1	0	1 L
Vespertilionidae			
Kerivoula dongduongana	1	1 P (1 emb)	
Murina harpioloides	1	1 NR	
Murina huttoni	5	1 P (2 emb)	1 L, 3VJF, 1 VJM
Myotis ater	3	3 P (2-1 emb, 1 ND)	
Myotis horsfieldii	3	1 P (1 emb), 1NR	1 L
Phoniscus jagorii	1	0	1 VJF
Pipistrellus coromandra	7	5 P (3-2 emb each, 1 emb-1, rel-1)	2 L
Scotomanes ornatus	1	1 NR	

Abbreviations: L = lactating, M = male, F = female, *n* = number of females examined, ND = not determined, NR = not reproductive, rel = released without dissection, emb = embryos, P = pregnant, VJ = volant juvenile.

Table 4. Descriptive statistics ($\bar{X} \pm SD$, range) for echolocation calls of frequency modulated (FM) and FM/quasi-constant frequency (Q-CF) emitting species of bats recorded at Bidoup Nui Ba National Park (BNBNP) in comparison with echolocation data reported from other locations in Asia

Species	*n* bats	*n* calls	Start frequency (kHz)	End frequency (kHz)	Frequency of maximum energy (kHz)	Midpoint frequency (kHz)	Duration (ms)	Bandwidth (kHz)	Locations with echolocation calls generally consistent with BNBNP	Locations with echolocation calls not consistent with BNBNP
Arielulus circumdatus	4	48	74.6 ± 3.2 (69.6–81.7)	33.6 ± 2.4 (29.0–38.4)	51.3 ± 4.3 (39.5–67.3)	54.1 ± 2.0 (50.8–59.0)	1.7 ± 0.4 (1.0–2.7)	41.0 ± 4.0 (33.3–48.4)	China (Guangdong)[1]	Vietnam (unspecified, BNBNP)[2,19]
Eptesicus pachyomus	1	12	60.5 ± 3.8 (55.7–66.7)	25.7 ± 0.8 (24.3–27.4)	47.1 ± 1.0 (44.8–48.3)	43.1 ± 2.0 (40.0–46.4)	3.1 ± 0.9 (1.7–4.2)	34.7 ± 3.8 (30.1–40.7)	None found	None found
Kerivoula titania	1	12	189.6 ± 3.2 (183.6–191.5)	74.4 ± 5.3 (63.6–84.3)	131.2 ± 6.4 (121–138)	132.0 ± 3.4 (127–136)	3.5 ± 0.3 (2.9–4.0)	115.2 ± 5.5 (107.2–127.9)	Thailand[3]	None found
Murina cyclotis	1	12	160.1 ± 6.4 (144.9–165.2)	61.1 ± 3.8 (55.4–65.5)	114.7 ± 25.6 (70.8–143.5)	110.6 ± 2.7 (105–114)	2.6 ± 0.6 (1.6–3.3)	99.0 ± 9.0 (79.9–107.9)	Thailand[4,5,6,7] Malaysia (peninsular)[8,9,11] India (Karnataka)[10] Vietnam (Quang Ngai)[12]	None found
Murina harpioloides	1	12	163.8 ± 6.4 (152.8–172.9)	65.7 ± 2.7 (61.4–69.6)	122.5 ± 15.1 (99.5–138.4)	114.8 ± 3.2 (110– 121)	1.6 ± 0.4 (1.3–2.8)	98.2 ± 7.4 (85.9–109.4)	None found	None found
Murina huttoni	9	108	151.5 ± 5.3 (149.5–161.1)	56.4 ± 3.4 (50.0–64.3)	108.9 ± 15.7 (75.2–141.5)	104.0 ± 3.0 (96.5–110.5)	2.5 ± 1.2 (1.3–6.0)	95.2 ± 6.5 (74.9–106.2)	None found	China (Guangdong)[13]
Myotis ater	3	36	100.8 ± 10.6 (83.7–121.1)	45.65 ± 1.2 (36.3–56.5)	59.7 ± 4.9 (51.4–70.7)	73.2 ± 6.3 (62.7–86)	4.9 ± 3.2 (1.7–14.3)	55.1 ± 13.0 (28.4–80.7)	Vietnam (Bac Kan)[14] Vietnam (Quang Ngai)[12]	None found
Myotis horsfieldii	5	60	103.2 ± 10.6 (78.5–122.9)	43.8 ± 3.7 (37.7–51.7)	64 ± 7.2 (54.9–101.8)	73.5 ± 5.9 (60.5–80.9)	3.2 ± 0.7 (1.7–4.9)	59.4 ± 10.6 (35.9–85.2)	Vietnam (unspecified)[2] India (Andaman Islands)[15] Thailand[7] India (Tamil Nadu)[18]	None found
Nyctalus cf. *plancyi*	1	12	52.6 ± 0.9 (51.4–54.0)	24.1 ± 1.1 (22.3–26.4)	45.4 ± 0.6 (44.1–45.9)	38.4 ± 0.9 (36.9–40.2)	1.6 ± 0.1 (1.4–1.8)	28.5 ± 1.1 (27.2–30.4)	No comparisons made	No comparisons made
Phoniscus jagorii	1	12	158.9 ± 13.7 (147.6–185.3)	83.0 ± 2 .4 (79.3–88.2)	100.0 ± 2.0 (97.6–103.6)	121.0 ± 6.5 (116–132)	2.5 ± 0.3 (2.1–3.1)	75.9 ± 14.9 (59.6–106.0)	Malaysia (peninsular)[8,9,11]	Thailand[6,17]
Pipistrellus coromandra	7	84	88.3 ± 7.1 (76.3–105.5)	36.8 ± 2.4 (32.4–43.3)	48.8 ± 5.8 (40.4–69.7)	62.5 ± 4.3 (55.8–73.9)	2.4 ± 0.6 (1.3–4.4)	51.5 ± 6.2 (40.4–63.3)	India (Karnataka)[10] India (Andaman Islands)[15] Vietnam (unspecified)[2]	None found
Scotomanes ornatus	2	24	87.0 ± 9.4 (73.4 – 103.5)	38.3 ± 5.2 (30.8–46.9)	58.5 ± 8.2 (43.5–68.3) 2nd harmonic	62.7 ± 6.8 (53.9–74.5)	2.1 ± 0.4 (1.4–3.0)	48.6 ± 6.7 (38.6–65.1)	China (Mianyang, Sichuan)[16] Vietnam (Bac Kan,1[st] harmonic)[14] Vietnam (Quang Ngai)[12] Vietnam (BNBNP, 1[st] harmonic)[2,19]	None found

All calls were recorded from bats in flight at night within the enclosure described in Materials and methods, except *Nyctalus* cf. *plancyi* (hand-held only). See Supplementary Table S2 for more detailed information on call measurements as reported in the literature.

[1] Zhang et al. 2014; [2] Kruskop 2013; [3] Douangboubpha et al. 2016; [4] Soisook 2013; [5] Soisook et al. 2013; [6] Phommexay 2009; [7] Hughes et al. 2011; [8] Schmieder et al. 2010; [9] Schmieder et al. 2012; [10] Raghuram et al. 2014; [11] Kingston et al. 1999; [12] Son et al. 2016; [13] Zhou et al. 2011; [14] Furey et al. 2009; [15] Srinivasulu et al. 2017; [16] Liu et al. 2011; [17] Thong et al. 2006; [18] Wordley et al. 2014; [19] Abramov et al. 2009.

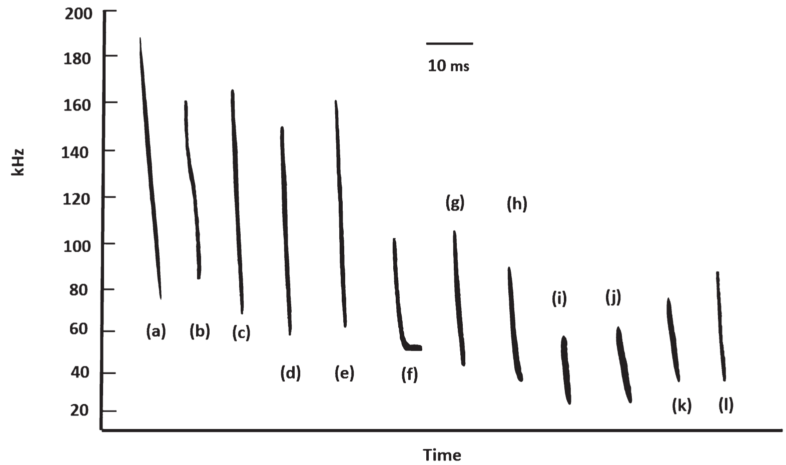

Fig. 2. Shapes of calls from time-frequency spectrograms of bat species that emit frequency modulated (FM) and FM/quasi-constant frequency (Q-CF) ultrasonic echolocation calls as recorded at Bidoup Nui Ba National Park, Vietnam. All calls except *Nyctalus* cf. *plancyi* (hand-held) were recorded from bats in flight at night within the enclosure described in Materials and methods. Species are (a) *Kerivoula titania*, (b) *Phoniscus jagorii*, (c) *Murina harpioloides*, (d) *Murina huttoni*, (e) *Murina cyclotis*, (f) *Myotis ater*, (g) *Myotis horsfieldii*, (h) *Pipistrellus coromandra*, (i) *Nyctalus* cf. *plancyi*, (j) *Eptesicus pachyomus*, (k) *Arielulus circumdatus*, and (l) *Scotomanes ornatus* (second harmonic).

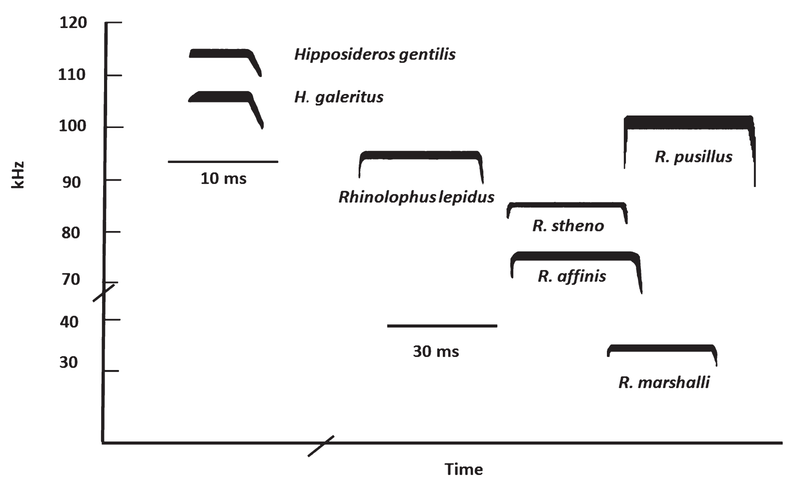

Fig. 3. Shapes of calls from time-frequency spectrograms of bat species that emit constant frequency (CF), frequency modulated (FM)/CF, and FM/CF/FM ultrasonic echolocation calls as recorded at Bidoup Nui Ba National Park, Vietnam. All calls were recorded from bats in flight at night within the enclosure described in Materials and methods.

Echolocation

We recorded calls of 19 species of bats. Twelve species were FM or FM/Q-CF emitting bats (Table 4, Fig. 2). Echolocation call characteristics for two of these species (*Eptesicus pachyomus* and *Murina harpioloides*) to our knowledge have not been previously reported. Calls of two other species (*Kerivoula titania* and *M. huttoni*) have been recorded previously only at single locations in Asia; calls of *K. titania* at BNBNP are consistent with those recorded in Thailand whereas those of *M. huttoni* are not consistent with calls recorded in China (Table 4, Supplementary Table S2). The calls of the remaining eight FM or FM/Q-CF emitting species are generally consistent with those recorded by others at most other locations in Asia (Table 4, Supplementary Table S2).

We recorded echolocation calls of seven species of CF, CF/FM, or FM/CF/FM emitting rhinolophid and hipposiderid bats captured at BNBNP (Table 5, Fig. 3). Variation in FMAXE was low compared to other acoustic measurements (*CV* 0.3–1.4%, Supplementary Table S3). Comparisons with measurements of the same species made at many other locations in Asia are consistent with

Table 5. Descriptive statistics ($\bar{X} \pm SD$, range) for echolocation calls of constant frequency (CF), frequency modulated (FM)/CF, and FM/CF/FM emitting species of bats recorded at Bidoup Nui Ba National Park (BNBNP), Vietnam in comparison with echolocation data reported from other locations as reported in the literature

Species	*n* bats	*n* calls	CF component FMAXE (kHz)	FM rise (kHz)	FM tail (kHz)	Duration (ms)	Locations with echolocation measures consistent with BNBNP	Locations with echolocation measures not consistent with BNBNP
Hipposideros galeritus	9	108	106.9 ± 1.4 (102.4–109.0)	0	11.8 ± 2.4 (4.1–16.8)	6.6 ± 1.6 (4.6–14.3)	Vietnam (Cat Tien NP)[1]; Lao PDR[2]; Cambodia[3]; Malaysia (Sabah)[2,4]; India (Telangana and Karnataka)[5]	Thailand[6]; Malaysia (peninsula)[2,4]; India (Karnataka)[7]
Hipposideros gentilis	1	12	114.5 ± 0.4 (113.5–114.8)	0	17.7 ± 1.1 (16.6–19.8)	6.5 ± 0.6 (5.5–7.4)	None found	As *H. pomona*: Malaysia (peninsular)[8]; Thailand[36]; Myanmar[38]; Lao PDR[2,4]China[9]; Hong Kong[37]
Rhinolophus affinis	13	156	74.2 ± 1.0 (72.6–75.5)	10.6 ± 4.3 (1.9–20.0)	18.9 ± 2.4 (9.8–24)	35.6 ± 7.5 (17.5–54.4)	Vietnam (Cat Ba NP)[10]; Vietnam (Tam Do NP)[10] Vietnam (BNBNP)[11]; Vietnam (Bac Kan)[12]; Vietnam (Quang Ngai)[16]; Cambodia[3,13]; Lao PDR[2,4]; China (Hainan, Guangdong, Guangxi, Fujian)[9]; Malaysia (peninsula)[2,4,15,19,20]; Indonesia (Sumatra, Lombok)[19,35]; Thailand[14,19,20,26]; China (Hong Kong)[37]	Vietnam (Cat Tien NP)[1,17]; Vietnam (Kon Tum)[17]; Vietnam (Vu Quang, Langbian Plateau); China (Jiangxi, Yunnan)[9,33]; China (unspecified)[18]; Malaysia (Sarawak)[19]; Java[19], Thailand[6], Thailand (Tarutao islands)[19], Thailand (Koh Surin, Phang Nga)[19], Borneo[19]
Rhinolophus lepidus	6	72	93.7 ± 1.3 (91.5–96.8)	9.8 ± 4.8 (0–16.2)	15.4 ± 3.6 (4.2–22.0)	34.3 ± 10.1 (14.3–51.3)	China (Yunnan)[9,30,31]; India (Karnataka)[7]; India (Tamil Nadu)[22], Thailand[14]	China (unspecified)[18]; Malaysia (peninsula, Tioman Island)[2,4,15,20,28]; Singapore[21]; Thailand[6]; India (unspecified, Delhi)[27,29]
Rhinolophus cf. *marshalli*	1	12	34.1 ± 0.2 (33.7–34.6)	4.1 ± 1.4 (2.6–6.1)	7.0 ± 2.2 (4.7–10.1)	29.7 ± 1.4 (27.5–31.4)	None found	China (unspecified)[18]; China (Yunnan, Guangxi)[9,23]; Vietnam (Cat Ba, other)[24,34]; Lao PDR[2]
Rhinolophus pusillus	6	72	100.1 ± 0.9 (98.9–103.5)	11.0 ± 4.1 (2.0–21.5)	17.6 ± 5.6 (5.0–37.3)	35.4 ± 7.2 (18.6–48.8)	Vietnam (Quang Ngai)[16]; Vietnam (Bac Kan)[12]; Vietnam (Tam Do NP)[10]; Lao PDR[4]; China (multiple locations)[9]; China (Yunnan)[25,31]; China (Hong Kong)[37]	Vietnam (Cat Tien NP)[1]; Vietnam (Cat Ba NP)[10]; Thailand[6,26,27]; Lao PDR[2]; Cambodia[3]; China (Beijing, Guangxi)[9]; China (unspecified)[18]; China (10 locations)[25]; Indonesia (Lombok)[35]
Rhinolophus stheno	5	60	84.7 ± 0.6 (83.6–85.4)	11.1 ± 3.8 (2.1–20.2)	17.7 ± 4.4 (5.2–26.0)	33.9 ± 8.6 (15.5–48.6)	Vietnam (Cat Tien NP)[1]; Malaysia (peninsula)[2,4,15,20]; Thailand[6,14,26,27,32]; China (Yunnan)[9]	Vietnam (Bac Kan)[12]; Lao PDR (as *R. microglobosus*)[2]; Cambodia (as *R. microglobosus*)[3]; Thailand (as *R. microglobosus*)[6]

All calls recorded from bats in flight at night within the enclosure described in Materials and methods. See Supplementary Table S3 for more detailed information on call measurements reported in the literature.

Sources of information on locations of recordings: [1] Thong 2015; [2] Francis 2008, 2019; [3] Phauk et al. 2013; [4] Francis and Habersetzer 1998; [5] Srinivasulu et al. 2015; [6] Hughes et al. 2010; [7] Raghuram et al. 2014; [8] Murray et al. 2018; [9] Zhang et al. 2009; [10] Thong 2014; [11] Abramov et al. 2009; [12] Furey et al. 2009; [13] Kingsada et al. 2011; [14] Phommexay 2009; [15] Kingston et al. 2000; [16] Son et al. 2016; [17] Thong 2011; [18] Wu et al. 2015; [19] Ith et al. 2015, 2016; [20] Heller and von Helversen 1989; [21] Pottie et al. 2005; [22] Wordley et al. 2014; [23] Liu et al. 2009; [24] Thong et al. 2007; [25] Jiang et al. 2010; [26] Robinson 1996; [27] Soisook et al. 2016; [28] Chua and Aziz 2019; [29] Mishra et al. 2018; [30] Li et al. 2014 ; [31] Shi et al. 2009; [32] Soisook et al. 2008; [33] Jiang et al. 2008; [34] Kruskop 2013; [35] McKenzie et al. 1995; [36] Douangboubpha et al. 2010; [37] Shek and Lau 2006; [38] Struebig et al. 2005.

those from CF bats at BNBNP, However, FMAXE of echolocation calls from some locations differ substantially from calls we report for BNBNP. These include reported FMAXE outside of the statistical ranges recorded at BNBNP (Supplementary Table S3) for *Hipposideros galeritus* (study areas in India, peninsular Malaysia, and Thailand), *Rhinolophus affinis* (Borneo, Cambodia, Java, Indonesia, and study areas within China, Malaysia, Thailand, and Vietnam), *R. lepidus* (Thailand, and study areas within China, India, and peninsular Malaysia), and *R. pusillus* (Cambodia, Indonesia, Thailand, and study areas in China, Lao PDR, and Vietnam). Echolocation calls of one species with morphological uncertainties to identification (*R.* cf. *marshalli*) and the single *H. gentilis* are unlike reports from elsewhere (Table 5). Inconsistencies among reports regarding FMAXE of *R. stheno* are likely attributable to species differences with *R. microglobosus* (see Materials and methods).

Discussion

We captured 20 species of bats not previously reported from BNBNP. Abramov et al. (2009) documented 13 species of bats in a preliminary survey of the park. Seven of these species also were taken in our study, three of which were among the most abundant species in both studies: *Rhinolophus affinis*, *R. lepidus*, and *Pipistrellus coromandra*. Four other species (*Arielulus circumdatus*, *Murina harpioloides*, *Myotis horsfieldii*, and *Scotomanes ornatus*) were also taken in both surveys but were less common. No species of fruit bats were recorded by Abramov et al. (2009). Six species documented by Abramov et al. (2009) but not taken during our survey were *Hipposideros armiger*, *Coelops frithii*, *Myotis muricola*, *M. phanluongi*, *Harpiocephalus harpia*, and *Miniopterus magnater*. These species were rare in the earlier study, with five species documented by single captures and one captured twice (Abramov et al. 2009). Our sampling was biased towards species that use habitats lower to the ground, and species that forage at or above canopy level may have been missed.

At least 33 species of bats in five families have now been documented at BNBNP. This is a moderately high species richness among the parks and other nature reserves in Vietnam. Several studies have reported inventories of bats in parks and reserves that recorded 12 to 24 species (Hendrichsen et al. 2001; Son et al. 2016; Tu et al. 2016) although these varied in completeness and intensity. Studies of six other areas have documented 30 or more species of bats. Thong (2015) reported 47 species at the well-surveyed Cat Tien National Park in southern Vietnam, noting that seven of these needed modern taxonomic confirmation, whereas others may represent members of species complexes not yet recognized. Hendrichsen et al. (2001) reported 32 to 39 species at three national parks in karst areas of northern Vietnam: Phong Nha-Ke Bang, Cuc Phuong, and Pu Mat. Minh et al. (2011) documented 43 species in Pu Mat National Park. Records of 39 species were compiled for Hong Lien Son National Park and surrounding areas in northern Vietnam (Kruskop and Shchinov 2010). Furey et al. (2010) captured 36 species in five families with 694 captures at the karst-dominated landscape at Kim Hy Nature Reserve in northern Vietnam. The Kim Hy study was based on nearly 40 000 m^2 h combined net and harp trap sampling systematically throughout the year. Six more species were confirmed at Kim Hy Nature Reserve by additional studies, increasing the total to 42 (Furey et al. 2010). We have no doubt that further research will increase the number of known species from BNBNP. Predicted species richness estimates based on doubling of the sample size in our survey suggested an additional 8–9 species of bats [totaling 35 to 36 species without those documented by Abramov et al. (2009)], but with an upper 95% confidence limit of 19 additional species. Kruskop and Abramov (2011) suggested that four species of bats not documented by Abramov et al. (2009) were known from surrounding areas and were likely to occur in BNBNP. Two of these were detected in our survey [*Cynopterus sphinx* and *Hipposideros gentilis*, reported as *H. pomona* in Kruskop and Abramov (2011)] but two have not yet been captured within the park (*H. larvatus* and *Miniopterus fuliginosus*).

Similar to Cat Tien National Park but unlike reserves in northern Vietnam, BNBNP does not have an extensive karst substrate (Gillieson 2005). BNBNP therefore has fewer roosting opportunities for cave-obligate species of bats. However, the variation in roosting habits of Vietnamese bats reported mostly from caves is not well known. Some species of bats in Vietnam considered to be cave dwellers also will roost in rock crevices (*Rhinolophus affinis*; Kruskop 2013), hollow trees, and foliage. Kruskop (2013) and Francis (2019) described many species documented at BNBNP as known to roost in hollow trees (e.g., *Coelops frithii*, *Cynopterus sphinx*, *R. affinis*, *R. pusillus*, *R. stheno*, *Kerivoula dongduongana*, *Myotis ater*, *Nyctalus* cf. *plancyi*) or in foliage (e.g., *C. sphinx*, *Macroglossus sobrinus*, *K. dongduongana*, *Myotis muricola*, *M. ater*, *Murina cyclotis*, *Pipistrellus coromandra*, *R. pusillus*, *Scotomanes ornatus*). All of the species we documented are known to inhabit forested areas (Kruskop 2013). The faunal affinities of the species found at BNBNP are mixed, ranging from Indonesian and Malaysian elements to Himalayan and Palearctic species (Kruskop 2013). The higher elevation landscapes of BNBNP make this park suitable habitat for species that are tolerant of cooler temperatures; many of the species of bats at BNBNP are known to utilize forested habitats at mid to higher elevations elsewhere in Vietnam (Kruskop 2013). Future research should seek to determine if bat distributions follow elevational differences at BNBNP, or if our observations on elevational differences among species simply reflect biases in local abundance due to sampling effort or proximity of roosts at sampling locations. Similarly, additional sampling combined with extensive ground-truthing of vegetation where bats have been documented will be required to determine if some species of bats are found disproportionately in any particular vegetation type. Our measurement and analysis of forest cover was insufficient to conclusively make such distinctions.

Like many areas in southeast Asia, the Dalat Plateau has an annual pattern of predictable wet and dry seasons. In our area March marks the terminus of the winter dry season, with the summer rains beginning in April and persisting through October (Pham-Thanh et al. 2019). We found that the insectivorous bats at BNBNP show a reproductive phenology wherein pregnancy is seen in many of our samples from March, with lactation and the presence of volant juveniles but no pregnancies evident in June. This pattern of late dry season pregnancies and wet season production of young is common in insectivorous bats from many other tropical parts of the world (Fleming et al. 1972; Bernard and Cumming 1997; Racey and Entwistle 2000), with increasing evidence for similar patterns now accumulating from different study areas in Vietnam (Furey et al. 2011; Kruskop 2013; Son et al. 2016). Future bat community surveys elsewhere in Vietnam should attempt to include both seasons in their sampling to further verify this pattern. Determination of litter size is also important demographic information rarely reported for many southeast Asian bats, as evidenced by our seemingly unusual finding of twin embryos in *Murina huttoni*.

Southeast Asian bats can contain complexes of morphologically similar species that may be distinguishable in part based on divergence in fundamental aspects of their ultrasonic calls (Francis 2008). For example, in Vietnam *Rhinolophus pusillus* and *R. lepidus* are thought to be part of "an extremely tangled" species complex that has not been fully resolved (Kruskop 2013: 124). At BNBNP morphological examination with limited DNA confirmation suggested that the frequency of maximum energy in echolocation calls do not overlap between these two species (Table 5, Supplementary Table S3). The patterns in echolocation traits we found, however, are not consistent within species across studies from different locations (Table 5), suggesting the need for further taxonomic and acoustic study of these two species. The possibility of cryptic species diversity based on echolocation calls also cannot be ruled out for some of the other species we recorded that show distinct differences across locations. Two possible examples from our study at BNBNP include the *Hipposideros gentilis* and *R.* cf. *marshalli* (Table 1). In other cases, significant variability in echolocation patterns can occur within species. For example, both geographic and habitat variability occur in the echolocation calls of *R. affinis* throughout its southern range (Ith et al. 2015, 2016). The possibility of geographic and habitat variability in echolocation calls also cannot be ruled out for some of the species we recorded at BNBNP that were distinct from reports in the literature. Incorporation of descriptive patterns in echolocation calls will be a necessary adjunct to all bat community surveys in Vietnam and elsewhere in southeast Asia to help unravel the sources in variation of echolocation calls apparent from the literature.

Supplementary data

Supplementary data are available at *Mammal Study* online.

Supplementary Table S1. Results of genetic comparisons using 685 bps of Cytochrome c oxidase subunit 1 (COI)

Supplementary Table S2. Echolocation call characteristics of bats with frequency modulated (FM) and FM/quasi-constant frequency (Q-CF) emitting calls recorded at Bidoup Nui Ba National Park, Vietnam, in comparison with calls of the same species as reported elsewhere in Asia

Supplementary Table S3. Echolocation call characteristics of constant frequency (CF), frequency modulated (FM)/CF, and FM/CF/FM emitting bats recorded at Bidoup Nui Ba National Park, Vietnam, in comparison with calls of the same species as reported elsewhere in Asia

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