



## New Data on Distribution, Morphology and Echolocation of *Hipposideros khaokhouayensis* Guillén-Servent & Francis, 2006 (Chiroptera: Hipposideridae)

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**Abstract:** *Hipposideros khaokhouayensis* is a globally rare and vulnerable species. Since information about its distribution and echolocation was very limited, the author conducted a series of bat surveys in northwestern Vietnam with an emphasis on this species between 2022 and 2023. Bats were captured using harp traps and mist nets then identified in the field based on their morphological diagnoses. Echolocation calls were recorded under three different situations (free-flying while emerging from caves, handheld, and flying within a flight tent) using the PCTape system. A colony of the species was discovered in Son La Province. The adults of this colony were found to be considerably larger than all individuals described in previous publications. The species emits multiharmonic calls with the most energy in the second harmonic. Each usual call comprises two components: a constant-frequency (CF) component followed by a downward frequency-modulated terminal sweep (tFM). Special calls, which were not mentioned in any literature, were recorded in-between usual calls. Each special call comprises three distinct components: an upward frequency-modulated initial sweep (iFM) followed by a CF and a tFM. The frequency of the CF component and the pulse duration of the adult bats from Son La Province are higher and longer than those in published descriptions. The present study results indicate that *H. khaokhouayensis* emits a single call or calls in groups up to seven signals. The new distributional record, morphological features and echolocation characteristics demonstrated herewith, provide essential information for monitoring and conservation of this vulnerable species at national and international scales.

**Key words:** bat, biodiversity, distribution, echolocation, special calls

### Introduction

Phou Khao Khouay leaf-nosed bat *Hipposideros khaokhouayensis* Guillén-Servent & Francis, 2006 was first described from Phou Khao Khouay National Park in Lao People's Democratic Republic (Lao PDR) (GUILLÉN-SERVENT & FRANCIS 2006). The species has been listed as Vulnerable (VU) in the IUCN Red List of Threatened Species (DOUANGBOUBPHA 2019). Due to limited published records, *Hipposideros khaokhouayensis* was even misunderstood

as a species endemic to Lao PDR (TUNEU-CORRAL 2019). In fact, both Lao PDR and Vietnam are native countries for this species (THONG & FUREY 2008, THONG et al. 2008, ABRAMOV & KRUSKOP 2012, KRUSKOP 2013, THONG et al. 2016, DOUANGBOUBPHA 2019, THONG et al. 2020, THONG et al. 2021). The first record of *H. khaokhouayensis* from Vietnam was published by THONG et al. (2008). Before the present study, the species was still rarely documented with few published records throughout its distributional range including the type locality in

Lao PDR and the Cat Ba National Park in Vietnam (THONG & FUREY 2008, THONG et al. 2008, ABRAMOV & KRUSKOP 2012, THONG et al. 2016, THONG et al. 2021). Remarkably, almost all previous studies just focused on taxonomy and conservation status of the species. Only the CF value and pulse duration were included in several publications (GUILLÉN-SERVENT & FRANCIS 2006, THONG et al. 2021). Between 2022 and 2023, the author conducted a series of field surveys in different localities in northwestern Vietnam with an emphasis *H. khaokhouayensis*. This paper provides a detailed description of echolocation calls with first records of special signals and new distributional and morphological information of the species.

## Materials and Methods

### Bat capture and identification

Six field surveys were conducted in Son La Province, northwestern Vietnam: between 2022 and 2023. Mist nets of 6.0 m (height)  $\times$  9.0-12.0 m (length), mesh size 16  $\times$  16 mm and four-bank harp traps (FRANCIS 1989) were used to capture bats. They were set up in front of caves and under the canopy of plantation and natural vegetation (Fig. 1).

Bats were captured and handled following guidelines recommended by the American Society

of Mammalogists (SIKES & GANNON 2011, SIKES R.S. & ACUCASM 2016). Each netted or trapped bat was carefully removed then examined in reproductive status and age following RACEY (2009) and BRUNET-ROSSINNI & WILKINSON (2009). Morphological measurements of each adult captured individual were measured for identification in a comparison with data of the species in previous publications (GUILLÉN-SERVENT & FRANCIS 2006, THONG et al. 2008, ABRAMOV & KRUSKOP 2012, KRUSKOP 2013, THONG et al. 2016, THONG et al. 2021). Seven external measurements were taken using a digital callipers (ABSOLUTE Coolant Proof Calliper Series 500, Mitutoyo America Corporation, Illinois 60502, IL, USA) to the nearest 0.1 mm: FA, forearm length - from the extremity of the elbow to the extremity of the carpus with the wings folded; EH, ear height - length of ear conch; EW, ear width - the greatest width of ear conch; NL, anterior nose-leaf width - the greatest width of the anterior leaf; Tail, tail length - from the anal opening to the tip of the tail; TIB, tibia length - from the knee joint to the ankle; HF, hind-foot length - from the extremity of the heel behind the os calcis to the extremity of the longest digit, excluding the hairs or claws. Photographs were taken before released at the capture sites. Data from juveniles were excluded from analyses to reduce the influence of age variations.



**Fig. 1.** A four-bank harp trap set up under the canopy of natural vegetation nearby Tham Village, Tong Lanh Commune, Thuan Chau District, Son La Province, northwestern Vietnam.

### Echolocation recordings and analyses

Echolocation recordings and analyses were carried out in the field following THONG (in press). Calls were recorded using the PCTape system (480 kHz, 16 bit) at three different situations: emerging from caves, handheld, and flying inside a flight tent [5 m (width), 5 m (length), 3 m (height)]. Batman software, which displays colour sonograms of the detected echolocation signals in real-time, was used to obtain high-quality sound sequences. Selected sound sequences were subsequently analysed using the Selenia software. The PCTape, Batman and Selenia are all custom-made programs (version May 2008) developed by the University of Tübingen, Germany. As a hipposiderid bat species, Phou Khao Khouay leaf-nosed bat uses multiharmonic echolocation calls with the highest energy in the second harmonic. Its calls were described following Tian and Schnitzler (TIAN & SCHNITZLER 1997). Each entire harmonic of usual calls comprises two components: constant-frequency (CF) followed by a downward frequency-modulated terminal sweep (tFM). A number of special calls, which comprises three components [an upward frequency-modulated initial sweep (iFM) followed by a CF and a tFM], were recorded over the surveys. Selected recordings were displayed as sonograms with an FFT (Fast Fourier Transformation) of 256, Hann-window, and zero-padding. Six following sound parameters of the second harmonic of usual calls [CF frequency, tFM frequency, tFM bandwidth, CF duration, tFM duration, pulse duration] and three additional sound parameters (iFM frequency, iFM bandwidth

and iFM duration) of the special calls were measured. The iFM frequency, iFM bandwidth, CF frequency, tFM frequency and tFM bandwidth were measured in kilohertz (kHz) while iFM duration, CF duration, tFM duration, and pulse duration were measured in milliseconds (ms).

## Results

### New distributional and morphological records

Eight individuals of *H. khaokhouayensis* were captured at an unnamed natural vegetation area near Tham Village, Tong Lanh Commune, Thuan Chau District, Son La Province, Vietnam (21°25'26.93"N, 103°44'44.02"E, 569.3 meters above sea level). Two of those individuals were juvenile females while six other individuals including three males and three females were adult. None of these adults was reproductively active. These new records considerably extend the species' distributional range northwards. The captured individuals clearly demonstrated the diagnostic morphological features of *H. khaokhouayensis* as follows: the noseleaf is narrow with an expanded internarial septum which forms an oval disc-like shape; no supplementary leaflets under the anterior leaf; lateral margins of the posterior and anterior leaves are connected at their bases (Fig. 2). There is a narrow median emargination on the frontal margin of the anterior leaf. Ears are broad with blunt tips. The pelage colour of the adult individuals varies between light grey-brown and dark brown whereas the juveniles' pelage is dark grey. Exter-



Fig. 2. Lateral (left) and frontal (right) views of a *H. khaokhouayensis* from Son La Province.

**Table 1.** Seven external measurements (in mm) of the six captured adults from Son La Province. Data are presented as sample size (n), mean  $\pm$  standard deviation and range (minimum-maximum). For abbreviations, see Materials and Methods.

| n | Sex | FA                          | EH                          | EW                          | NL                       | Tail                        | TIB                         | HF                       |
|---|-----|-----------------------------|-----------------------------|-----------------------------|--------------------------|-----------------------------|-----------------------------|--------------------------|
| 3 | ♂♂  | 47.5 $\pm$ 3.8<br>44.1-51.6 | 27.4 $\pm$ 1.5<br>25.8-28.6 | 18.8 $\pm$ 1.0<br>17.9-19.8 | 6.3 $\pm$ 0.5<br>5.9-6.8 | 35.8 $\pm$ 1.0<br>35.1-36.9 | 19.4 $\pm$ 1.0<br>18.6-20.5 | 5.9 $\pm$ 0.4<br>5.6-6.3 |
| 3 | ♀♀  | 47.7 $\pm$ 2.7<br>45.1-50.5 | 27.4 $\pm$ 1.3<br>25.9-28.2 | 18.7 $\pm$ 0.6<br>18.1-19.2 | 6.2 $\pm$ 0.1<br>6.1-6.3 | 35.5 $\pm$ 0.3<br>35.3-35.9 | 19.3 $\pm$ 0.5<br>18.9-19.8 | 6.0 $\pm$ 0.2<br>5.8-6.2 |

nal measurements of the six captured adults show no sexual difference (Table 1). One male and one female from Son La Province appear as the largest known individuals of this species.

### New acoustic records with special signals

The usual calls of *H. khaokhouayensis* comprise a typical “CF-FM” signal structure of a hipposiderid bat species (Fig. 3). In usual calls, the values of CF frequency, tFM frequency, tFM bandwidth are in ranges of 91.8-94.4 kHz, 76.6-83.6 kHz, 8.5-16.9 kHz, whereas CF duration, tFM duration, pulse duration are in ranges of 4.5-8.3 ms, 0.8-1.7 ms, 5.3-9.7 ms, respectively (Tables 2). Remarkably, its special calls, which comprise three components (iFM, CF, tFM), were recorded while an observed individual was flying through a narrow cave mouth (Fig. 4). In these special calls, iFM frequency, iFM bandwidth, CF frequency, tFM frequency and tFM bandwidth are in ranges of 79.8-85.5 kHz, 8.9-14.6 kHz, 94.2-94.4 kHz, 79.4-80.3 kHz and 14.1-15.0 kHz, respectively whereas iFM duration, CF duration, tFM duration, and pulse duration are in ranges of 0.5-1.9 ms, 5.8-6.3 ms, 1.0-1.3 and 7.6-9.0 ms (Table 2).

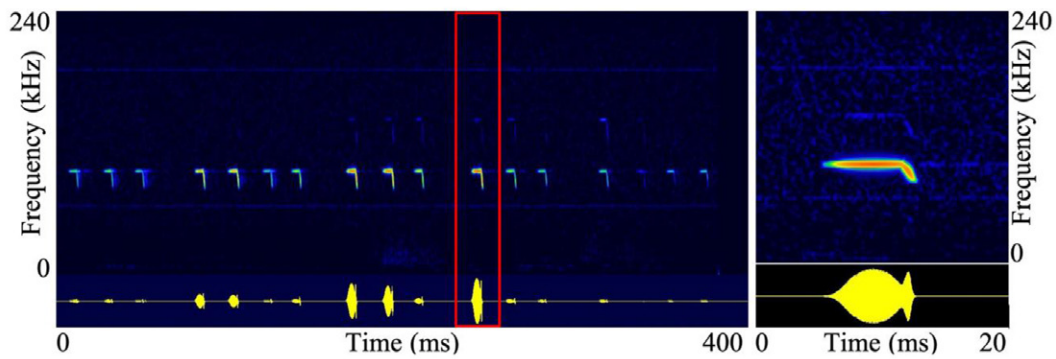
The bat in Fig. 3 emitted 5 groups of either 3 or 4 CF-tFM signals most likely in the rhythm of the wing beat. The bat in Fig. 4 emitted a long group of many CF-tFM signals which ended with a special iFM-CF-tFM call and was followed by two single calls with an interval of about 76 ms which most probably corresponds to the wing beat cycle (Fig. 4). The CF frequency, CF duration, tFM frequency, tFM bandwidth and tFM duration of the special calls are also overlapped and identical to those of usual calls (Table 2). Data in Table 2 indicate that the CF values (91.8-92.5 kHz) from the ‘handheld’ and ‘flight tent’ recording situations are identical while the CF frequency from the ‘emerging’ recording situation is considerably higher (93.9-94.4 kHz). Among the sound parameters of special calls, the frequency and bandwidth of iFM are almost identical to those of tFM while the duration of iFM is considerably wider than that of tFM.

During flight (emerging from the roosting site) and flying inside a flight tent, *H. khaokhouayensis* emitted single CF-FM call or calls in groups up to seven signals (Figs. 3 and 4). Observational and recording data indicated that, when flying inside a flight tent or close to a cave wall, this species emitted echolocation calls in groups. A single call was detected and recorded while the bats were flying far from the cave wall or foraging under a vegetation canopy.

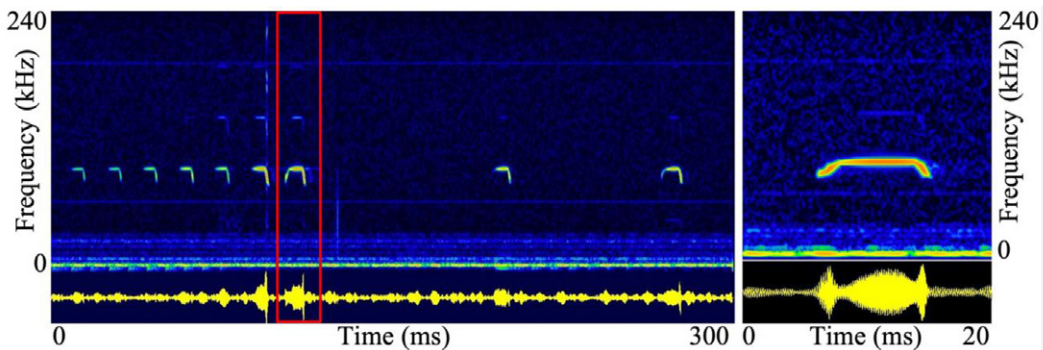
The Tham Cave is around one kilometre in length with two narrow but high mouths. Its floor has been used as a local road connecting two adjacent local communities. It is surrounded by different habitat types including natural vegetation on mountainous area, paddy fields, villages with bamboo, fruit trees and other vegetation (Fig. 5). A colony of up to ten individuals of *H. khaokhouayensis* were detected by the PCTape and observed within a dark chamber in the middle section of the cave during the field surveys.

## Discussion

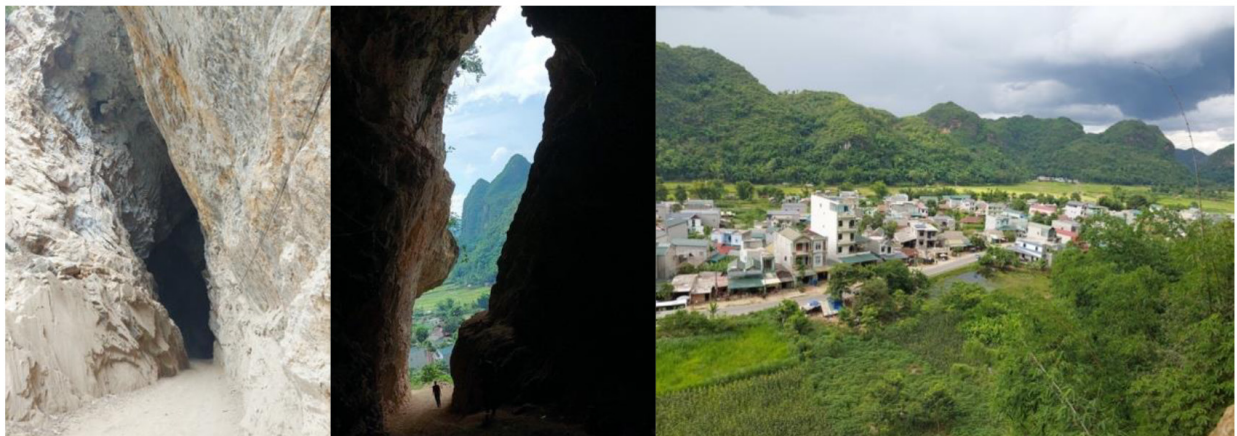
*Hipposideros khaokhouayensis* was only known from two localities, the type locality in Lao PDR and in Cat Ba National Park in Vietnam (GUILLÉN-SERVENT & FRANCIS 2006, THONG & FUREY 2008, THONG et al. 2008, ABRAMOV & KRUSKOP 2012, KRUSKOP 2013, THONG et al. 2016, DOUANGBOUPHA 2019, TUNEU-CORRAL 2019, THONG et al. 2020, THONG et al. 2021). Records of this species from Son La Province not only extend its distributional range, but also provide new morphological and acoustic data (Fig. 6). The pelage colour of the species was described as a variation between light and dark brown (THONG et al. 2008, GUILLÉN-SERVENT & FRANCIS 2006, ABRAMOV & KRUSKOP 2012, KRUSKOP 2013, TUNEU-CORRAL 2019, THONG et al. 2021). However, two female adults from Son La Province were greyish-brown with uniformly coloured individual hairs. Based on morphological measurements, one male and one female from Son La Province are considerably larger than any individuals described in previous publications (Tables 1 and 3).



**Fig. 3.** Sonograms and oscillograms of a 400-millisecond sound sequence (left) and a closed-up view of a usual call (right) of *H. khaokhouayensis* recorded during emergence from the Tham Cave.



**Fig. 4.** Sonograms and oscillograms of a 300-millisecond sound sequence (left) and a closed-up view of a special call (right) of *H. khaokhouayensis* recorded during emergence from the Tham Cave.



**Fig. 5.** Views from the outside (left) and inside (central) of the Tham Cave and surrounding habitats (right).

The current distributional range of the species is clearly disjunct, comprising two mainland and one nearshore island localities (Fig. 6). This species was found at different habitats in elevations of 6–400 meters above sea level (GUILLÉN-SERVENT & FRANCIS 2006, THONG et al. 2008, DOUANGBOUBPHA 2019, THONG et al. 2021). The Tham Cave (situated at 569.3 meters above sea level) appears as the high-

est known localities at which this species has been recorded.

*Hipposideros khaokhouayensis* can be regarded as a cave-dwelling species since all records have been obtained from caves and surrounding habitats within karst areas. Based on natural conditions including karst cave systems and highly diverse vegetations among the three localities (Fig. 6), it is very

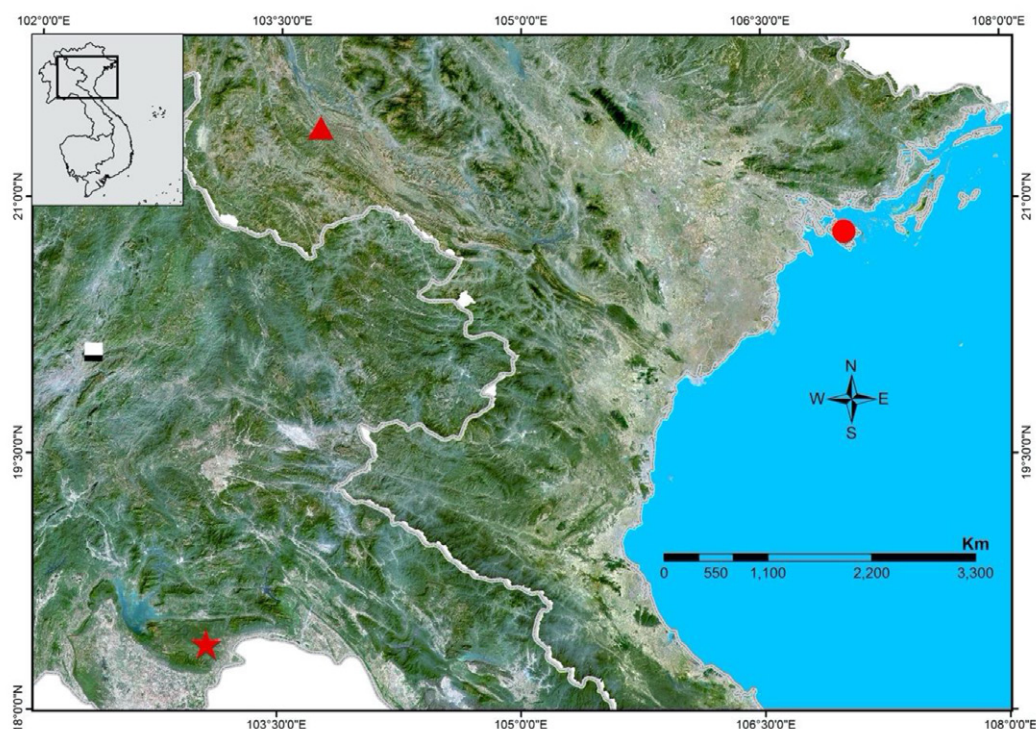
**Table 2.** Selected sound parameters of *H. khaokhouayensis* in different recording situations. Sample sizes are the numbers of signals measured within a selected sound sequence of 1000 milliseconds. Data are presented as sample size (n), mean  $\pm$  standard deviation, and range (minimum-maximum). For abbreviations, see Materials and Methods.

| Recording situation | Call type | n  | iFM frequency               | iFM bandwidth              | iFM duration             | CF frequency                | CF duration              | tFM frequency               | tFM bandwidth               | tFM duration             | Pulse duration           |
|---------------------|-----------|----|-----------------------------|----------------------------|--------------------------|-----------------------------|--------------------------|-----------------------------|-----------------------------|--------------------------|--------------------------|
| Emerging            | Special   | 4  | 83.0 $\pm$ 2.5<br>79.8-85.5 | 11.4 $\pm$ 2.5<br>8.9-14.6 | 1.3 $\pm$ 0.6<br>0.5-1.9 | 94.3 $\pm$ 0.1<br>94.2-94.4 | 6.0 $\pm$ 0.2<br>5.8-6.3 | 79.7 $\pm$ 0.4<br>79.4-80.3 | 14.7 $\pm$ 0.4<br>14.1-15.0 | 1.2 $\pm$ 0.1<br>1.0-1.3 | 8.5 $\pm$ 0.6<br>7.6-9.0 |
| Emerging            | Usual     | 17 | -                           | -                          | -                        | 94.3 $\pm$ 0.1<br>93.9-94.4 | 6.0 $\pm$ 1.1<br>4.5-7.9 | 80.0 $\pm$ 1.3<br>77.0-82.2 | 14.3 $\pm$ 1.2<br>12.2-16.9 | 1.1 $\pm$ 0.2<br>0.8-1.7 | 7.1 $\pm$ 1.2<br>5.3-9.1 |
| Handheld            | Usual     | 26 | -                           | -                          | -                        | 92.1 $\pm$ 0.1<br>91.8-92.1 | 6.1 $\pm$ 0.6<br>4.7-7.3 | 81.5 $\pm$ 1.4<br>78.4-93.6 | 10.6 $\pm$ 1.4<br>8.5-13.7  | 1.1 $\pm$ 0.1<br>0.8-1.3 | 7.2 $\pm$ 0.6<br>5.8-8.2 |
| Flight tent         | Usual     | 34 | -                           | -                          | -                        | 92.4 $\pm$ 0.2<br>91.8-92.5 | 7.0 $\pm$ 0.7<br>5.7-8.3 | 78.4 $\pm$ 1.2<br>76.6-82.2 | 14.0 $\pm$ 1.1<br>10.3-15.9 | 1.2 $\pm$ 0.1<br>0.9-1.5 | 8.2 $\pm$ 0.7<br>6.9-9.7 |

likely that *H. khaokhouayensis* naturally inhabits many other karst areas in Lao PDR and Vietnam. Unfortunately, its echolocation calls were poorly studied due to limited records throughout the known distributional range (Table 4). The previous publications provided values of only two sound parameters, CF frequency and pulse duration (GUILLÉN-SERVENT & FRANCIS 2006, THONG et al. 2008, THONG et al. 2021). The present study provides the values of six specific sound parameters (CF frequency, CF duration, tFM frequency, tFM bandwidth, tFM duration and pulse duration) which would be useful for further studies including acoustic identification and monitoring. The CF frequency and pulse duration of the adult bats from Son La Province are partly overlapped and considerably higher and longer than the respective ones described in previous publications (Table 4). Special signals, which comprise three distinct components (iFM, CF, tFM), were emitted in-between usual signals when an observed bat individual flew throughout a narrow mouth of the Tham Cave. This special call structure was not described or mentioned in any previous literature. An intensive study is required to understand the echolocation behaviour of this species. In general, the CF component is used for detection and classification of fluttering objects or prey whereas the FM components may be important for obstacle avoidance in flight (NEUWEILER et al. 1987, SCHNITZLER & DENZINGER 2011, SCHOEPLER, pers. com.). It may be assumed that the observed bat individual emitted the special calls with iFM to increase its call values for more accurate detection, identification or avoidance of objects in surrounding environments.

## Conclusions

The present study resulted in new information on the distribution, morphology and echolocation of a globally rare and vulnerable bat species. Morphologically, the discovered colony in Son La Province includes the so far known largest individuals of *H. khaokhouayensis*. In term of echolocation, the highest CF frequency and longest pulse duration were also recorded during the present study. The species emits signal call or calls in groups up to seven signals. Special calls comprising three components (iFM, CF, tFM) were first recorded for a hipposiderid bat species. The new distributional record, morphological features and echolocation characteristics demonstrated herewith, provide essential information for monitoring and conservation of the species at national and international scales.



**Fig. 6.** Distributional records of *H. khaokhouayensis* from the type locality (star) in Lao Popular Democratic Republic, Cat Ba National Park (circle) and Tham Cave (triangle) in Vietnam. Diagram prepared by Nguyen Tran Vy.

**Table 3.** A comparison of external measurements (in mm) of the six captured bats from Son La Province with previously published data. Data are presented as sample size (n), mean  $\pm$  standard deviation, and range (minimum-maximum). For abbreviations, see Materials and Methods.

| Data sources                     | FA              | EH              | EW             | NL            | Tail           | TIB            | HF            |
|----------------------------------|-----------------|-----------------|----------------|---------------|----------------|----------------|---------------|
| This study                       | 47.6 $\pm$ 3.0  | 27.4 $\pm$ 1.2  | 18.8 $\pm$ 0.7 | 6.3 $\pm$ 0.3 | 35.7 $\pm$ 0.7 | 19.4 $\pm$ 0.7 | 6.0 $\pm$ 0.3 |
|                                  | 44.1-51.6       | 25.8-28.6       | 17.9-19.8      | 5.9-6.8       | 35.1-36.9      | 18.6-20.5      | 5.6-6.3       |
| GUILLÉN-SERVENT & FRANCIS (2006) | 45.5–48.6       | 24.4–25.2       | –              | 5.2–6.7       | 35.0–37.5      | 20.2–22.1      | 7.1–8.3       |
| THONG et al. (2008)              | 41.6            | 22.7            | 17.3           | 5.4           | 34.7           | 17.1           | 5.7           |
| TUNEU-CORRAL (2019)              | 46.0-49.0       | 24.0-26.0       | –              | –             | –              | –              | –             |
| THONG et al. (2021)              | 43.1 $\pm$ 42.2 | 22.4 $\pm$ 20.6 | 17             | 5.5           | 28.2           | 28.2           | 6.4           |

**Table 4.** Sound parameters of *H. khaokhouayensis* from Son La Province in comparison with previously published data. Data are presented as sample size (n), mean  $\pm$  standard deviation, and range (minimum-maximum). Sample sizes from this study are the numbers of signals measured within the three selected 1000-millisecond sound sequences. For abbreviations, see Materials and Methods.

| Data sources                     | n  | CF frequency                | CF duration              | tFM frequency               | tFM bandwidth              | tFM duration             | Pulse duration           |
|----------------------------------|----|-----------------------------|--------------------------|-----------------------------|----------------------------|--------------------------|--------------------------|
| This study                       | 81 | 92.8 $\pm$ 0.9<br>91.8-94.4 | 6.4 $\pm$ 0.9<br>4.5-8.3 | 79.8 $\pm$ 1.8<br>76.6-83.6 | 13.0 $\pm$ 2.0<br>8.5-16.9 | 1.1 $\pm$ 0.2<br>0.8-1.7 | 7.6 $\pm$ 0.9<br>5.3-9.7 |
| GUILLÉN-SERVENT & FRANCIS (2006) | 6  | 87.2-91.1                   | -                        | -                           | -                          | -                        | 3.0-5.0                  |
| THONG et al. (2008)              | 1  | 94.2                        | -                        | -                           | -                          | -                        | -                        |
| THONG et al. (2021)              | 2  | 91.2-92.1                   | -                        | -                           | -                          | -                        | 7.7–8.8                  |

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## References

- ABRAMOV A. V. & KRUSKOP S. V. 2012. The mammal fauna of Cat Ba Island, northern Vietnam. *Russian Journal of Theriology* 11 (1): 57–72.
- BRUNET-ROSSINI A. K. & WILKINSON G.S. 2009. *Ecological and Behavioural Methods for the Study of Bats*, Methods for age estimation and the study of senescence in bats, 2nd Edition, The John Hopkins University Press, pp. 315–325.
- DOUANGBOUPHA B. 2019. *Hipposideros khaokhouayensis* (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2020: e.T136819A166602959. <https://dx.doi.org/10.2305/IUCN.UK.2020-1.RLTS.T136819A166602959.en>.
- FRANCIS C. M. 1989. A comparison of mist nets and two designs of harp traps for capturing bats. *Journal of Mammalogy* 70 (4): 865–870.
- GUILLÉN-SERVENT A. & FRANCIS C. M. 2006. A new species of bat of the *Hipposideros bicolor* group (Chiroptera: Hipposideridae) from Central Laos, with evidence of convergent evolution with Sundaic taxa. *Acta Chiropterologica* 8 (1): 39–61. doi.org/10.3161/1733-5329(2006)8[39:ANSOBO]2.0.CO;2
- KRUSKOP S.V. 2013. *Bats of Vietnam: Checklist and an identification manual*. Moscow, Russia. 299 p.
- NEUWEILER G., METZNER W., HEILMANN U., RIIBSAMEN R., ECKRICH M. & COSTA H.H. 1987. Foraging behaviour and echolocation in the rufous horseshoe bat (*Rhinolophus rouxi*) of Sri Lanka. *Behavioral ecology and sociobiology* 20: 53–67. doi.org/10.1007/BF00292166
- RACEY P.A. 2009. *Ecological and Behavioural Methods for the Study of Bats*, Reproductive assessment of bats, 2nd Edition, The John Hopkins University Press, pp. 249–264.
- SCHNITZLER H.-U. & DENZINGER A. 2011. Auditory fovea and Doppler shift compensation: adaptations for flutter detection in echolocating bats using CF-FM signals. *Journal of Comparative Physiology A* 197: 541–559. doi 10.1007/s00359-010-0569-6.
- SIKES R.S. & ACUCASM (ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS). 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97 (3): 663–688.
- SIKES R.S. & GANNON W.L. 2011. The Animal Care and Use Committee of the American Society of Mammalogists. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92 (1): 235–253.
- THONG V.D. & FUREY N.M. 2008. The bat fauna of Cat Ba Biosphere Reserve. *Journal of Biology (=Academia Journal of Biology)* 30 (3): 73–77. (In Vietnamese, with English abstract).
- THONG V.D. (in pres). Remarks on the diversity and echolocation calls of hipposiderid bats (Chiroptera: Hipposideridae) in Cuc Phuong National Park, northeastern Vietnam. *Academia Journal of Biology*.
- THONG V.D., DENZINGER A., SANG N.V., HUYEN N.T.T., THANH H.T., LOI D.N., NHA P.V., VIET N.V., TIEN P.D., TUANMU M.-N., HUANG J.C.-C., LADTHAVONG T., LUONG N.T. & SCHNITZLER H.-U. 2021. Bat Diversity in Cat Ba Biosphere Reserve, Northeastern Vietnam: A Review with New Records from Mangrove Ecosystem. *Diversity* 13 (376): 1–29.
- THONG V.D., DIETZ C., SCHNITZLER H.-U., DENZINGER A., FUREY N.M., BORISENKO A.V. & BATES P.J.J. 2008. First record of *Hipposideros khaokhouayensis* (Chiroptera: Hipposideridae) from Vietnam. *HNUE Journal of Science* 53 (5): 138–143.
- THONG V.D., DUNG D.T. & THANH N.V. 2016. An overview of bat research in Cat Ba biosphere reserve with remarks on previous records. *Proceedings of the 2nd national scientific conference on biological research and teaching in Vietnam*, Publishing House of the Vietnam National University, pp. 737–744.
- THONG V.D., SICHANH S. & NHA P.V. 2020. The conservation status of bats (Mammalia: Chiroptera) in Cat Ba National Park, northeastern Vietnam. *HNUE Journal of Science* 65: 92–98.
- TIAN B. & SCHNITZLER H.-U. 1997. Echolocation signals of the greater horseshoe bat (*Rhinolophus ferrumequinum*) in transfer flight and during landing. *The Journal of the Acoustical Society of America* 101(4): 2347–2364.
- TUNEU-CORRAL C. 2019. *Handbook of the mammals of the world*. Phou Khao Khouay leaf-nosed bat (*Hipposideros khaokhouayensis*). Barcelona: Lynx Edicions, p. 255.

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