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NOTES ON GEOGRAPHIC DISTRIBUTION

First records of *Mops johorensis* (Dobson, 1873), Northern Free-tailed Bat (Chiroptera, Molossidae), from Borneo, with new information on their genetics and echolocation calls

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Abstract. This study presents the first confirmed records of *Mops johorensis* (Dobson, 1873) (Chiroptera, Molossidae) from Borneo. Specimens were recorded at three sites: Sabah (Sungai Kangkawat, 50 m a.s.l) and Sarawak (Lubok Antu, 30 m a.s.l and Mount Penrissen, 1200 m a.s.l). Echolocation analysis revealed site-based variation in call frequencies. Morphological comparisons showed subtle differences between Bornean and Peninsular populations. Genetic analysis using the mitochondrial COI gene showed minimal divergence between Bornean and Peninsular individuals. Spatial modelling identified hotspots for Molossidae in northern Sabah and central Sarawak, with habitat suitability strongly influenced by bat and cave density, climate, and land use.

Key words. Canopy, diversity, forest species, new record, Sarawak, Sabah

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INTRODUCTION

The family Molossidae, commonly known as free-tailed bats, exhibits a broad distribution in both the Old and New Worlds, comprising 134 recognised species (Simmons and Cirranello 2025). These bats possess elongated, narrow wings that facilitate rapid and agile flight, along with a unique free tail that extends beyond the uropatagium (Payne et al. 1985; Francis 2008; Phillipps and Phillipps 2016). In Southeast Asia, 15 species of Molossidae in seven genera have been documented, with four species, namely *Mops johorensis* (Dobson, 1873), *M. mops* (de Blainville, 1840), *M. plicatus* (Buchannan, 1800), and *Cheiromeles torquatus* Horsfield, 1824 reported from Malaysia (Payne et al. 1985; Kingston et al. 2006; Francis 2008; Lim et al. 2017; Phillipps and Phillipps 2016).

Previously, the known distribution of *M. johorensis* was limited to Peninsular Malaysia (Pulai, Johor; Krau Wildlife Reserve, Pahang; Mount Jerai, Kedah; Belukar Bukit, Terengganu) and Sumatra, Indonesia (Wilson and Reeder 2005; Kingston et al. 2006; Jayaraj et al. 2013; Roslan et al. 2016). This species was previously assigned to the genus *Chaerephon* Dobson, 1874 and was revised to *Mops* in 2024 (Mammal Diversity Database 2024). It is categorized as Vulnerable by the IUCN Red List 2025 due to its restricted range and likely small population size (Senawi et al. 2020). The species prefers high-canopy foraging (Kingston et al. 2006; Francis 2008), which complicates capture efforts. Most studies have focused on forest habitats, with sampling techniques leaning towards understory bats. Since this species prefers open spaces, it has been rarely recorded, and there is not much known about its ecology, echolocation, and genetics in Malaysia.

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This research provides the initial verified records of *M. johorensis* in Borneo, thereby expanding its known distribution to Sabah and Sarawak. This report presents new distribution records, along with detailed ecological, genetic, and morphological data, addressing the significant knowledge gaps regarding this elusive species. Specifically, this report: (1) confirms the presence of *M. johorensis* in Borneo through genetic and morphological data, (2) describes its echolocation call structure and compares it with its sister species in Borneo, *M. mops* for which call data are available, (3) details its morphological characteristics including external and skull measurements, (4) maps the potential habitat suitability of Malaysian Molossidae across Borneo using a weighted overlay analysis of key ecological and spatial variables.

STUDY AREA

Field surveys were conducted at three locations in Borneo: Sungai Kangkawat Research Station, Imbak Canyon Conservation Area, Sabah (117.0596°E, 005.0748°N, 50 m a.s.l), Lubok Antu, Sarawak (111.817°E, 001.2894°N, 30 m a.s.l) and Mount Penrissen, Sarawak (110.2167°E, 001.1167°N, 1200 m a.s.l) (Figure 1). These sites encompass mixed dipterocarp forest with highland and lowland areas.

METHODS

Bats were captured using high mist nets (~10 m above ground)**,** deployed from 1800 hours to 2200 hours for five sampling nights. Captured individuals were identified, sexed, and measured in the field before release. External measurements recorded included forearm length (FA), ear length (E), tibia length (TB), hind foot length (HF), tail-vent length (TV), and body weight (Wt)**.** The craniodental measurements include condyle-canine length (CCL), interorbital constriction (IOC), zygomatic width (ZW), width of braincase (WOB), mastoid width (MW) width from left upper canine to right upper canine (WUC1), width from left upper last molar to right upper last molar (WUM^3), length from upper canine to upper last molar (CM^3), mandible (MDB) and lower canine to lower last molar length (CM_3) (Yoshiyuki and Lim 2005; Velazco and Petterson 2014; Morni et al. 2016). A few individuals of the target species were taken as voucher specimens for reference of the new records and deposited in the UNIMAS Zoological Museum (MZU).

Echolocation calls were recorded using a Pettersson M500-384 USB Ultrasound Microphone (Pettersson Elektronik AB, Sweden). Bats were recorded in two conditions to analyze call variation: first in a room, flying less than 5 m above the ground, and second in open space, more than 10 m above the ground after release. Recording calls in both settings is important, as *M. johorensis* is a frequency-modulating bat that modifies its call structure according to the surrounding environment. The structure of each recorded call was analyzed using Kaleidoscope Call Viewer v. 4.5.5 (Wildlife Acoustic Incorporated, USA). All sonograms were generated using software's standard default FFT size and overlap settings. For each call pulse, the following parameters were measured: F_{start} refers to the initial frequency of the selected pulse (kHz); F_{end} denotes the terminal frequency of the selected pulse (kHz); F_{peak} indicates the frequency at which maximum energy occurs (kHz); PD represents the duration of the pulse (ms); and PI is the interval between the start of one pulse and the start of the subsequent pulse (ms) (Kingston et al. 2003; Douangboubpha et al. 2014; Morni et al. 2016; Yoh et al. 2022). The calls were analysed in comparison to those of *M. mops*, a closely related species which call data are available in our lab.

Tissue samples (muscle and liver) were preserved in absolute ethanol for genetic analysis. DNA was

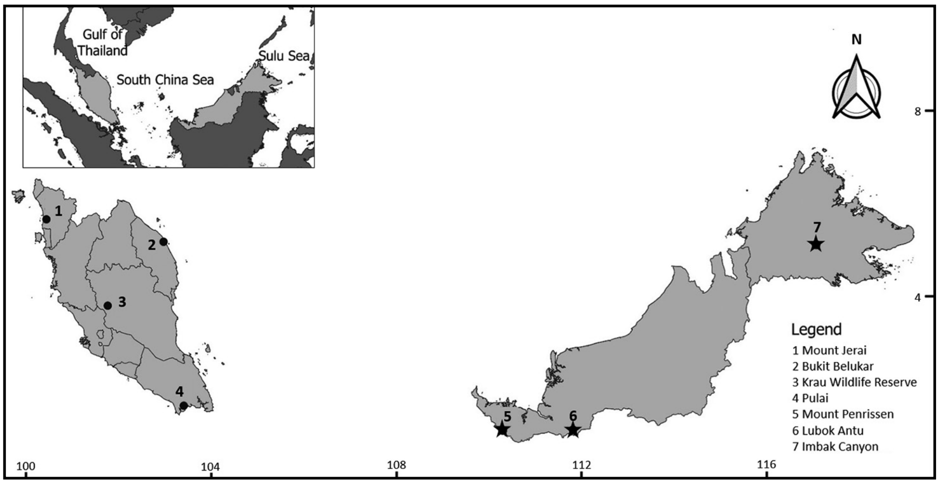

Figure 1. Previously known (black dot) and new localities of *Mops johorensis* in Malaysia; new records are from Mount Penrissen and Lubok Antu, Sarawak and Sungai Kangkawat, Sabah (black star). Inset map: position of Malaysia in South-east Asia.

extracted using a DNeasy Blood & Tissue Kit (Qiagen, Germany) following manufacturer protocols. A 602-bp fragment of the cytochrome oxidase subunit I (COI) gene region was amplified using VR1 (5′-AGACTTCT-GGGTGGCCAAAGAATCA-3′) and VF1 (5′-TTCTCAACCAACCACAAAGACATTGG-3) primers with the following PCR parameters: initial denaturation (94 °C for 3 min), denaturation (94 °C for 1 min), annealing (50 °C for 1 min), extension (72 °C for 2 min), final extension (72 °C for 5 min), and soaking (4°C). The PCR products were visualised, and successful products were outsourced to a private company for Sanger sequencing. In addition, a sequence of *M. johorensis* from Mount Jerai, kindly shared by Isham Azhar, was included in the analysis. Three additional sequences of *Tadarida latouchei* (Thomas, 1920), *T. teniotis* (Rafinesque, 1814) and *Otomops wroughtoni* Thomas, 1913 from GenBank were included to provide better resolution of Molossidae in Southeast Asia. No other molosid bat sequences from this region are currently available. Phylogenetic analyses were conducted in MEGA11 (Tamura et al. 2021) using the maximum-likelihood (ML) method. The best-fit nucleotide substitution model was determined in MEGA11 using the "Find Best DNA/Protein Models (ML)" function, which identified the Tamura Nei + Gamma distributed with Invariant Sites (TN93+G+I) as the most suitable model (Akaike Information Criterion (AIC): 5868.861). ML analyses were performed with 1000 bootstrap replications to assess node support. Pairwise genetic distances were calculated in MEGA11 using the Kimura 2-parameter (K2P) model. Analyses were based on the same 602-bp COI alignment used for the ML tree without any missing data.

Due to the paucity of occurrence records for *M. johorensis*, species-level distribution mapping was not feasible. To avoid misinterpretation, the data were pooled at the family level, which allow for more comprehensive and ecologically meaningful analyses. A total of 36 occurrence records for these species were compiled from this study and UNIMAS Zoological Museum collections (Table 1). To analyse the distribution of molossid bats and assess their habitat suitability in Borneo, a weighted overlay analysis was conducted using ArcGIS Pro (ESRI 2024). Five environmental parameters were included: bat density, cave density, annual precipitation, annual mean temperature, and land use data (Table 2). Kernel Density Analysis was employed to visualize bat activity based on spatial point data, with bat density represented by a red gradient on the map. Cave density was derived from locations of known karst and cave sites published in google maps. Annual precipitation and annual mean temperature data were obtained from the WorldClim v. 2.1 database (~1 km² resolution) (Fick and Hijmans 2017). Land-use data were sourced from the European Space Agency, Land Cover CCI dataset. Each factor was assigned a weight based on its ecological significance in determining suitable habitats for Molossidae. The model categorized habitat suitability into five classes, ranging from very low to very high. Although the number of sampling sites is limited, the development of this model is important to provide insights into spatial and habitat suitability of this family, especially for generating information in areas with limited data and identifying areas with similar ecosystem that may be suitable for these species.

RESULTS

Chiroptera, Molossidae

***Mops johorensis* (Dobson, 1873)**
Figures 2, 3

New records. BORNEO — SABAH • Tongod, Imbak Canyon, Sungai Kangkawat; 117.0596°E, 005.0748°N; 50 m alt.; 10.VIII.2018; F.A.A. Khan leg.; disturbed lowland forest, canopy-level mist-netting; 1 ♀, ICCA18-048 — SARAWAK • Sri Aman, Lubok Antu; 111.817°E, 001.2894°N; 30 m alt.; 12.IX.2011; I. Azhar leg.; 1♀, MZU/M/4629 • Padawan, Mount Penrissen; 110.2167°E, 001.1167°N; 1200 m alt.; 9.XII.2015; I. Azhar leg.; montane forest, canopy-level mist-netting; 1♂, BH15-078.

Identification. All three individuals have similar phenotype, as described by Francis (2008). They possess dark-brown upperparts and paler underparts. The upper lip is wrinkled. A "pocket" is present between the ears, formed by a flap of skin which is raised at the middle and extends backwards. Inside this pocket, long tuft hairs were detected. A high wing aspect ratio was observed, as these individuals have a long, narrow wing with pointed wingtips similar what has been reported by Norberg and Rayner (1987). The upper premolars have a small anterior one. The sagittal and lambdoid crests are not that obvious, whereas the anterior palatal crest is well developed. The skull characteristics of observed specimens match with those provided by Freeman (1981) and Francis (2008).

Echolocation. The echolocation recordings revealed frequency differences between Sabah and Sarawak individuals. The Sarawak individual exhibited a higher F_{peak} (36.1–37.3 kHz), while the Sabah individual had a broader F_{peak} range (23.3–35.1 kHz). The echolocation calls of *M. johorensis* were also compared to *M. mops*, which produced lower F_{peak} at 22.6–23.9 kHz (Figure 3, Table 3).

Table 1. Occurrence records of Malaysian molossid species used for species distribution modelling.

Species	Collection ID	Locality	Latitude	Longitude
Mops johorensis	ICCA18031	Malaysia:Sabah, Sungai Kangkawat	005.050	117.116
	BH15078	Malaysia: Sarawak, Lubok Antu	01.289	111.817
	BH15079	Malaysia: Sarawak, Mount Penrissen	01.117	110.217
Mops plicatus	MNP046	Malaysia: Sarawak, Mulu NP	04.092	114.896
	MNP069	Malaysia: Sarawak, Mulu NP	04.092	114.896
	MNP077	Malaysia: Sarawak, Mulu NP	04.092	114.896
	MNP051	Malaysia: Sarawak, Mulu NP	04.092	114.896
	MNP987	Malaysia: Sarawak, Mulu NP	04.092	114.896
	MNP066	Malaysia: Sarawak, Mulu NP	04.092	114.896
	MNP047	Malaysia: Sarawak, Mulu NP	04.092	114.896
	MZU/M/256	Malaysia: Sabah, Gomantong Cave	05.530	118.075
	MZU/M/257	Malaysia: Sabah, Gomantong Cave	05.530	118.075
	MZU/M/258	Malaysia: Sabah, Gomantong Cave	05.530	118.075
	MZU/M/259	Malaysia: Sabah, Gomantong Cave	05.530	118.075
	MZU/M/302	Malaysia: Sabah, Gomantong Cave	05.530	118.075
	MZU/M/266	Malaysia: Sabah, Gomantong Cave	05.530	118.075
	MZU/M/303	Malaysia: Sabah, Gomantong Cave	05.530	118.075
	MZU/M/544	Malaysia: Sabah, Kunak	04.683	118.250
	MZU/M/545	Malaysia: Sabah, Kunak	04.683	118.250
	MZU/M/546	Malaysia: Sabah, Kunak	04.683	118.250
	MZU/M/547	Malaysia: Sabah, Kunak	04.683	118.250
	MZU/M/548	Malaysia: Sabah, Kunak	04.683	118.250
	MZU/M/549	Malaysia: Sarawak, Kuching	01.557	110.344
Mops mops	KNP110923	Malaysia: Sarawak, Kubah NP	01.596	110.181
	BA1246	Malaysia: Sarawak, Batang Ai NP	01.289	111.817
	NNP14555	Malaysia: Sarawak, Niah NP	03.797	113.788
	MZU/M/611	Malaysia: Sarawak, Bakun NP	02.762	114.055
Cheiromeles torquatus	MZU/M/765	Malaysia: Sabah, Pulau Banggi	07.129	117.075
	MZU/M/833	Malaysia: Sabah, Tabin WR	05.267	118.650
	MZU/M/459	Malaysia: Sabah, Tenom	05.121	115.942
	MNP24556	Malaysia: Sarawak, Mulu NP	04.092	114.896
	MZU/M/1123	Malaysia: Sarawak, Miri	04.415	114.009
	MZU/M/1432	Malaysia: Sarawak, Kapit	01.517	112.167
	MZU/M/1175	Malaysia: Sarawak, Batang Ai	01.289	111.817

* BA = Batang Ai, BH = Borneo Highland, ICCA = Imbak Canyon Conservation Center, MNP = Mulu National Park, MZU/M = UNIMAS Zoological Museum/Mammal.

Table 2. Layers and variables used in suitability analysis, with details on resolution, category, year, and source.

Layer	Parameter	Resolution	Category/unit	Year	Source/Citation
Environmental layer	Land use	~300 m	Land cover classes	2020	European Space Agency, Land Cover CCI dataset
Bioclimatic variable	Annual mean temperature	~1 km^2	°C	1970–2000	WorldClim v2.1 (Fick and Hijmans 2017)
Bioclimatic variable	Annual mean precipitation	~1 km^2	mm/year	1970–2000	WorldClim v2.1 (Fick and Hijmans 2017)
Spatial data	Bat-density map	N/A	Kernel density (records)	Various	This study + UNIMAS Zoological Museum collections
Spatial data	Cave-density map	N/A	Kernel density (sites)	Various	12 caves identified through Google Map

Morphology. External and craniodental measurements of the Bornean *M. johorensis* specimens exhibited differ from previously recorded individuals from Peninsular Malaysia. The forearm length ranged from 48 to 50 mm, which is slightly longer than the mean value of 45.36 mm reported in earlier study (Roslan et al. 2016) (Table 4). Skull measurements showed variation in specific traits, with some measurements, such as mandibular breadth (MDB) indicating larger dimensions, while others suggested differences in shape and proportion rather than an overall increase in size (Table 5). The Bornean specimens also displayed a relatively broader mandible (MDB) with a comparable length of the lower dentary, suggesting variation in mandibular robustness rather than a uniform enlargement in size. Given the small sample sizes, these observations should be interpreted with caution. Additional specimens are required to determine whether the observed

Figure 2. Latero-ventral view of *Mops johorensis*, from Sungai Kangkawat, Imbak Canyon Conservation Area, Sabah (specimen ICCA18031).

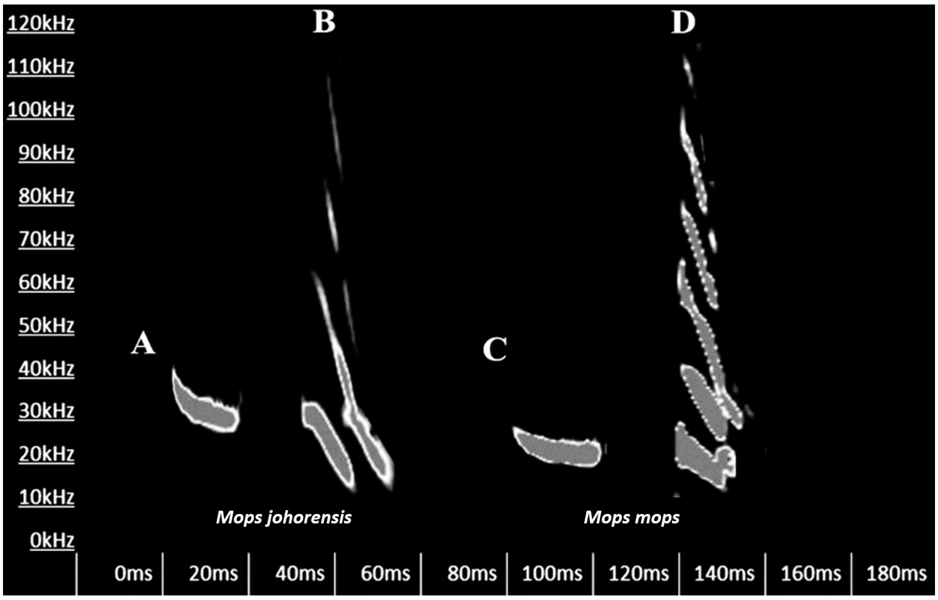

Figure 3. Sonogram on the structure of echolocation calls of *Mops johorensis* and *M. mops*. For each pair of the species calls, first call's structure, (**A–C**) indicate high-frequency calls recorded in the open space at an altitude >10 m; second calls structure, (**B–D**) indicate low frequency calls recorded in a room <5m from ground.

differences represent true population-level variation, individual morphological variability, or potential inconsistencies in measurement approaches between studies.

Genetics. The study generated 22 new COI sequences, including four sequences of *M. johorensis*, four sequences of *M. mops*, 11 sequences of *M. plicatus*, and three sequences of *C. torquatus* (Table 6). The analysis of the COI gene (602 bp) revealed minimal genetic distance between Bornean and Peninsular Malaysian populations of *M. johorensis*, with only one transition mutation at position 504 (K2P: 0.2%). The ML tree strongly supported the monophyly of *M. johorensis* (bootstrap 100%), with its closest relative being *M. plicatus* (K2P distance: 9%; bootstrap 86%), and *M. mops* forming a more distant clade (K2P: 12.8%; bootstrap 81%) (Figure 4, Table 7). The study also generated the first COI sequences for *C. torquatus*, contributing new genetic data for Southeast Asian molossid bats.

Table 3. Call parameters of *Mops johorensis*. Parameters: F_{start} = start frequency (kHz), F_{end} = end frequency (kHz); F_{peak} = peak frequency (kHz), PD = pulse duration (ms), PI = pulse interval (ms).

Species	Recording conditions	Call pulses	F_{start} (kHz)	F_{end} (kHz)	F_{peak} (kHz)	PD (ms)	PI (ms)
M. johorensis (*n* = 1)	i: High calls	7	43.9±4.9	30.6±3.0	36.8±0.6	6.3±1.4	104.3±20.2
Sarawak			39.0–48.8	27.6–33.6	36.2–37.3	4.9–7.8	84.1–124.4
	ii: Low calls at ≤5 m from ground	7	35.4±4.5	13.7	25.1±0.7	4.3±0.3	80.0±8.5
			30.9–39.9		24.4–25.8	4.0–4.6	71.5–88.5
M. johorensis (*n* = 1)	i: High calls	5	54.8 ± 13.4	30.4 ± 6.4	25.9 ± 5.1	8.8 ± 5.7	120. 1 ± 46.6
Sabah			34.2 – 67.8	20.1 – 36.7	23.3 – 35.1	4.5 – 18.2	77.9 – 180.4
	ii: Low calls at ≤5 m from ground	5	26.8 ± 4.3	22.9 ± 2.3	28.5 ± 5.6	3.6 ± 1.2	124.6 ± 45.5
			25.3 – 31.6	20.4 – 24.9	25 – 34.9	2.5 – 4.9	79.9 – 170.9
M. mops	i: High calls	12	37.4±2.3	16.9±1.3	23.3±0.6	11.8±1.9	275.6±26.6
(*n* = 1)			35.1–39.8	15.7–18.2	22.6–23.9	9.9–13.7	249.0–302.2
Sarawak	ii: Low calls at ≤ 5m from ground	8	23.4	7.3±1.4	19.3±0.1	2.1±0.5	84.6±8.6
				5.9–8.7	19.1–19.4	1.6–2.6	76.1–93.2

Table 4. External measurements (mm) and weight (g) for three specimens of *Mops johorensis* from Sungai Kangkawat, Imbak Canyon Conservation Area, Sabah, together with measurements of specimens from Francis (2008) and Roslan et al. (2016).

Character	This study (*n* = 3)	Roslan et al. 2016 (*n* = 1)	Francis 2008 (*n* = not specified)
Forearm (FA)	48.83 ± 1.045 (48–50)	45.36	44–49
Head and body (HB)	72.58 ± 3.43 (70.15–75)	64.35	NA
Tail to ventral (TV)	43.9 ± 1.91 (41.7–45)	34.02	36–43
Hind foot (HF)	10.93 ± 2.10 (8.8–11)	10.51	NA
Tibia (TB)	19.87 ± 0.82 (19–20.63)	16.65	NA
Ear length (E)	21.02 ± 3.57 (18.08–25)	11.36	NA
Weight (g)	21.33 ± 1.53 (20–23)	20.6	15–25

Spatial analysis and habitat modelling. The density map of Molossidae in Borneo reveals distinct spatial patterns in hotspot distribution, influenced by variations in annual mean temperature. The highest density hotspots, ranging from 142 to 160, are concentrated in northern Sabah and central-northern Sarawak. Smaller, scattered hotspots are observed along the southern and western coastal areas. The background grayscale gradient illustrates annual mean temperatures, with lighter shades representing warmer regions and darker shades indicating cooler areas (Figure 5). Molossidae density was assigned the highest weight (30%) due to its indication of favorable environmental conditions and available roosting sites. Regions with very high suitability (red areas on the map) coincide with high bat density clusters, predominantly in central and northern Sabah and northern Sarawak (Figure 6). Cave density, weighted at 25%, also plays a crucial role, as many molossid species rely on caves for roosting and reproduction. High-suitability zones are observed around known limestone karst regions. Annual precipitation (20%) and annual mean temperature (20%) capture climatic influences on habitat viability, with high precipitation supporting lush vegetation and insect abundance, while warm temperatures optimize bat metabolic processes and activity. Land use, assigned a lower weight (5%), remains an important factor, with natural forests and protected areas showing higher suitability, while agricultural and urban areas exhibit lower suitability.

DISCUSSION

Range expansion and new records. *Mops johorensis* was previously considered confined to Peninsular Malaysia and Sumatra, with limited records from these areas (Wilson and Reeder 2005; Kingston et al. 2006; Jayaraj et al. 2013; Roslan et al. 2016; Lim et al. 2017). The identification of this species in Borneo, specifically

Table 5. Craniodental measurements (mm) for three specimens of *Mops johorensis* from Sungai Kangkawat, Imbak Canyon Conservation Area, Sabah, together with measurements of specimens from Jayaraj et al. (2013).

Character	This study ($n = 3$)	Jayaraj et al. 2013 ($n = 1$)
Condylo-canine length (CCL)	18.21 ± 0.34 (18–18.61)	17.66
Interorbital constriction (IOC)	4.92 ± 0.06 (4.88–4.99)	4.60
Zygomatic width (ZW)	12.13 ± 0.14 (12.04–12.29)	12.05
Width of braincase (WOB)	9.90 ± 0.042 (9.61–10.07)	9.74
Mastoid width (MW)	11.02 ± 0.12 (10.9– 11.15)	11.00
Width from left upper canine to right upper canine (WUC1)	4.48 ± 0.05 (4.44–4.54)	4.24
Width from left upper last molar to right upper last molar (WUM3)	8.45 ± 0.12 (8.35–8.59)	8.94
Length from upper canine to upper last molar (CM^3)	7.2 ± 0.16 (7.02–7.32)	7.05
Mandible (MDB)	13.96 ± 0.18 (13.2–13.57)	12.57
Length from lower canine to lower last molar (CM_3)	7.86 ± 0.21 (7.69–8.10)	7.52

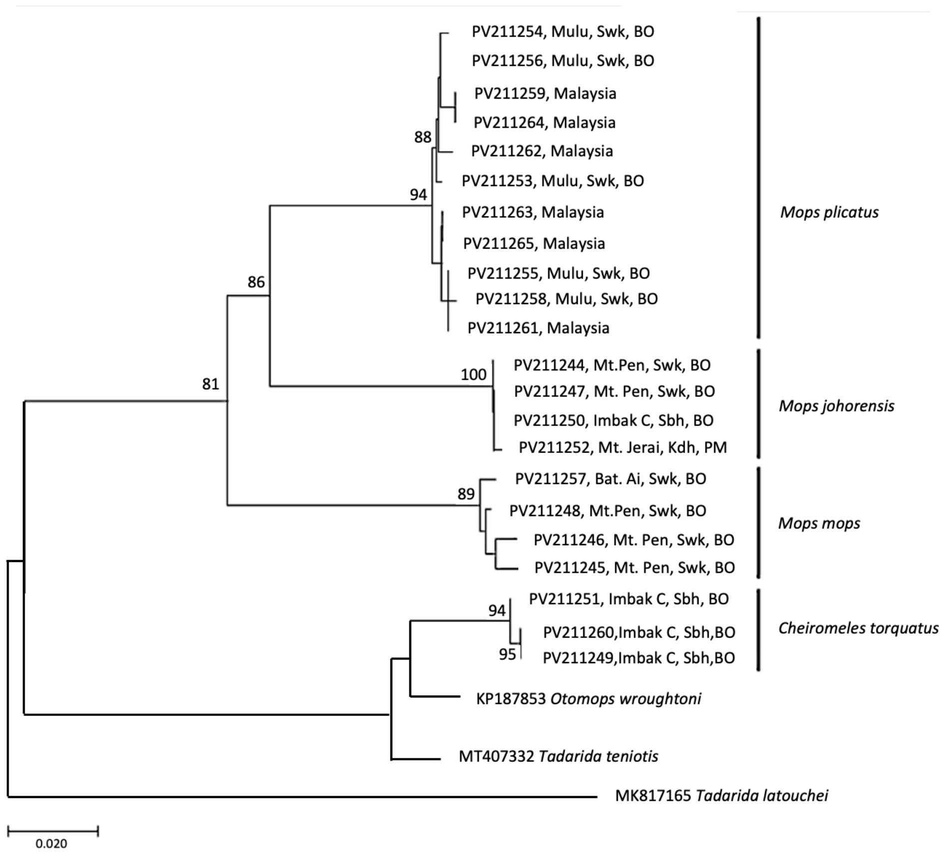

Figure 4. Maximum-likelihood (ML) tree of molossid bats in Southeast Asia. The phylogeny was generated with 1000 bootstrap replicates. Phylogenetic analysis was conducted in MEGA11. Sample locality information is provided after the GenBank accession number (BO = Malaysian Borneo; PM = Peninsular Malaysia; Malaysia = only country level information available). Full locality details are presented in Table 6.

Table 6. New cytochrome oxidase I sequences of Molossids from Batang Ai, Imbak Canyon, Mount Jerai, Mount Penrissen and Mulu NP generated from this study

Species	Locality	GenBank accession number
Mops johorensis (*n* = 4)	Malaysian Borneo: Sarawak, Mount Penrissen	PV211244
	Malaysian Borneo: Sarawak, Mount Penrissen	PV211247
	Malaysian Borneo: Sabah, Imbak Canyon	PV211250
	Peninsular Malaysia: Kedah, Mount Jerai	PV211252
Mops mops (*n* = 4)	Malaysian Borneo: Sarawak, Mount Penrissen	PV211245
	Malaysian Borneo: Sarawak, Mount Penrissen	PV211246
	Malaysian Borneo: Sarawak, Mount Penrissen	PV211248
	Malaysian Borneo: Sarawak, Batang Ai NP	PV211257
Mops plicatus (*n* = 11)	Malaysian Borneo: Sarawak, Mulu NP	PV211253
	Malaysian Borneo: Sarawak, Mulu NP	PV211254
	Malaysian Borneo: Sarawak, Mulu NP	PV211255
	Malaysian Borneo: Sarawak, Mulu NP	PV211256
	Malaysian Borneo: Sarawak, Mulu NP	PV211258
	Malaysia	PV211259
	Malaysia	PV211261
	Malaysia	PV211262
	Malaysia	PV211263
	Malaysia	PV211264
	Malaysia	PV211265
Cheiromeles torquatus (*n* = 3)	Malaysian Borneo: Sabah, Imbak Canyon	PV211249
	Malaysian Borneo: Sabah, Imbak Canyon	PV211251
	Malaysian Borneo: Sabah, Imbak Canyon	PV211260

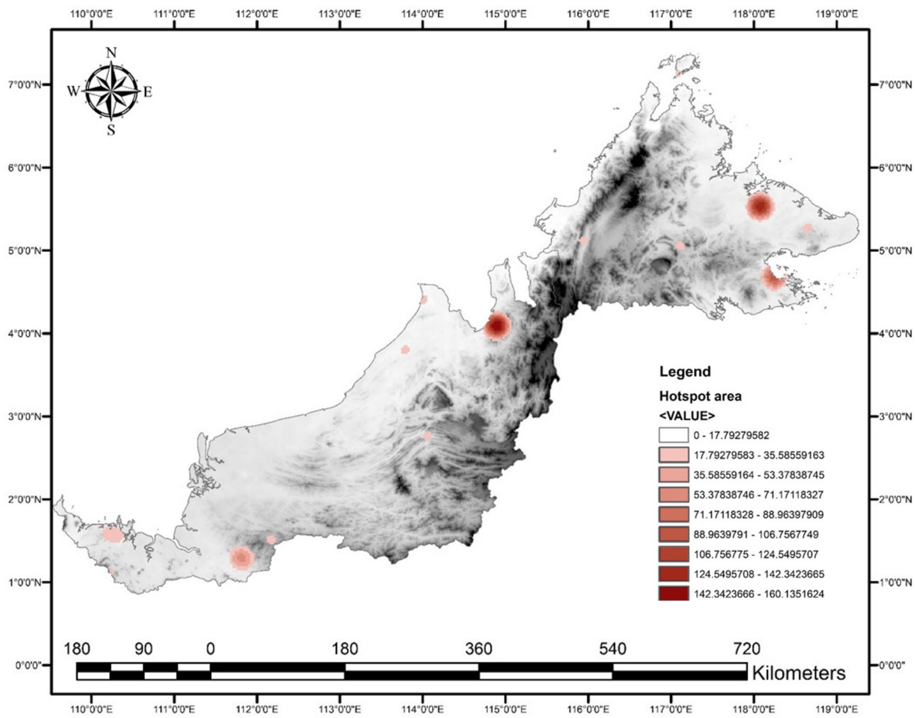

Figure 5. Density map of Molossidae in Borneo

at Sungai Kangkawat, Imbak Canyon in Sabah, and Lubok Antu and Mount Penrissen in Sarawak, has substantially broadened its reported range. This indicates that *M. johorensis* may possess a broader distribution than previously recorded, yet it has gone undetected due to its elusive characteristics and tendency for high-altitude foraging (Kingston et al. 2003). Despite this range expansion, the species continues to be rarely observed.

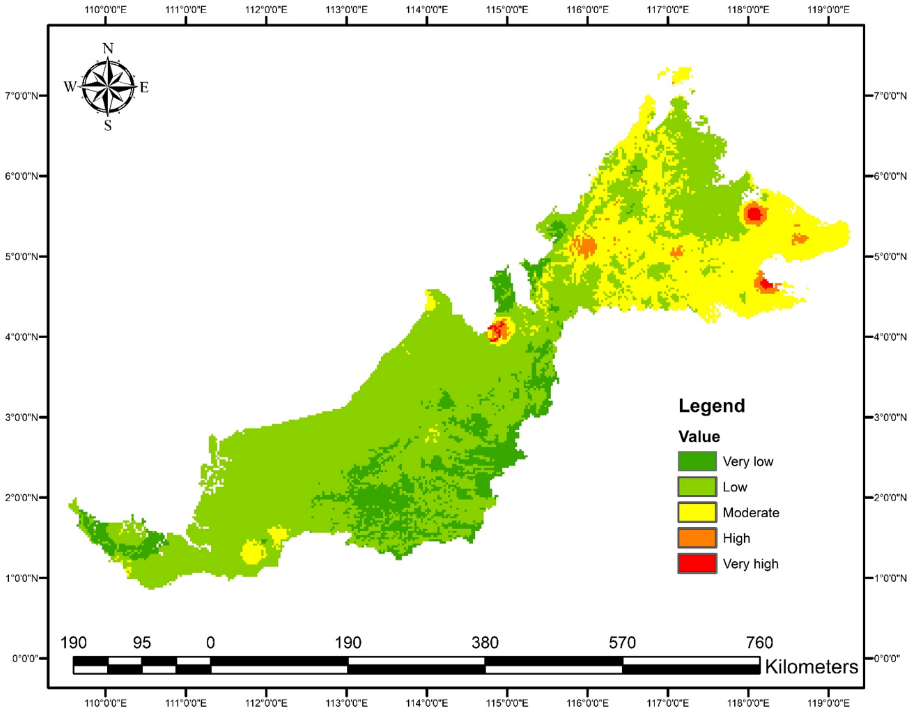

Figure 6. Suitability analysis model of Malaysian molossids.

Table 7. Pairwise distance test of Malaysian molossids (Kimura 2-parameter model).

	[1]	[2]	[3]
[1] *Mops johorensis* (*n* = 4)			
[2] *Mops plicatus* (*n* = 11)	9.0		
[3] *Mops mops* (*n* = 4)	12.8	11.2	
[4] *Cheiromeles torquatus* (*n* = 3)	20.8	20.5	21.6

During several nights of sampling, only a single individual of *M. johorensis* was captured at Sungai Kangkawat (from 83 bats), while one individual was recorded at Mount Penrissen (from 48 bats). This low capture rate is consistent with previous findings from Belukar Bukit, Terengganu, where the species was similarly observed in very low numbers (Roslan et al. 2016). One of the key contributing factors is likely its preference for foraging in high-canopy or open-space environments, making traditional ground-level mist-netting largely ineffective for its detection (Holbech 2020).

Unlike earlier studies, this survey employed stratified mist-netting techniques that included canopy-level nets set at approximately 10–15 m above the ground, in addition to ground-level nets. These high-net placements, implemented using high poles across canopy gaps, enabled access to vertical foraging strata often missed by conventional methods. This approach likely contributed to the successful capture of *M. johorensis* and aligns with previous ecological characterizations of open-space aerial foragers, which are typically underrepresented in ground-based surveys (Lacki et al. 2007; Furey et al. 2009). While passive acoustic monitoring has the potential to enhance detection of such elusive species, its effectiveness is currently limited by the lack of a comprehensive and validated echolocation call library for *M. johorensis*. As such, targeted stratified mist-netting remains a vital method for detecting and studying rare, canopy-foraging bat species.

Ecological flexibility. These new records expand the known distribution of the species beyond Peninsular Malaysia and Sumatra. Notably, our observations also extend the known ecological range of *M. johorensis*, which had previously only been reported from lowland evergreen forests (50–117 m a.s.l) (Wilson and Reeder 2005; Kingston et al. 2006; Jayaraj et al. 2013; Roslan et al. 2016). In contrast, we recorded individuals from a montane site at approximately 1200 m a.s.l. (Mount Penrissen) and from a disturbed forest area (Sungai Kangkawat), highlighting the species' broader habitat tolerance than previously understood.

Echolocation. *Mops johorensis* exhibits alternating call frequencies, a characteristic commonly associated with open-space aerial foragers (Jung et al. 2007; Ellerbrok et al. 2023). The Sarawak individual demonstrated high F_{peak} (36.17–37.33 kHz), whereas the Sabah individual displayed a wider F_{peak} range (23.3–35.1 kHz). Although these could reflect habitat structure and foraging behaviour (e.g. Falcão et al. 2021; Gilmour et al.

2021), the sample size of this study is very limited, therefore these observations needed to be treated with caution. The contrast between the montane Sarawak site (approximately 1200 m elevation, montane forest, dense canopy cover) and the lowland Sabah site (open flight space) is consistent with the idea of surrounding habitat structure may influence call parameters (Roeleke et al. 2022; Liu et al. 2024; Silva et al. 2024). Given the limited sample size of *M. johorensis*, this interpretation should be considered preliminary and requires confirmation by collecting more samples.

Genetics. Genetic analysis through COI sequencing indicates that *M. johorensis* from Borneo (Sabah and Sarawak) and Kedah (Peninsular Malaysia) constitutes a monophyletic group with minimal genetic divergence. The sequences exhibited a single transition mutation at position 504 of 602 base pairs, indicating a close relationship between Bornean and Peninsular populations, which may have undergone recent divergence or gene flow. Phylogenetic analyses indicate that *M. johorensis* is most closely related to *M. plicatus*, exhibiting a genetic divergence of 9%, while its divergence from *M. mops* is 12.8%. The findings corroborate previous morphological descriptions highlighting similarities in dental structure and skull morphology between *M. johorensis* and *M. plicatus* (Freeman 1981; Francis 2008). Despite their genetic similarity, differences in call frequencies, geographic ranges, and wing morphologies indicate ecological differentiation, preventing niche overlap. Although *C. torquatus* is a more common species compared to other Malaysian molossids (Jayaraj et al. 2013), no COI gene sequence is available GenBank. This study provides the first COI gene sequences for *C. torquatus* and *M. johorensis*.

Spatial analysis and habitat modelling. The observed distribution pattern suggests that Molossidae hotspots are more prevalent in warmer lowland regions, likely due to the availability of abundant insect prey and suitable roosting sites (Janzen and Schoener 1968; Morni et al. 2018; Rosli et al. 2018; Jinggong et al. 2022; van Dijk et al. 2024; Morni et al. 2025). Notably, the prominent northern hotspot in Sabah may be associated with extensive karst ecosystems, which are critical for bat roosting. Likewise, the dense hotspot in central Sarawak is likely connected to limestone karst formations, recognized as important habitats for Molossidae species (McFarlane et al. 2015; Voight et al. 2019).

Understanding the relationship between temperature and bat distribution is essential for predicting potential range shifts under future climate scenarios. The suitability model highlights how multiple environmental factors interact to shape bat habitat preferences. The concentration of high-suitability areas in less disturbed forested landscapes underscores the importance of conserving these regions. Conservation efforts should focus on protecting key hotspots, particularly those associated with unique habitats such as caves and fragmented forests, to safeguard molossid populations.

The accuracy of spatial and habitat modelling is influenced by the sampling of both occurrence data and environmental predictors (Fourcade et al. 2014). This study focused on distribution modelling of Molossidae in Malaysian Borneo, where some hotspots predicted in the analyses showed areas close to borders with Brunei and Indonesia. Due to the absent of occurrence records from these neighboring countries, the predictions near these borders may have reduced resolution. Inclusion of data from Brunei and Indonesia in future studies would enable a more comprehensive assessment of molossid distributions across Borneo.

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ADDITIONAL INFORMATION

Conflict of interest

The authors declare that no competing interests exist.

Ethical statement

All specimens were handled in accordance with the procedures for animal care and use in accordance with ARRIVE guidelines.

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Author contributions

Conceptualization: FAAK. Data curation: MAM. Formal analysis: MAM, JWD, ERJ, SNR. Funding acquisition: FAAK. Investigation: JWD, JVK, ERJ, PR, QSR, NM, WNWA, USD, AA, LAB, AM, NHH, JS, IA. Methodology: FAAK, JWD, ERJ, PR, QSR, NM, WNWA, USD, AA, LAB, AM. Resources: FAAK. Validation: JVK, SNR, AM, NHH, JS, IA. Visualisation: MAM, ERJ, IA, SNR. Writing – original draft: FAAK, MAM. Writing – review and editing: FAAK, JVK, SNR, NHH, JS, IA.

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Data availability

All data that support the findings of this study are available in the main text and the GenBank genetic sequence records will be release online upon publication of the manuscript.

REFERENCES

Douangboubpha B, Bumrungsri S, Soisook P, Karapan S, Bates PJJ (2014) The discovery of *Kerivoula krauensis* (Chiroptera: Vespertilionidae) in southern peninsular Thailand provides new information on the distribution and conservation status of this data deficient species. Songklanakarin Journal of Science and Technology 36 (5): 577-582.

Ellerbrok JS, Farwig N, Peter F, Rehling F, Voigt CC (2023) Forest gaps around wind turbines attract bat species with high collision risk. Biological Conservation 288: 110347. https://doi.org/10.1016/j.biocon.2023.110347

Esri (2024) ArcGIS Pro (Version 3.3). Environmental Systems Research Institute. https://www.esri.com/en-us/arcgis/products/arcgis-pro/. Accessed on: 2025-03-14.

Falcão F, Dodonov P, Caselli CB, dos Santos JS, Faria D (2021) Landscape structure shapes activity levels and composition of aerial insectivorous bats at different spatial scales. Biodiversity and Conservation 30 (8): 2545–2564. https://doi.org/10.1007/s10531-021-02210-x

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37 (12): 4302–4315. https://doi.org/10.1002/joc.5086

Francis CM (2008) A field guide to the mammals of South-East Asia: Thailand, Peninsular Malaysia, Singapore, Myanmar, Laos, Vietnam and Cambodia. New Holland Publishers, London, United Kingdom, 392 pp.

Freeman PW (1981) A multivariate study of the family Molossidae (Mammalia: Chiroptera): Morphology, ecology, evolution. Fieldiana Zoology 7: 1–173. https://doi.org/10.5962/bhl.title.3128

Furey NM, Mackie IJ, Racey PA (2009) The role of ultrasonic bat detectors in improving inventory and monitoring surveys in Vietnamese karst bat assemblages. Current Zoology 55 (5): 327–341. https://doi.org/10.1093/czoolo/55.5.327

Fourcade Y, Engler JO, Rödder D, Secondi J (2014) Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PloS One 9 (5): e97122. https://doi.org/10.1371/journal.pone.0097122

Gilmour LR, Holderied MW, Pickering SP, Jones G (2021) Acoustic deterrents influence foraging activity, flight and echolocation behaviour of free-flying bats. Journal of Experimental Biology 224 (20): jeb242715. https://doi.org/10.1242/jeb.242715

Holbech LH (2020) The elevated mist-net frame: A robust and versatile manoeuvrable design for capturing upper strata birds. Methods in Ecology and Evolution 11 (9): 1086–1091. https://doi.org/10.1111/2041-210X.13425

Janzen DH, Schoener TW (1968) Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49 (1): 96–110. https://doi.org/10.2307/1933565

Jayaraj VK, Azhar MI, Daud SHM (2013) A new record of *Chaerephon johorensis* at Mount Jerai Kedah, Malaysia. Malayan Nature Journal 65: 233–235.

Jinggong ER, Rajasegaran P, Morni MA, William-Dee J, Denel A, Khan FAA (2022) Bats of Mount Silabur, Sarawak, and its potential for conservation. Borneo Journal of Resource Science and Technology 12 (1): 141–156. https://doi.org/10.33736/bjrst.4235.2022

Jung K, Kalko EAV, Von Helversen O (2007) Echolocation calls in Central American emballonurid bats: signal design and call frequency alternation. Journal of Zoology 272 (2): 125–137. https://doi.org/10.1111/j.1469-7998.2006.00250.x

Kingston T, Lim BL, Akbar Z (2006) Bats of Krau Wildlife Reserve. Penerbit Universiti Kebangsaan Malaysia, Selangor, Malaysia, 145 pp.

Kingston T, Jones G, Akbar Z, Kunz TH (2003) Alternation of echolocation calls in 5 species of aerial-feeding insectivorous bats from Malaysia. Journal of Mammalogy 84 (1): 205–215. https://doi.org/10.1644/1545-1542(2003)084%3C0205:AOECIS%3E2.0.CO;2

Lacki MJ, Amelon SK, Baker MD (2007) Foraging ecology of bats in forests. In: Lacki MJ, Hayes JP, Kurta A (Eds.) Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, Maryland, 83–127pp.

Lim VC, Ramli R, Bhassu S, Wilson JJ (2017) A checklist of the bats of Peninsular Malaysia and progress towards a DNA barcode reference library. PLoS One 12 (7): e0179555. https://doi.org/10.1371/journal.pone.0179555

Liu Y, Geng Y, Si M, Zhu D, Huang Z, Yin H, Jiang T (2024) Trait responses, nonconsumptive effects, and the physiological basis of *Helicoverpa armigera* to bat predation risk. Communications Biology 7 (1): 1436. https://doi.org/10.1038/s42003-024-07166-6

Mammal Diversity Database 2024. Mammal Diversity Database. Version 1.13. https://doi.org/10.5281/zenodo.12738010. Accessed on: 2025-03-14.

McFarlane DA, Van Rentergem G, Ruina A, Lundberg J, Christenson K (2015) Estimating colony size of the wrinkle-lipped bat, *Chaerephon plicatus* (Chiroptera: Molossidae) at Gomantong, Sabah, by quantitative image analysis. Acta Chiropterologica 17 (1): 171–177. https://doi.org/10.3161/15081109ACC2015.17.1.014

Morni MA, William-Dee J, Jinggong ER, Sabaruddin NA, Azhar NAA, Iman MA, Larsen PA, Seelan JSS, Bilung LM, Khan FAA (2025) Gut microbiome community profiling of Bornean bats with different feeding guilds. Animal Microbiome 7 (1): 21. https://doi.org/10.1186/s42523-025-00389-w

Morni MA, Khan FAA, Rosli QS, Dee JW, Tingga RCT, Rahman MRA (2018) Bats roost site preferences in Wind Cave Nature Reserve, Bau, Sarawak. Malaysian Applied Biology 47: 57–64.

Morni MA, Tahir NFDA, Rosli QS, Dee JW, Azhar I, Roslan A, Zahidin MA, Abdullah MT, Khan FAA (2016) New record of *Rhinolophus chiewkweeae* (Chiroptera: Rhinolophidae) from the east coast of Peninsular Malaysia with new information on their echolocation calls, genetics and their taxonomy. Raffles Bulletin of Zoology 64: 242–249.

Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalian: Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of Royal Society of London B 316: 335–427

Payne J, Francis CM, Phillipps K (1985) A field guide to the mammals of Borneo. The Sabah Society and World Wildlife Fund Malaysia, Kota Kinabalu, Malaysia, 332 pp.

Phillips Q, Phillips K (2016) Phillips's field guide to the mammals of Borneo and their ecology. John Beaufoy Publishing Ltd, Oxford, United Kingdom, 400 pp.

Roeleke M, Schlägel UE, Gallagher C, Pufelski J, Blohm T, Nathan R, Voigt CC (2022) Insectivorous bats form mobile sensory networks to optimize prey localization: The case of the common noctule bat. Proceedings of the National Academy of Sciences 119 (33): e2203663119. https://doi.org/10.1073/pnas.2203663119

Roslan A, David G, Zahidin MA, Rosmidi FH, Ahmad NII, Abdullah MT (2016). A new distributional record of *Chaerephon johorensis* (Chiroptera: Molossidae) at Belukar Bukit, Hulu Terengganu, Terengganu, Malaysia. Journal of Wildlife and Parks 31: 1–11

Rosli QS, Khan FAA, Morni MA, William-Dee J, Tingga RCT, Mohd-Ridwan AR (2018) Roosting behaviour and site mapping of cave dwelling bats in Wind Cave Nature Reserve, Bau, Sarawak, Malaysian Borneo. Malaysian Applied Biology 47 (1): 231–238.

Senawi J, Csorba G, Kingston T (2020) *Chaerephon johorensis*. The IUCN Red List of Threatened Species 2020: e.T4313A22019065. https://dx.doi.org/10.2305/IUCN.UK.20202.RLTS.T4313A22019065.en. Accessed on: 2025-03-03.

Silva DA, Holanda I, Aguiar L (2024) Clutter rejection and echolocation adaptations in urban-dwelling molossid bats. Acta Chiropterologica 26 (2): 237–248. https://doi.org/10.3161/15081109ACC2024.26.2.008

Simmons NB, Cirranello AL (2025) Bat Species of the World: A taxonomic and geographic database. Version 1.7. https://batnames.org/. Accessed on: 2025-02-03.

Tamura K, Stecher G, Kumar S (2021) MEGA11: molecular evolutionary genetics analysis version 11. Molecular Biology and Evolution 38 (7): 3022–3027. https://doi.org/10.1093/molbev/msab120

van Dijk LJ, Fisher BL, Miraldo A, Goodsell RM, Iwaszkiewicz-Eggebrecht E, Raharinjanahary D, Tack AJ (2024) Temperature and water availability drive insect seasonality across a temperate and a tropical region. Proceedings of the Royal Society B 291 (2025): 20240090. https://doi.org/10.1098/rspb.2024.0090

Velazco PM, Patterson BD (2014) Two new species of yellow-shouldered bats, genus *Sturnira* Gray, 1842 (Chiroptera, Phyllostomidae) from Costa Rica, Panama and western Ecuador. ZooKeys 402: 43–66. https://doi.org/10.3897/zookeys.402.7228

Voigt CC, Bumrungsri S, Roeleke M (2019) Rapid descent flight by a molossid bat (*Chaerephon plicatus*) returning to its cave. Mammalian Biology 95: 15–17. https://doi.org/10.1016/j.mambio.2019.01.001

Wilson DE, Reeder DM (2005) Mammal species of the world: a taxonomic and geographic reference. The John Hopkins University Press, Baltimore, United States, 2142 pp.

Yoh N, Kingston T, McArthur E, Aylen OE, Huang JCC, Jinggong ER, Struebig MJ (2022) A machine learning framework to classify Southeast Asian echolocating bats. Ecological Indicators 136: 108696. https://doi.org/10.1016/j.ecolind.2022.108696

Yoshiyuki M, Lim BL (2005) A new horseshoe bat, *Rhinolophus chiewkweeae* (Chiroptera, Rhinolophidae), from Malaysia. Bulletin of the National Science Museum Tokyo, Series A 31 (1): 29–36.