museu de ciències naturals de Barcelona

Animal Biodiversity and Conservation 49.1 (2026)
DOI: 10.32800/abc.2026.49.0008

Research paper

Seasonal and spatial variations in the diet of the Asiatic lesser yellow house bat (*Scotophilus kuhlii*) in Cambodian artificial guano farms

S. Sin[1], S. Kheam[1], S. Ith[1], N. O. Uk[1], J. D. Jong[2], S. Phauk[1,3]

Author affiliations:
[1] Royal University of Phnom Penh, Phnom Penh, Cambodia.
[2] Swedish University of Agricultural Sciences, Uppsala, Sweden.
[3] Uppsala University, Uppsala, Sweden.

Corresponding author:
Sopha Sin
sopha.sin@rupp.edu.kh

Handling Editor:
Sidney F. Gouveia

Received: 22/04/2025
Cond. acceptance: 11/11/2025
Final acceptance: 23/03/2026
Published: 29/04/2026

Cite:
Sin S, Kheam S, Ith S, Uk NO, Jong JD, Phauk S, 2026. Seasonal and spatial variations in the diet of the Asiatic lesser yellow house bat (*Scotophilus kuhlii*) in Cambodian artificial guano farms. *Animal Biodiversity and Conservation* 49.1, e0008. DOI: https://doi.org/10.32800/abc.2026.49.0008

Abstract

Seasonal and spatial variations in the diet of the Asiatic lesser yellow house bat (Scotophilus kuhlii) *in Cambodian artificial guano farms*. Insectivorous bats play an important ecological role in regulating insect populations and contributing to nutrient cycling. Although seasonal dietary shifts have been investigated in bats on guano farms, the diet of the Asiatic lesser yellow house bat, *Scotophilus kuhlii*, remains poorly understood in this context. This study examined seasonal and spatial variations in the diet of *S. kuhlii* across three artificial guano farms in the provinces of Kandal, Kampong Cham, and Pursat, in Cambodia. We analysed 240 faecal samples collected during dry and wet seasons and identified 18 prey types representing 13 insect families from seven orders, as well as Acari. Scarabaeidae and Lygaeidae were the primary prey during the dry season, whereas Blattellidae dominated the diet in the wet season. Dietary composition was broadly similar among guano farms in the dry season but differed significantly among sites in the wet season. Seasonal dietary shifts were largely driven by nine insect groups: Blattellidae, Lygaeidae, Formicidae, Scolytinae, unclassified Coleoptera, Pentatomidae, Scarabaeidae, Hydrophilidae, and Delphacidae. Our findings indicated that *S. kuhlii* is an opportunistic predator, with dietary shifts influenced by both seasonal change and spatial differences in prey available among sampling sites. The study highlights the ecological importance of insectivorous bats in guano farming systems, where they contribute not only to organic fertilizer production but also to sustained regulation of insect populations in surrounding agricultural landscapes.

Key words: Bat farm, Conservation, Faecal analysis, Ecosystem services, Coleoptera, Cambodia

Introduction

Bats are flying mammals belonging to the order Chiroptera, the second most diverse mammalian order comprising over 1,450 species worldwide, including 83 species recorded in Cambodia (Simmons and Cirranello 2023, Roberts et al 2024). In recent years, both farmers and conservationists have recognized the important role of bats in regulating insect pest populations within agricultural systems (Boyles et al 2011, Maine and Boyles 2015). Insectivorous bats can consume insects that amount to 80-100% of their body weight each night, highlighting their significant ecological role as natural pest control agents. This feeding capacity indicates their value in sustainable agriculture, where they provide valuable ecosystem services (Kunz et al 2011). Dietary studies consistently show that insectivorous bats prey on a range of nocturnal agricultural pests, including hemipterans, coleopterans, heteropterans, and lepidopterans (Whitaker 1988, Leelapaibul et al 2005, Oliveira et al 2015). Collectively, these findings reinforce the critical role of bats as natural pest regulators (Boyles et al 2011, Kasso and Balakrishnan 2013, Maine and Boyles 2015). Given their importance in agricultural pest suppression, understanding spatial and seasonal variations in bat diet is essential for assessing their effectiveness in regulating insect populations throughout the year.

Spatial and seasonal variations strongly influence prey availability across habitats and climatic conditions, resulting in corresponding changes in bat diet composition. Previous studies have shown that insectivorous bats adjust their diets in response to habitat structure and seasonal fluctuations in insect abundance (Whitaker et al 1996, Ober and Hayes 2008). Dietary diversity tends to be higher in warmer months when insect populations peak. In contrast, in temperate regions, bats experience severely restricted diets in winter because insects are largely absent, and many bat species enter hibernation

© [2026] Copyright belongs to the authors, who license the journal *Animal Biodiversity and Conservation* to publish the paper under a Creative Commons Attribution 4.0 License.

ISSN: 1578-665 X eISSN: 2014-928 X

during this period (Kunz et al 1995, Hope and Jones 2012). In tropical ecosystems, seasonal dietary shifts have also been observed in various bat species. For example, in Thailand, *Mops plicatus* (Buchanan, 1800) adjusts its diet in response to seasonal changes, feeding on available prey across different habitats (Srilopan et al 2018, Suksai and Bumrungsri 2019, Thongjued et al 2021). These studies demonstrate species-specific foraging adaptability and emphasize the dynamic predatory role of bats in the ecosystem. Understanding dietary shifts across habitats and seasons, particularly in artificial guano farms, is crucial for evaluating the ecological and conservation roles of bats in agricultural landscapes. Artificial bat guano farms, designed to encourage bat roosting and guano collection, have gained increasing attention as a sustainable strategy of improving soil fertility and enhancing pest management (Propper et al 2023). These farms typically consist of artificial roosting structures that support bat colonies and facilitate the accumulation of natural guano for agricultural use (Kunz et al 2011).

Cambodia and Vietnam have successfully established bat farms for guano production (Furey 2012). Large colonies of *Scotophilus kuhlii* Leach, 1821, have been documented roosting in guano farms across Kandal, Kampong Cham, Pursat, and Takeo provinces, in Cambodia. These farms often use dome-shaped roosts made of palm leaves, either hoisted into trees or mounted on artificial structures to attract bats (Chhay 2012). The collected guano is used or sold by local farmers as organic fertilizer. With a growing emphasis on organic farming, Cambodia has benefited from these artificial guano farms, which provide a sustainable, nutrient-rich fertilizer that enhances crop production (Racey 2009). Bat guano increases soil microbial activity, promotes healthier crop growth, and reduces dependence on chemical fertilizers (Furey and Racey 2016).

Additionally, the presence of insectivorous bats in these artificial structures contributes significantly to pest suppression, as these bats consume large quantities of agricultural pests, reducing the need for synthetic pesticides (Boyles et al 2011, Thi et al 2014, Sek 2018). Despite these benefits, proper management and conservation are essential to ensure bat health and prevent ecological disruptions associated with excessive guano harvesting. Overharvesting can destabilize roost substrates and disturb colonies during sensitive periods such as lactation or juvenile development (Mildenstein et al 2016, Voigt and Kingston 2016). Human disturbance, such as frequent entry, noise, or bright lights can increase stress, trigger roost abandonment, and reduce reproductive success (Voigt and Kingston 2016). Inadequate maintenance of roosting structures, including insufficient darkness, poor microclimate conditions, or a lack of predator control, further threatens colony persistence (Kunz et al 2011, Russo and Ancillotto 2015). Addressing these risks underscores the importance of well-managed artificial guano farms for conserving bat populations while supporting sustainable agriculture.

One species that plays a crucial role in these artificial guano farms in Cambodia is the Asiatic lesser yellow house bat, *Scotophilus kuhlii* (Tuttle 2015). This insectivorous bat species, native to South and Southeast Asia, forms colonies ranging from 1,000 to 10,000 individuals (Bates and Harrison 1997, Francis 2019). Its common presence in agricultural landscapes and human settlements makes it particularly suited to roosting in artificial structures designed for guano production (Hisheh et al 2004). *Scotophilus kuhlii* exhibits a strong preference for foraging in agricultural and urban environments (Sun et al 2008, Zhu et al 2012). Previous studies reveal that it primarily consumes nocturnal insects, including agriculturally significant pests such as beetles (Coleoptera) and moths (Lepidoptera), positioning it as a natural biocontrol agent that could reduce reliance on chemical pesticides in agroecosystems (Srinivasulu et al 2010). However, despite its ecological importance, *S. kuhlii* remains understudied in the context of artificial guano farming, a practice more commonly associated with cave-dwelling bat species (Fujita and Tuttle 1991). A study in Cambodia showed that *S. kuhlii* frequently forages around lowland rice paddy fields, where pest insects make up a substantial portion of its diet (Sek 2018). Clarifying its dietary composition is therefore important for evaluating its contribution to insect population suppression in agricultural systems.

Prioritizing research on this species can strengthen the link between sustainable agriculture and bat conservation, supporting both food security and ecosystem resilience. This study aimed to investigate the dietary preferences of *S. kuhlii* in Cambodia by examining its prey composition across artificial guano farms and seasons. We predicted that dietary composition would vary seasonally and among guano farms, with *S. kuhlii* consuming a wide range of insect groups. By clarifying its overall dietary composition, this study provides important insights into how *S. kuhlii* responds to seasonal and habitat-specific variations in prey availability within agricultural landscapes. These findings also contribute to a broader understanding of how artificial guano farms can support the long-term conservation of bat colonies and maintain key ecological functions associated with insectivorous bats.

Material and methods

Study area

This study was conducted at three artificial bat guano farms hosting *Scotophilus kuhlii* colonies, all located within lowland rice paddy landscapes in Cambodia (fig. 1A). Each site represents a distinct agricultural environment featuring artificial roosts constructed to support bat populations.

The first site (fig. 1B) is located in Kandal province (11° 22.874' N, 105° 1.166' E) near the Tonle Bassac River, and lies at the confluence of the Tonle Sap and Mekong River distributaries. This region contains nutrient-rich floodplains supporting rice cultivation and mixed crops such as long beans, cucumbers, and cabbage. The area experiences a humid tropical climate (26-35 °C) with annual rainfall averaging 1,200-1,400 mm, concentrated in the wet season (May-October). The average annual precipitation during the dry season (December to April) is approximately 196 mm (World Bank 2021).

The second site (fig. 1C), in Kampong Cham province (11° 54.620' N, 105° 8.049' E), is located approximately 75 km from the first site and within the central Mekong lowlands. The agricultural landscape is similar, characterized by expansive rice fields and additional cultivated crops. The climate is quite humid (25-36 °C) with rainfall

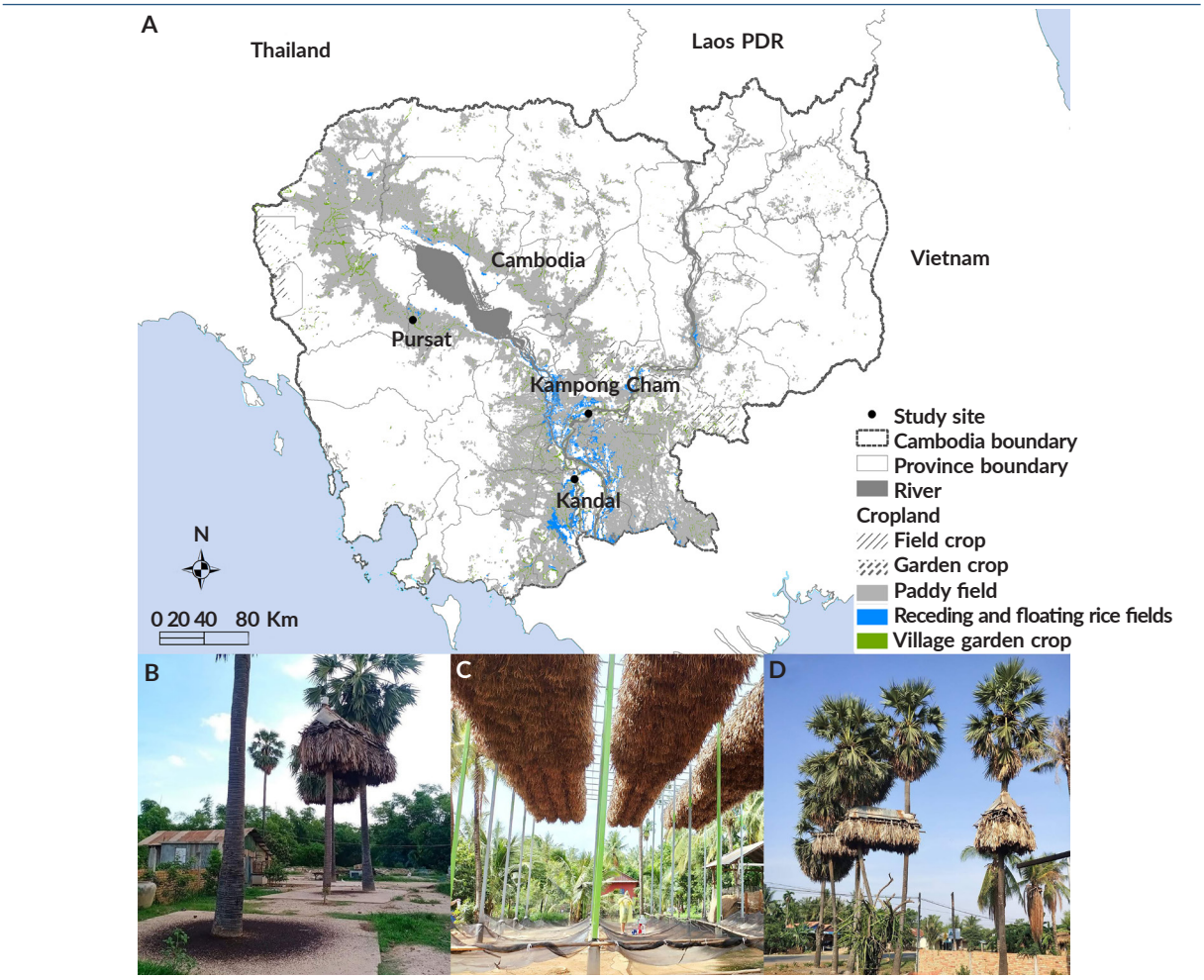

Fig. 1. Bat guano farms of *Scotophilus kuhlii* in the lowland paddy fields of Cambodia: A, map of the study areas; B-D, bat guano farms; B, Kandal province; C, Kampong Cham (©Thavry Hoem); and D, Pursat (©KimSeng Keng).

slightly higher than in Kandal (1,400-1,600 mm annually) due to its position within the Mekong floodplain. During the dry season, water levels drop markedly, but proximity to the Mekong River helps buffer extreme drought conditions (World Bank 2021).

The third site (fig. 1D) is located in Pursat province (12° 39.520' N, 103° 40.434' E), and lies approximately 270 km northwest of the other two locations. The landscape is dominated by paddy fields interspersed with cucumber plantations and palm trees. The area is situated near the Tonle Sap floodplain, and experiences a tropical monsoon climate (24-35 °C). Rainfall is highest among the three sites, averaging 1,600-1,800 mm per year, influenced by moisture from Tonle Sap Lake. Seasonal flooding is common during peak monsoon months (July-September). The dry season is characterized by lower humidity, stronger winds, and reduced water availability, affecting local agricultural production (World Bank 2021).

Faecal sampling and analysis

Faecal (guano) samples were collected on four sampling occasions at each farm in 2021, encompassing both the dry season (March and April) and the wet season (June and July). To minimise variation introduced by farm owners, all collectors received identical written and verbal instructions on sampling procedures. Fresh samples were obtained immediately after bats returned to the roost at dawn, allowing newly deposited pellets to be clearly distinguished from older material. Samples were delivered to the first author on the same day. For each sampling occasion, 20 faecal pellets were randomly selected from each farm, yielding a total of 240 pellets (20 × 4 sampling occasions × 3 farms). These pellets were selected for analysis across all farms and sampling occasions. Each pellet was treated as an individual sample for dietary analysis. All samples were preserved in 70 % ethanol and transported to the Cambodian Entomology Initiatives (CEI) laboratory at the Royal University of Phnom Penh for analysis. Faecal samples were analysed using standard methods for food habits analysis (Whitaker 1988, Whitaker et al 2009) and protocols from previous studies (Sin et al 2020). Prey fragments were carefully separated using needles or fine forceps and examined under an Olympus SZ51 microscope. Identification to

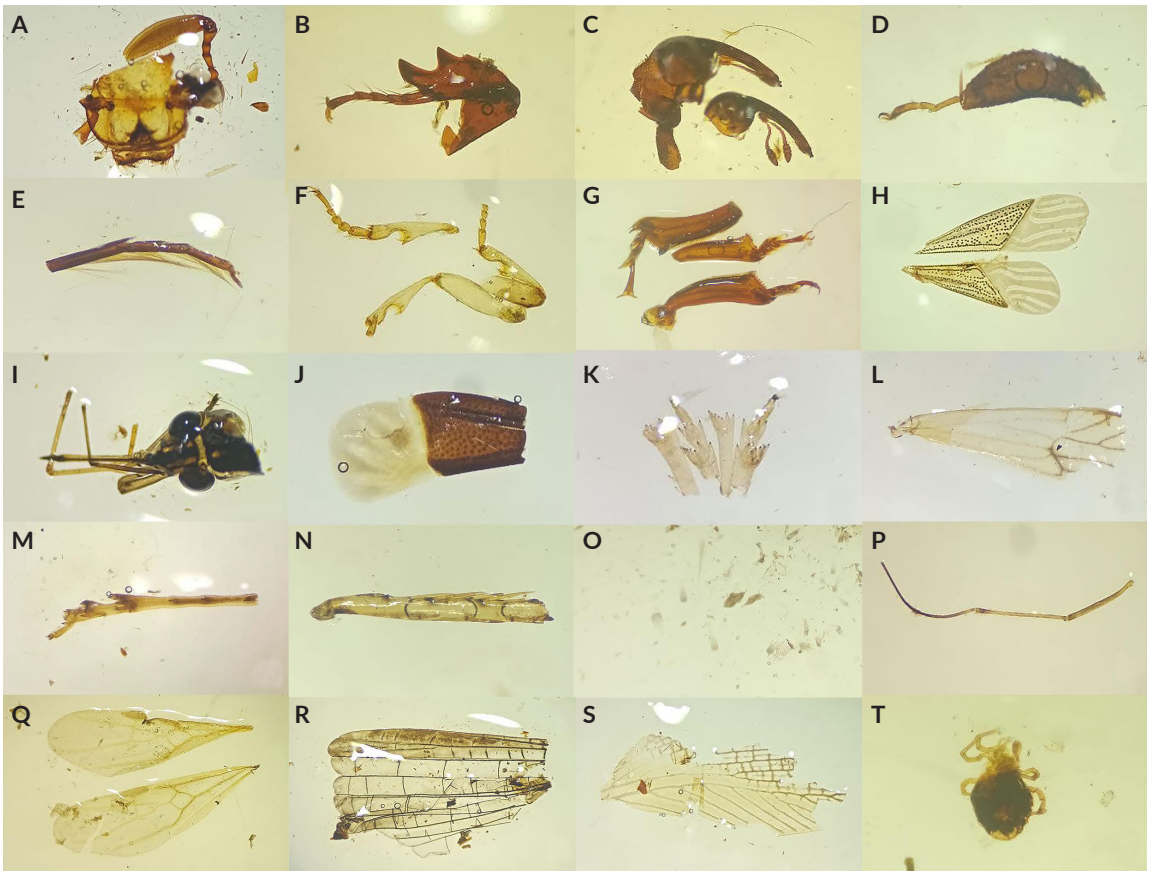

Fig. 2. Fragments of prey types represent in the diet of *Scotophilus kuhlii*: A-B, Scarabaeidae; A, head and antennae; B, leg; C, Curculionidae-head; D, Scolytinae-leg; E, Hydrophilidae-swimming leg; F, Carabidae-legs; G, Nitidulidae-legs; H-I, Lygaeidae; H, wings; I, head; J, Pentatomidae-wing; K-L, Delphacidae; K, legs; L, wing; M, Cixiidae-leg; N, Cicadellidae; O, Lepidoptera - wing scales; P, Diptera-leg; Q, Formicidae-wings; R, Orthoptera-wing; S, Blattellidae-wing; and T, Acari-body. Not to scale.

order and family levels was conducted using taxonomic keys and illustrations from Whitaker (1988), McAney et al (1991), Wilson and Claridge (1991), Johnson and Borror (2005), Pokhrel and Budha (2014), Waghiiwimbom et al (2019), and Sin et al (2020).

Statistical analysis

Identified prey types were visually quantified, and their percentage volume (PV) and percentage frequency (PF) were calculated following Whitaker (1988) and Whitaker et al (2009). PV represents the proportion of each prey type in the composite sample, while PF indicates the percentage of samples in which a prey type occurred across seasons and sites. Presence-absence data for identified prey types (orders and families) were also recorded, following the approach of Leelapaibul et al (2005). Because soft-bodied insects are easily digestible and often underrepresented in PV, both PV and PF were used to reduce bias when comparing seasonal and geographical variation in the diet. Differences in diet composition among seasons and guano farms were tested using the non-parametric *Kruskal-Wallis* test, followed by *Dunn's post-hoc* comparisons. Ordination analyses were conducted to assess dissimilarities among sample groups, and visualized using a non-metric multidimensional scaling (NMDS) plot. Analysis of Similarities (ANOSIM) was used to evaluate differences between seasonal variations and guano farms. Indicator Species Analysis (ISA; De Cáceres et al 2010) was performed to identify prey groups significantly associated with seasons and guano farms. All statistical analyses were conducted in R version 4.2.2 (R Core Team, 2022) using the *vegan* and *ggplot2* packages for NMDS and ANOSIM, and the *indicspecies* package for ISA. Statistical significance was set at $p < 0.05$.

Results

Diet composition

A total of 240 faecal samples, comprising 80 pellets from each guano farm, were analysed to identify the prey types consumed by *S. kuhlii*. Eighteen distinct prey types were recorded, representing seven insect orders: Coleoptera (unclassified Coleoptera, Scarabaeidae, Curculionidae, Scolytinae, Hydrophilidae, Carabidae, and Nitidulidae), Hemiptera (Lygaeidae and Pentatomidae, Delphacidae, Cixiidae and Cicadellidae), Lepidoptera, Diptera, Hymenoptera (Formicidae), Orthoptera and Blattodea (Blattellidae), along with Acari (mites) (fig. 2).

Table 1. Percentage volume (PV) mean ± SD and percentage frequency (PF) of prey types identified in the diet of *Scotophilus kuhlii* during the dry and wet seasons at the three artificial guano farms: Kandal, Kampong Cham, and Pursat provinces, Cambodia.

	Kandal				Kampong Cham				Pursat			
	Dry		Wet		Dry		Wet		Dry		Wet	
Prey type	PV	PF	PV	PF	PV	PF	PV	PF	PV	PF	PV	PF
Coleoptera												
Unclassified												
Coleoptera	0	0	1.0 ± 4.5	5	0.2 ± 1.6	3	0	0	0	0	13.9 ± 23.6	38
Scarabaeidae	28.2 ± 26.4	83	15.0 ± 22.9	53	44.4 ± 33.7	98	29.3 ± 23.6	78	15.5 ± 22.5	65	11.7 ± 13.7	53
Curculionidae	16.7 ± 21.6	65	11.1 ± 23.9	33	18.2 ± 23.3	58	12.7 ± 19.6	48	2.3 ± 6.0	18	5.0 ± 11.4	25
Carabidae	1.3 ± 4.0	13	0.4 ± 1.7	8	3.8 ± 6.5	35	2.6 ± 4.8	33	0.6 ± 2.3	8	4.4 ± 6.4	40
Nitidulidae	2.0 ± 6.9	13	1.6 ± 6.7	8	1.6 ± 3.6	18	0.7 ± 3.3	5	0	0	0.6 ± 2.3	8
Hydrophilidae	0.1 ± 0.3	3	0.2 ± 0.8	5	0	0	0.2 ± 1.0	5	0	0	0.3 ± 1.1	5
Scolytinae	0	0	12.0 ± 29.6	23	0	0	10.4 ± 22.6	28	0	0	0	0
Hemiptera												
Lygaeidae	30.6 ± 22.8	83	3.5 ± 5.4	43	19.1 ± 18.2	73	8.9 ± 8.4	65	62.2 ± 36.4	85	9.1 ± 10.6	75
Pentatomidae	1.3 ± 7.9	5	0.7 ± 2.3	8	5.7 ± 10.2	43	0.3 ± 1.1	5	9.7 ± 21.1	33	1.7 ± 4.0	18
Delphacidae	10.4 ± 17.6	53	1.4 ± 6.5	10	0.3 ± 1.3	8	0.8 ± 2.9	8	1.1 ± 4.1	13	2.7 ± 4.2	35
Cicadellidae	3.4 ± 5.5	40	6.2 ± 12.5	35	1.7 ± 5.2	28	3.4 ± 5.9	33	2.3 ± 6.0	25	2.9 ± 4.9	30
Cixiidae	0	0	0.1 ± 0.7	3	0	0	0	0	0	0	1.5 ± 5.3	10
Lepidoptera	0.5 ± 1.4	13	0.6 ± 1.5	20	0.3 ± 1.2	10	0.5 ± 1.4	15	1.2 ± 2.9	20	1.8 ± 2.3	50
Diptera	0.3 ± 2.0	3	0.3 ± 1.0	8	0.1 ± 0.7	3	0.1 ± 0.6	3	0.3 ± 0.9	18	0	0
Hymenoptera												
Formicidae	2.2 ± 6.3	20	12.3 ± 24.5	45	2.1 ± 3.9	30	1.7 ± 5.0	15	1.0 ± 3.4	13	11.1 ± 15.3	50
Orthoptera	2.6 ± 5.6	30	2.0 ± 4.9	18	1.0 ± 2.2	20	3.5 ± 6.3	33	3.5 ± 4.7	53	2.6 ± 8.0	18
Blattodea												
Blattellidae	0.3 ± 1.6	3	31.5 ± 37.3	68	1.3 ± 3.8	13	25.0 ± 29.7	78	0.1 ± 0.8	3	30.7 ± 24.9	98
Acari	0.2 ± 0.8	5	0.2 ± 0.6	13	0.03 ± 0.1	3	0.1 ± 0.4	5	0.1 ± 0.4	10	0.2 ± 0.6	10

Based on percentage volume (PV), the most abundant prey families were Scarabaeidae (23.9 ± 26.6 %), Lygaeidae (22.0 ± 27.9 %), and Blattellidae (14.4 ± 25.5 %), followed by Curculionidae (10.8 ± 19.4 %), and Formicidae (5.0 ± 13.1 %). Less frequently consumed groups included Delphacidae, Cicadellidae, Cixiidae, Lepidoptera, Diptera, Orthoptera, and mites (table 1).

Percentage frequency (PF) showed a similar pattern with Scarabaeidae (71 %), Lygaeidae (70 %), Blattellidae (43 %), and Curculionidae (41 %) being the most commonly detected prey families. Other groups occurred less frequently, generally below (40 %) of samples (table 1). Overall, these results indicate that *S. kuhlii* primarily feeds on beetles and true bugs, with cockroaches and ants representing important secondary dietary components.

Seasonal and spatial variation in diet

The analysis of seasonal dietary composition revealed that the two most significant food sources for *S. kuhlii* were Lygaeidae and Scarabaeidae, which dominated the diet. Other major prey groups included Curculionidae, Pentatomidae, and Delphacidae based on both PV and PF values across all guano farms, except for Curculionidae in Pursat and Pentatomidae in Kandal during the dry season (table 1). Consumption of these prey decreased significantly during the wet season, whereas Blattellidae, Formicidae, and Scolytinae increased, except for Formicidae in Kampong Cham and Scolytinae in Pursat province. Additional prey types, including Coleoptera, Lepidoptera, Carabidae, and Cixiidae, were also observed in the Pursat site. Remaining prey groups were infrequently detected in both seasons.

Kruskal-Wallis test for PV revealed a minor but significant difference among guano farms during the dry season ($H_{(2)} = 6.09$, $P = 0.047$), indicating slight variation in prey composition among farms during this period. A stronger effect was observed during the wet season ($H_{(2)} = 13.35$, $P = 0.001$), reflecting greater dietary differences among farms when prey diversity is higher. *Dunn's post-hoc* test showed that these differences were driven primarily by

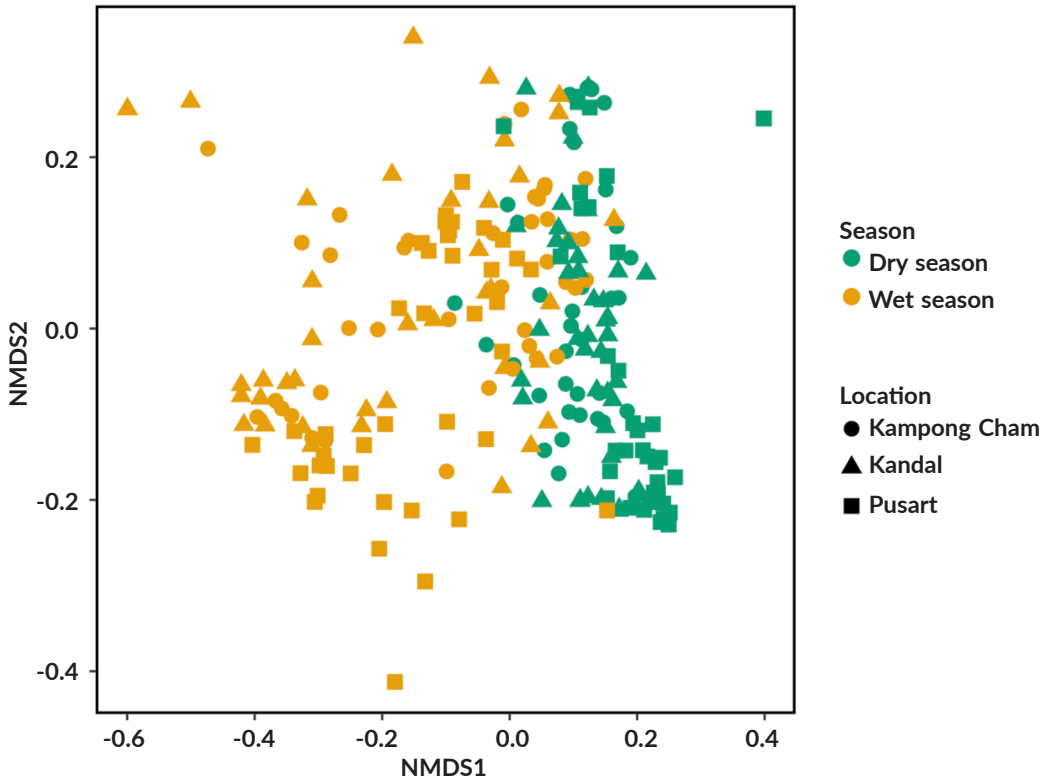

Fig. 3. Two-dimensional NMDS ordination of the diet of *Scotophilus kuhlii* in the seasonal variation from guano farms at Kandal, Kampong Cham, and Pursat provinces, Cambodia.

contrasts between Kandal and Pursat (dry: $P = 0.038$; wet: $P = 0.0008$), while no significant differences were observed between other farm pairs in either season. For PF, no significant differences among guano farms were found in the dry season ($H_{(2)} = 5.75$, $P = 0.056$), suggesting a broadly similar feeding pattern across sites when prey resources are limited. However, significant differences in the wet season ($H_{(2)} = 15.299$, $P = 0.0004$) reveal that PF composition varies more substantially among farms when seasonal prey diversity increases. *Dunn's post hoc* test indicated that the guano farm in Pursat differed significantly from both Kampong Cham ($P = 0.019$) and Kandal ($P = 0.0003$). *NMDS* visualisation showed clear seasonal separation in dietary composition, indicating distinct shifts in prey consumption between the dry and wet seasons (fig. 3). *ANOSIM* analysis confirmed a significant difference in diet between the dry and wet seasons ($R = 0.323$, $P = 1e\text{-}04$). Spatial differences among guano farms were smaller but still significant ($R = 0.087$, $P = 1e\text{-}04$), indicating that seasonal factors exert a stronger influence than site-level differences. These results suggest that *S. kuhlii* shows stronger dietary differentiation among sites during the wet season, likely reflecting seasonal differences in prey availability.

Indicator species analysis

Indicator species analysis (ISA) identified 13 specific prey types significantly associated with seasons or guano farms (table 2). During the dry season, most indicator prey belonged to Lygaeidae and Pentatomidae, followed by Scarabaeidae and Delphacidae. In the wet season, Blattellidae was the strongest indicator, followed by Scolytinae, Formicidae, and unclassified Coleoptera, and minor association of Hydrophilidae. Spatially, ISA revealed variations in prey consumption across the guano farms. In Pursat, the most important prey indicator included Lygaeidae, unclassified Coleoptera, and Lepidoptera, followed by Cixiidae and Pentatomidae. In Kandal, Delphacidae was the only significant indicator prey, whereas Scarabaeidae was the primary indicator prey in Kampong Cham. Additional associations were observed across multiple farms, including Curculionidae and Scolytinae (Kandal and Kampong Cham), Carabidae (Kampong Cham and Pursat), and Formicidae (Kandal and Pursat). These associations highlight both seasonal and spatial variation in prey availability and demonstrate the flexible foraging behaviour in *S. kuhlii*.

Discussion

Diet composition

The diet of *Scotophilus kuhlii* contained insects from several orders, including Hemiptera (Lygaeidae, Pentatomidae), Coleoptera (Scarabaeidae, Curculionidae, Scolytinae), Blattodea (Blattellidae), and Hymenoptera (Formicidae), indicating broad dietary flexibility. This pattern is consis-

Table 2. Indicator species analysis (ISA) of prey types consumed by *S. kuhlii* associated with the different seasons and guano farms at Kandal, Kampong Cham, and Pursat provinces, Cambodia. Asterisks indicate significant in percentage frequency of prey types for specific seasonal and spatial variations (*p-value < 0.05, ** p-value < 0.01, *** p-value < 0.001). The indicator value (IndVal) index measures the association between a prey taxon and a season/site group.

	Season				Bat guano farms				
Prey type	Dry	Wet	IndVal	p-value	Kandal	Kampong Cham	Pursat	IndVal	p-value
Coleoptera									
Unclassified									
Coleoptera	–	***	0.222	0.0001	–	–	***	0.285	0.0001
Scarabaeidae	**	–	0.203	0.0012	–	***	–	0.339	1e-04
Curculonidae	–	–	–	–	***	***	–	0.262	0.0003
Carabidae	–	–	–	–	–	**	**	0.189	0.0081
Hydrophilidae	–	*	0.137	0.0457	–	–	–	–	–
Scolytinae	–	***	0.233	0.0001	*	*	–	0.165	0.0212
Hemiptera									
Lygaeidae	***	–	0.533	0.0001	–	–	***	0.341	0.0001
Pentatomidae	***	–	0.218	0.0002	–	–	*	0.161	0.0277
Delphacidae	*	–	0.134	0.0339	***	–	–	0.254	4e-04
Cixiidae	–	–	–	–	–	–	*	0.151	0.0354
Blattodea									
Blattellidae	–	***	0.542	0.0001	–	–	–	–	–
Hymenoptera									
Formicidae	–	***	0.249	0.0001	*	–	*	0.168	0.0218
Lepidoptera	–	–	–	–	–	–	***	0.248	0.0006

tent with previous findings from southern China, where Coleoptera, Hemiptera, Lepidoptera, and Hymenoptera were the major dietary components of *S. kuhlii* (Zhu et al 2012). Similar patterns have also been reported in other *Scotophilus* species, such as *S. heathi* (Horsfield, 1831) and *S. leucogaster* (Cretzschmar, 1826), further demonstrating that members of this genus commonly exploit a wide range of insect groups in agricultural and urban habitats (Advani 1983, Barclay 1985). The diversity of prey detected in this study suggested that *S. kuhlii* is an opportunistic predator capable of adjusting its diet to locally available prey. Consequently, it may interact with a broad array of insect taxa, including groups that contain important agricultural pests (e.g., Lygaeidae, Pentatomidae, Delphacidae, Cixiidae, and Cicadellidae). However, the population-level impact on these insect groups remains uncertain. The faecal analyses in our study reflect only the prey consumed and do not provide information on the relative abundance of insects in the surrounding environment. It remains unclear whether these dietary patterns result from active prey selection or simply from variation in local insect availability. Future studies combining faecal analysis with concurrent assessments of insect community composition would enable a more robust evaluation of the potential role of *S. kuhlii* in pest suppression within agricultural landscapes.

A notable finding was the low proportion of Lepidoptera (moths) in the diet of *S. kuhlii*, despite moths being abundant nocturnal insects and an important prey group for many bat species (Alviola et al 2023). A likely explanation is the temporal mismatch between the foraging activity of *S. kuhlii*, which typically occurs approximately 2 hours after nightfall (Atiqah et al 2015), and the peak activity of many moths, which often occurs closer to the early morning hours (Whitaker et al 1996). This reduced temporal overlap may limit encounters between predator and prey, resulting in fewer moths being consumed (Fullard et al 1994). Another possible explanation concerns the prey capture strategy. Moths often require highly manoeuvrable flight and specialized foraging behaviours to be captured effectively (Schnitzler and Kalko 2001). Probably, *S. kuhlii* may not be morphologically or behaviourally adapted for effective moth capture (Norberg and Rayner 1987). Overall, these factors suggest that *S. kuhlii* relies more heavily on insect groups that are both abundant and more easily accessible during its peak activity foraging period, reflecting an opportunistic feeding strategy.

Acari (mites) were present in very low proportions across seasons and guano farms. Their presence was most likely incidental, as mites commonly occur on beetles, cockroaches, and in guano-rich environments (Walter and

Proctor 2013, Krantz and Walter 2009). Because *S. kuhlii* frequently consumed Scarabaeidae and Blattellidae, mites may have been ingested unintentionally along with these primary prey. In addition, parasitic mites (e.g., Spinturnicidae and Macronyssidae), which inhabit bat skin and fur, may also be consumed during grooming (Morales-Malacara and López-Ortega 2001). Similar findings have been detected in *Rhinolophus shameli*, *Hipposideros larvatus*, and *H. gentilis* (Sin et al 2020), as well as in eight bat species of the genera *Rhinolophus* and *Hipposideros* documented in Nepal (Pokhrel and Budha 2014). Their presence highlights broader arthropod interactions in guano farm ecosystems. Future metabarcoding studies could help clarify whether mites are ingested passively or actively, and whether their occurrence varies seasonally or in relation to habitat conditions.

Although morphological analysis of prey fragments is crucial for understanding bat diet composition, this approach has inherent limitations because prey identification relies on recognizable chitinous fragments. As a result, detection may be biased toward heavily sclerotized insects such as beetles and true bugs, as soft-bodied or highly fragmented prey may be underrepresented in PF and PV estimates (Whitaker 1988, Clare et al 2009, Pompanon et al 2012). Molecular techniques, particularly DNA metabarcoding, can complement traditional morphological analyses by detecting prey DNA from degraded remains and improving taxonomic resolution, often allowing identification to the genus or species level (Clare et al 2009, Pompanon et al 2012, Deagle et al 2018). Integrating both approaches would provide a more comprehensive understanding of the dietary ecology of *S. kuhlii* and its ecological role in agricultural landscapes.

Seasonal and spatial variations in diet

Seasonal changes in dietary composition indicate that *S. kuhlii* closely tracks fluctuations in insect availability. Dietary diversity increased during the wet season, aligning with the expected rises in insect abundance associated with higher humidity, vegetation growth, and expanded breeding opportunities for many insect species (Janzen and Schoener 1968). The greater prey diversity observed during the wet season likely enables *S. kuhlii* to exploit a wider range of insect taxa, thereby reducing reliance on specific prey families. A similar pattern has been reported in rice-field landscapes in Peninsular Malaysia, where *Rhinolophus coelophyllus*, *R. malayanus*, *R. pusillus*, and *R. refulgens* exhibited seasonal shifts in the consumption of Coleoptera, Lepidoptera, Hemiptera, and Diptera reflecting adjustments in foraging behaviour in response to changing insect communities (Abdullah et al 2024). Despite these seasonal shifts, scarab beetles (Scarabaeidae) remained one of the most consistently consumed prey groups. This pattern aligns with the ecological dominance of Scarabaeidae across a wide range of habitats (Bogdanowicz et al 1999, Biedermann and Nuotclà 2020). Their robust exoskeletons and strong flight capabilities likely make them readily detectable to insectivorous bats, including *S. kuhlii* (Alviola et al 2023). Interestingly, although scarab beetles remained an important dietary component throughout the year, their proportion in the faecal samples was significantly higher during the dry season than the wet season. This pattern may reflect the increased availability of alternative prey groups in the wet season. As insect abundance and diversity increase, *S. kuhlii* may broaden its diet to include additional prey types, thereby reducing the relative contribution of scarab beetles (Janzen and Schoener 1968).

Scotophilus kuhlii showed a clear seasonal shift in prey composition, with Hemiptera-particularly Lygaeidae-becoming dominant during the dry season. This pattern is consistent with evidence that Lygaeidae populations, including *Nysius* species, tend to peak under dry conditions due to their multigenerational breeding cycles (Du Plessis et al 2011, Burdfield-Steel and Shuker 2014, Haouas et al 2019, Scaccini and Furlan 2021). These findings suggest that *S. kuhlii* closely responds to seasonal dynamics in insect abundance. In contrast, during the wet season, cockroaches (Blattellidae) became the primary prey, while the proportions of Lygaeidae and Scarabaeidae decreased significantly. Cockroaches are typically associated with dark, sheltered microhabitats such as leaf litter and roof structures (Johnson and Borror 2005). A study from Tanzania similarly reported a high prevalence of cockroaches in roof roosts, where they constituted a major prey item for *Chaerephon pumilus* (Aspetsberger et al 2003). Advani (1983) also noted that bats often forage near their roosting sites, particularly during the wet season, where cockroaches and beetles may be abundant. The construction of guano farms-especially those using dried palm leaves-likely provides favourable microhabitats for cockroaches, increasing their availability to foraging bats during periods of high moisture. Seasonal rainfall may further influence prey emergence patterns and bat foraging activity (Voigt et al 2011), contributing to the observed shifts in prey selection. Interestingly, seasonal variation in prey consumption was primarily associated with nine specific prey types, suggesting that *S. kuhlii* may exhibit dietary selectivity. However, without direct measurements of insect availability, it remains unclear whether these shifts are driven by changes in prey abundance or by bat foraging preferences.

In addition to seasonal differences, we also detected geographical variation in the diet of *S. kuhlii* across guano farms. These spatial patterns indicate that this bat species adjusts its diet in response to local prey availability, habitat structure, and landscape features. Significant differences in prey composition were observed among Kandal, Kampong Cham, and Pursat provinces, suggesting distinct dietary patterns across regions. This variation is consistent with previous studies documenting landscape-driven dietary shifts in bat species such as *Myotis sodalist*, *Taphozous melanopogon*, *Mops plicatus*, *Tylonycteris pachypus*, and *T. robustula* (Kurta and Whitaker 1998, Leelapaibul et al 2005, Srinivasulu and Srinivasulu 2005, Zhang et al 2005). The adaptability of bats to different food sources is strongly influenced by prey availability and habitat characteristics (Srinivasulu and Srinivasulu 2005), further supporting the idea that *S. kuhlii* is an opportunistic predator capable of adjusting its diet in response to changing environmental conditions. The dietary similarity between Kandal and Kampong Cham likely reflects shared ecological conditions along the Mekong River. In contrast, the distinct dietary profile in Pursat may be shaped by the unique hydrological regime and seasonal flood dynamics of the Tonle Sap floodplain, which influence local insect communities.

Conclusions

This study highlights the ecological role of *S. kuhlii* as a flexible and opportunistic predator capable of responding to both seasonal and spatial variation in insect communities. This dietary adaptability may enhance its contribution to ecosystem functioning, particularly in agricultural landscapes and guano farming systems. By supporting large bat colonies, guano farms provide a potential source of high-quality fertilizer, contributing to sustainable agricultural practices. Furthermore, these bat colonies may provide indirect benefits through the ecosystem service of insect pest suppression, suggesting that guano farms can function as multifunctional components of the agroecological landscapes. Understanding the dietary patterns of *S. kuhlii* can inform the design and management of artificial roosts to support healthy bat populations and optimise their ecological and economic benefits for local communities. Given that these benefits are threatened by illegal hunting (Mekong Eye 2024), targeted conservation and management efforts are needed to protect this bat species. Protecting *S. kuhlii* is likely to support biodiversity conservation while also contributing to the long-term sustainability of agricultural practices and ecosystem services in Cambodia.

References

Abdullah N-I, Elias N-A, Ohte N, Vincenot C, 2024. Resource partitioning among bat species in Peninsular Malaysia rice fields. *PeerJ* 12, e16657. DOI: 10.7717/peerj.16657

Advani R, 1983. Observations on the seasonal variations in food composition and some behavioral patterns of *Scotophilus h. heathi* (Chiroptera: Vespertilionidae) in Rajasthan. *Mammalia* 47, 215-219.

Alviola PA, Alviola MS, Taray KJ, Lucañas CC, De Guia AP, Dupo AL, Cuevas VC, Pampolina NM, Lit Jr IL, 2023. Dietary analysis of eight insectivorous bats (Chiroptera) from Puting Bato Cave Complex, Burdeos, Polillo Island, Philippines. *Journal of Asia-Pacific Biodiversity* 16(2023), 291-299. DOI: 10.1016/j.japb.2023.05.003

Aspetsberger F, Brandsen D, Jacobs DS, 2003. Geographic variation in the morphology, echolocation and diet of the little free-tailed bat, *Chaerephon pumilus* (Molossidae). *African Zoology* 38(2), 245-254. DOI: 5627020.2003.11407278

Atiqah N, Akbar Z, Syafrinna Ubaidah N, Foo NY, 2015. Comparison of the ranging behavior of *Scotophilus kuhlii* (Lesser Asiatic Yellow Bat) in the agricultural and urban landscape. In AIP *Conference Proceedings* 1678, 020026-1-6. DOI: 10.1063/1.4931211

Barclay RM, 1985. Foraging behavior of the African insectivorous bat, *Scotophilus leucogaster*. *Biotropica* 17, 65-70. DOI: 10.2307/2388381

Bates PJJ, Harrison D, 1997. Bats of the Indian Subcontinent. Harrison Zoological Museum, Sevenoaks, Kent, UK 258. ISBN 0-9517313-1-9. DOI: 10.1023/A:1017113501563

Biedermann PHW, Nuotclà JA, 2020. Social Beetles. *Encyclopedia of Social Insects* pp. 1-8.

Bogdanowicz W, Fenton MB, Daleszcyk K, 1999. The relationships between echolocation calls, morphology, and diet in insectivorous bats. *Journal of Zoology* 247, 381-393. DOI: https://doi.org/10.1111/j.1469-7998.1999.tb01001.x

Boyles JG, Cryan PM, Mccracken GF, Kunz TH, 2011. Economic importance of bats in agriculture. *Science* 332, 41-42. DOI: 10.1126/science.1201366

Burdfield-Steel ER, Shuker DM, 2014. The evolutionary ecology of the Lygaeidae. *Ecology and Evolution* 4(11), 2278-2301. DOI: 10.1002/ece3.1093

Chhay S, 2012. Cambodian bats: a review of farming practices and economic value of lesser Asiatic yellow house bat *Scotophilus kuhlii* (Leach, 1821). *Cambodian Journal of Natural History* 2012(2), 164-165.

Clare EL, Fraser EE, Braid HE, Fenton MB, Hebert PD, 2009. Species on the menu of a generalist predator, the eastern red bat (*Lasiurus borealis*): using a molecular approach to detect arthropod prey. *Molecular ecology* 18(11), 2532-2542. DOI: 10.1111/j.1365-294X.2009.04184.x

Deagle BE, Thomas AC, McInnes JC, Clarke LJ, Vesterinen EJ, Clare EL, Kartzinel TR, Eveson JP, 2018. Counting with DNA in metabarcoding studies: How should we convert sequence reads to dietary data? *Molecular ecology* 28(2), 391-406. DOI: 10.1111/mec.14734

De Cáceres M, Legendre P, Moretti M, 2010. Improving indicator species analysis by combining groups of sites. *Oikos* 119(10), 1674-1684. DOI: 10.1111/j.1600-0706.2010.18334.x

Du Plessis H, Van den Berg J, Byrne MJ, 2011. The effect of temperature on *Nysius natalensis* Evans (Hemiptera: Orsillidae) development and survival. *African Entomology* 19(3), 709-716.

Francis CM, 2019. *Field guide to the mammals of Southeast Asia* (2nd Edition). Bloomsbury Publishing, 409 pp.

Fujita MS, Tuttle MD, 1991. Flying foxes (Chiroptera: Pteropodidae): threatened animals of key ecological and economic importance. *Conservation Biology* 5(4), 455-463. DOI: 10.1111/j.1523-1739.1991.tb00352.x

Fullard JH, Simmons JA, Saillant PA, 1994. Jamming of bat echolocation: the dogbane tiger moth *Cycnia tenera* times its clicks to the terminal attack calls of the big brown bat *Eptesicus fuscus*. *Journal of Experimental Biology* 194, 285-298. DOI: 10.1242/jeb.194.1.285

Furey NM, 2012. Designing homes for tropical bats. Scientists explore artificial roosts for rebuilding forests. *Bats* 30, 7-9.

Furey NM, Racey PA, 2016. Conservation ecology of cave bats. *Advances in Ecological Research* 51, 287-325. DOI: 10.1007/978-3-319-25220-9_15

Haouas D, Glida-Gnidez H, Hafsi C, Nhaili H, Matocq A, 2019. *Nysius cymoides* (Heteroptera, Lygaeidae), is an emerging insect pest in Tunisia. *EPPO Bulletin* 49(2), 355-358. DOI: 10.1111/epp.12568

Hisheh S, How RA, Suyanto A, Schmitt LH, 2004. Implications of contrasting patterns of genetic variability in two vespertilionid bats from the Indonesian archipelago. *Biological Journal of the Linnean Society* 83(3), 421-431. DOI: 10.1111/j.1095-8312.2004.00401.x

Hope PR, Jones G, 2012. Warming up for dinner: torpor and arousal in hibernating Natterer's bats (*Myotis nattereri*) studied by radio telemetry. *Journal of Comparative Physiology B* 182, 569-578. DOI: 10.1007/s00360-011-0631-x

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. DOI: 10.2307/1933565

Johnson NF, Borror DJ, 2005. *Borror and DeLong's Introduction to the Study of Insects* (7th Ed.) Thomson, Brooks/Cole, USA.

Kasso M, Balakrishnan M, 2013. Ecological and economic importance of bats (Order Chiroptera). *International Scholarly Research Notices* 2013, 1-9. DOI: 10.1155/2013/187415

Krantz GW, Walter DE, 2009. *A manual of acarology* (3rd ed.). Texas Tech University Press.

Kunz TH, Torrez EBD, Bauer D, Lobova T, Fleming TH, 2011. Ecosystem services provided by bats. *Annals of the New York Academy of Sciences* 1223, 1-38. DOI: 10.1111/j.1749-6632.2011.06004.x

Kunz TH, Whitaker JJO, Wadanoli MD, 1995. Dietary energetics of the insectivorous Mexican free-tailed bat (*Tadarida brasiliensis*) during pregnancy and lactation. *Oecologia* 101(4), 407-415. DOI: 10.1007/BF00329419

Kurta A, Whitaker JJO, 1998. Diet of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *The American midland naturalist* 140(2), 280-286. DOI: 10.1674/0003-0031(1998)140[0280:DOTEIB]2.0.CO;2

Leelapaibul W, Bumrungsri S, Pattanawiboon A, 2005. Diet of wrinkle-lipped free-tailed bat (*Tadarida plicata* Buchannan, 1800) in central Thailand: insectivorous bats potentially act as biological pest control agents. *Acta Chiropterologica* 7, 111-119. DOI: 10.3161/1508110054527650

Maine JJ, Boyles JG, 2015. Bats initiate vital agroecological interactions in corn. *Proceedings of the National Academy of Sciences 112*(40), 12438-12443. DOI: 10.1073/pnas.1505413112

Mekong Eye, 2024. Bat guano collection in Southeast Asia: Conservation and zoonotic concerns. Mekong Eye. Available online at: https://www.mekongeye.com/2024/09/30/bat-guano [Accessed on 25/03/2025].

McAney C, Shiel C, Sullivan CM, Fairley JS, 1991. The analysis of bats droppings. *Mammal Society* 48 pp.

Mildenstein T, Tanshi I, Racey PA, 2016. Exploitation of bats for bushmeat and medicine. *Bats in the Anthropocene: conservation of bats in a changing world* 325-375. DOI: 10.1007/978-3-319-25220-9_12

Morales-Malacara JB, López-Ortega G, 2001. A new species of the genus *Periglischrus* (Acari: Mesostigmata: Spinturnicidae) on *Choeronycteris mexicana* (Chiroptera: Phyllostomidae) in central Mexico. *Journal of Medical Entomology* 38(2), 153-160. DOI: 10.1603/0022-2585-38.2.153

Norberg UM, Rayner JMV, 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society B* 316(1179), 335-427. DOI: 10.1098/rstb.1987.0030

Ober HK, Hayes JP, 2008. Prey selection by bats in forests of western Oregon. *Journal of Mammalogy* 89(5), 1191-1200. DOI: 10.1644/08-MAMM-A-025.1

Oliveira QL, Marciente L, Magnusson WE, Bobrowiec PE, 2015. Activity of the insectivorous bat *Pteronotus parnellii* relative to insect resources

and vegetation structure. *Journal of Mammalogy* 96(5), 1036-1044. DOI: 10.1093/jmammal/gyv108

Pokhrel S, Budha PB, 2014. Key to identify insects from droppings of some insectivorous bats of Nepal. *Journal of Institute of Science and Technology* 19(1), 129-136.

Pompanon F, Deagle BE, Symondson WO, Brown DS, Jarman SN, Taberlet P, 2012. Who is eating what: diet assessment using next generation sequencing. *Molecular ecology* 21(8), 1931-50. DOI: 10.1111/j.1365-294X.2011.05403.x

Propper CR, Singleton GR, Sedlock JL, Smedley RE, Frith OB, Shuman-Goodier ME, Lorica RP, Grajal-Puche A, Horgan FG, Prescott CV, Stuart AM, 2023. Faunal Biodiversity in Rice-Dominated Wetlands - An Essential Component of Sustainable Rice Production. In Closing Rice Yield Gaps in Asia: Innovations, Scaling, and Policies for Environmentally Sustainable Lowland Rice Production (pp. 93-120). Cham: Springer Nature Switzerland. DOI: 10.1007/978-3-031-37947-5_3

Racey PA, 2009. Reproductive assessment of bats. *Functional Ecology* 23(4), 773-786.

Roberts O, Holden J, Furey NM, de Kok R, Sean M, Oeung H, Chantha N, Chourn P, Barca B, Sinovas P, 2024. Virachey National Park Biodiversity Survey Report 2024, Cambodia. Fauna & Flora.

Russo D, Ancillotto L, 2015. Sensitivity of bats to urbanization: a review. *Mammalian Biology* 80(3), 205-212. DOI: 10.1016/j.mambio.2014.10.003

Scaccini D, Furlan L, 2021. *Nysius cymoides* (Hemiptera: Lygaeidae), a potential emerging pest: an overview of the information available to implement integrated pest management. *International Journal of Pest Management* 67(1), 73-88. DOI: 10.1080/09670874.2019.1666174

Schnitzler HU, Kalko EK, 2001. Echolocation by insect-eating bats: we define four distinct functional groups of bats and find differences in signal structure that correlate with the typical echolocation tasks faced by each group. *Bioscience 51*(7), 557-569. DOI: 10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2

Sek P, 2018. The activity of insectivorous bats over rice fields surrounding free-range bat guano farms in two provinces of Cambodia. Unpublished MSc Thesis, Royal University of Phnom Penh, Phnom Penh, 81 pp.

Sin S, Chhorn S, Doeurk B, Hak K, Ith S, Phauk S, Sor R, 2020. Diet preferences of insectivorous bats (Mammalia: Chiroptera) in Chambok, Kampong Speu Province, Cambodia. *Cambodian Journal of Natural History* 2020(2), 69-77.

Srilopan S, Bumrungsri S, Jantarit S, 2018. The wrinkle-lipped free-tailed bat (*Chaerephon plicatus* Buchannan, 1800) feeds mainly on brown planthoppers in rice fields of central Thailand. *Acta Chiropterologica* 20(1), 207-219. DOI: 10.3161/15081109ACC2018.20.1.016

Srinivasulu B, Srinivasulu C, 2005. Diet of the black-bearded tomb bat *Taphozous melanopogon* Temminck, 1841 (Chiroptera: Emballonuridae) in India. *Zoos' Print Journal* 20, 1935-1938.

Srinivasulu C, Racey PA, Mistry S, 2010. A key to the bats (Mammalia: Chiroptera) of South Asia. *Journal of Threatened taxa* 2(7), 1001-1076. DOI: 10.11609/JoTT.o2352.1001-76

Suksai P, Bumrungsri S, 2019. Water bodies are a critical foraging habitat for insectivorous bats in tropical agricultural landscapes of central Thailand. *Songklanakarin Journal of Science and Technology* 42(3), 521-532.

Sun K, Feng J, Jin L, Liu Y, Jiang Y, 2008. Identification of sympatric bat species by the echolocation calls. *Frontiers of Biology in China*, 3(2), 227-231. DOI: 10.1007/s11515-008-0017-y

Thi S, Furey NM, Jurgens JA, 2014. Effect of bat guano on the growth of five economically important plant species. *Journal of Tropical Agriculture* 52(2), 169-173.

Thongjued K, Chotigeat W, Bumrungsri S, Thanakiatkrai P, Kitpipit T, 2021. Direct PCR-DGGE technique reveals wrinkle-lipped free-tailed bat (*Chaerephon plicatus* Buchanan, 1800) predominantly consume planthoppers and mosquitoes in central Thailand. *Acta Chiropterologica* 23(1), 93-106. DOI: 10.3161/15081109ACC2021.23.1.008

Tuttle MD, 2015. Black gold from Cambodian bats. Merlin Tuttle's Bat Conservation. Available online at: https://www.merlintuttle.org/cambodian-farmers-friends-of-bats/ [Accessed on 13 November 2025].

Voigt CC, Kingston T, 2016. Bats in the Anthropocene. *Bats in the Anthropocene: conservation of bats in a changing world* 1-606. DOI: 10.1007/978-3-319-25220-9_1

Voigt CC, Schneeberger K, Voigt-Heucke SL, Lewanzik D, 2011. Rain increases the energy cost of bat flight. *Biology letters* 7(5), 793-795. DOI: 10.1098/rsbl.2011.0313

Waghiiwimbom MD, Moise BFE, Jules AP, Tamesse JL, 2019. The Diet Composition of Four Vesper Bats (Chiroptera: Vespertilionidae) from the Centre Region of Cameroon (Central Africa). *International Journal of Natural Resource Ecology and Management* 4(6), 153-163. DOI: 10.11648/j.ijnrem.20190406.11

Walter DE, Proctor HC, 2013. *Mites: Ecology, evolution & behaviour: Life at a microscale* (2nd ed.). Springer Science & Business Media.

Whitaker JO, McCracken GF, Siemers BM, 2009. Food habits analysis of insectivorous bats. In: Kunz, TH., Parsons, S., (Ed.), *Ecological and behavioural methods for the study of bats*. (2nd ed.) (pp. 567-592). Baltimore: Johns Hopkins University Press.

Whitaker JO, Neefus C, Kunz TH, 1996. Dietary variation in the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). *Journal of Mammalogy* 77(3), 716-724. DOI: 10.2307/1382676

Whitaker JO, 1988. Food habits analysis of insectivorous bats. In: Kunz, TH., & Racey, PA., (Ed), *Ecological and Behavioral Methods for the Study of Bats*. (pp. 309-325). Smithsonian Institution Press. Washington, DC.

Wilson MR, Claridge MF, 1991. *Handbook for the identification of leafhoppers and planthoppers of rice*. CAB International.

World Bank, 2021. Cambodia Climate Knowledge Portal. Available online at: https://climateknowledgeportal.worldbank.org/sites/default/files/country-profiles/16814-WB_Cambodia%20Country%20Profile-WEB.pdf [Accessed on 24.03.2025].

Zhang L, Jones G, Rossiter S, Ades G, Liang B, Zhang S, 2005. Diet of flat-headed bats, *Tylonycteris pachypus* and *T. robustula*, in Guangxi, South China. *Journal of Mammalogy* 86(1), 61-66. DOI: 10.1644/1545-1542(2005)086%3C0061:DOFBTP%3E2.0.CO;2

Zhu G, Chmura A, Zhang L, 2012. Morphology, echolocation calls, and diet of *Scotophilus kuhlii* (Chiroptera: Vespertilionidae) on Hainan Island, south China. *Acta chiropterologica* 14(1), 175-181. DOI: 10.3161/150811012X654394

Acknowledgements
The first author expresses sincere gratitude to the Swedish International Development Cooperation Agency (Sida) for their support through the "Sweden-Royal University of Phnom Penh Bilateral Program" (Contribution No. 11599). Additionally, thanks are extended to the Higher Education Improvement Project (HEIP), funded by the Cambodian Government (IDA Credit No. 6221-KH), for providing a research scholarship. The Centre for Biodiversity Conservation (CBC) and the Cambodian Entomology Initiatives (CEI) are also acknowledged for their invaluable research guidance and provision of laboratory facilities. Special thanks are owed to Mr. Seiha Hun, Mr. Kimseng Keng, Mr. Borin Koy, and Mr. Soem Sen for their assistance with bat faecal sample collection. Their contributions were instrumental to the success of this study.

Author contributions
S Sin performed fieldwork, writing original draft, reviewed and edited the manuscript, laboratory work, data collection, data curation, and data analysis; **S Phauk** performed data analysis, results, discussions, writing-review and edit; **S Keam**, **S Ith**, **NO Uk,** and **JD Jong** reviewed and revised the manuscript.

Conflicts of interest
The authors declare no conflict of interest.

Funding
Swedish International Development Agency (SIDA) for their support through the "Sweden-Royal University of Phnom Penh Bilateral program" (Contribution No. 11599), as well as to the Higher Education Improvement Project (HEIP) funded by the Cambodian Government (IDA Credit No. 6221-KH) for offering a research scholarship.

Complete affiliations
S Sin, Centre for Biodiversity Conservation (CBC); Department of Biology, Faculty of Science Royal University of Phnom Penh, Confederation of Russia Boulevard, Phnom Penh 120404, Cambodia.
S Kheam, Ecology Laboratory, Department of Biology, Faculty of Science, Royal University of Phnom Penh, Confederation of Russia Boulevard, Phnom Penh 120404, Cambodia,
S Ith, Department of Biology, Faculty of Science, Royal University of Phnom Penh, Confederation of Russia Boulevard, Phnom Penh 120404, Cambodia.
NO Uk, Department of Biology, Faculty of Science, Royal University of Phnom Penh, Confederation of Russia Boulevard, Phnom Penh 120404, Cambodia.
JD Jong, Swedish Biodiversity Centre (CBM), Swedish University of Agricultural Sciences, Uppsala, Sweden.
S Phauk, Cambodian Entomology Initiatives, Room 417A, Department of Biology, Faculty of Science, Royal University of Phnom Penh, Confederation of Russia Boulevard, Phnom Penh 120404, Cambodia; Department of Cell and Molecular Biology, Microbiology, Uppsala University, Uppsala, Sweden.

Animal Biodiversity and Conservation es manté neutral respecte a les reclamacions jurisdiccionals sobre mapes publicats i afiliacions institucionals
Animal Biodiversity and Conservation se mantiene neutral con respecto a reclamaciones jurisdiccionales sobre mapas publicados y afiliaciones institucionales
Animal Biodiversity and Conservation remains neutral with regard to jurisdictional claims in published maps and institutional affiliations