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ORIGINAL ARTICLE

Diet of insectivorous bats from mango orchards, Cambodia

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ABSTRACT

Insectivorous bats play important roles in agricultural ecosystems by regulating crop insect pests. However, bat diet composition in these areas remain understudied in Cambodia. In this study, we captured and analysed the diet of eight insectivorous bat species (*Rhinolophus pusillus*, *R. shameli*, *R. malayanus*, *Hipposideros* cf. *larvatus*, *H. gentilis*, *H. armiger*, *Myotis muricola,* and *Scotophilus kuhlii*) from mango orchards in Kampong Speu province. Eight insect orders were identified and quantified in the collected faecal samples of these bats. Coleoptera was the most dominant in the diet of *H. armiger* (100%), *H.* cf. *larvatus* (86.8%), *R. shameli* (86.2%), and *S. kuhlii* (84.5%). Lepidoptera, Hymenoptera, Diptera, and Dermaptera were frequently consumed by the remaining bat species. The combination of Coleoptera (49.2%), Hymenoptera (19.7%), and Lepidoptera (17.7%) from the eight bat species represents 86.6% of the total diet volume. This study demonstrates that different insectivorous bats consume diverse orders of insects, and the observed dominant insect orders from diets include many well-known agricultural pests, suggesting a critical role of bats as biological control agents for agriculture management.

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INTRODUCTION

Bats (Chiroptera) are the second most specious order of mammals after rodents, with over 1,450 species recorded worldwide (Simmons & Cirranello 2023). Based on their food preferences, insectivorous bats, fruit and nectar eaters, and carnivores (including vampire bats) represent over 70%, 29% and 1% of all species, respectively (Simmons 2005, Cedar 2023). Bats are remarkably diverse in the tropics (Willig 2001). Among the 81 bat species recorded in Cambodia, about 85.2% of them are insectivorous bats (Furey et al. 2021, Csorba & Furey 2022).

Insectivorous bats play an essential role in regulating nocturnal flying insect densities, including agricultural insect pests (Whitaker et al. 2009, Boyles et al. 2011, Maine & Boyles 2015). These bats can consume prey 30–100% of their body weight per night (Kunz et al. 2011). They consume diverse insect pests in agricultural areas, such as white-backed planthoppers and brown planthoppers (Homoptera: major pests of paddy fields) (Leelapaibul et al. 2005, Srilopan et al. 2018), corn earworm moths (Lepidoptera), brown/green stink bugs (Hemiptera), spotted cucumber beetles (Coleoptera), and fruit flies (Diptera) (Maine & Boyles 2015). With large colonies and high diversity, insectivorous bats can suppress millions of insect densities in ecosystems and agricultural landscapes (Whitaker 1996, Srilopan et al. 2018). These biological insect suppressions could save billions of dollars for the agricultural sector by reducing crop damage and pesticide usage (Boyles et al. 2011, Wanger et al. 2014, Maine & Boyles 2015). Specifically, Wrinkle-lipped free-tailed bats (*Mops plicatus*) save approximately 2,900 tons of rice and about 26,200 people's meals worth more than USD 1.2 million annually in Thailand (Wanger et al. 2014). *Tadarida brasiliensis* are primary moth control agents on cotton fields in south-central Texas (Lee & McCracken 2005), contributing an estimated value of 741,000 USD annually in the USA (Cleveland et al. 2006). Although a growing body of literature provides substantial evidence of the essential functions of insectivorous bats, the dietary habits of insectivorous bats in Southeast Asia remain poorly known.

The diet composition of insectivorous bats depends on the availability of insects in seasonal and geographical variations, the size of insects, and their foraging behaviours (Lee & McCracken 2005, Leelapaibul et al. 2005, Zhang et al. 2005). Kolkert et al. (2020) reported that most insectivorous bats positively selected Lepidoptera, while Coleoptera, Diptera, Hemiptera, Hymenoptera, Orthoptera, Tricoptera and Neuroptera were less consumed over cotton farms in Australia. They further found that 65% of prey were significant cotton pests in the bat diet compositions. Amongst different agricultural landscapes, paddy fields are known as the home of diverse insect pests (Pathak & Khan 1994, Dunn et al. 2023), and have been reported as the most favourable foraging habitats of *M. plicatus* (Leelapaibul et al. 2005). The dietary analysis of these bats showed that planthoppers (Homoptera: *Nilaparvata lugens* and *Sogatella furcifera*, considered as insect pests) were consumed by these bats on paddy fields in Thailand (Leelapaibul et al. 2005, Srilopan et al. 2018). All these studies indicate that different bat species may have different food preferences and foraging habitats, being good insect pest biological control agents in agricultural systems.

Only a few studies have been conducted on bat diet in Cambodia, such as Thavry et al. (2017) with the Cave Nectar Bat (*Eonycteris spelaea*) and Sin et al. (2020) with insectivorous bats at mountainous gradients. No studies have addressed the insectivorous bats' dietary analyses in mango orchards in Cambodia, therefore making it necessary to explore them to identify their potential benefits for sustainable crop management.

Mango is one of the most important fruit crops in Cambodia. To date, mango farmland covers about 152,073 hectares and yields up to 2.2 million tons or USD 0.44 million annually (MAFF 2022). Kampong Speu province is known for its 34,733 hectares of mango crops, representing about 22.84% of the total mango orchards in Cambodia. These orchards produce ca. 810,990 tons of mango annually (MAFF 2022). However, insect pests are the major challenge in mango production losses (Venkata et al. 2018). Six endemics and 45 quarantine species of insect pests have been recorded in mango orchards in Cambodia, of which fruit flies (Diptera: *Bactrocera* spp.), leaf and planthoppers (Homoptera), moths (Lepidoptera), leaf-eating beetles, and weevils (Coleoptera) are known as main insect pests (Hean 2003). Although chemical control measures are the most effective strategy to control pests in agricultural landscapes, the biological control strategy is widely practised to control insect pests. Therefore, it becomes crucial to understand whether insectivorous bats may play an important role in biological control in mango orchards.

Here, we aimed to capture as many insectivorous bat species as possible and analyse their diet compositions in mango orchards from the Kampong Speu province, the Southwest of Cambodia. We expected that diverse insectivorous bat species would be captured, and these bats would consume different proportions of various insect groups depending on the species.

MATERIAL AND METHODS

Study Area

This study was conducted in Chambok and Treng Trayueng communes (Fig. 1), which are considered the largest mango orchards in Kampong Speu province, the Southwest of Cambodia. Chambok and Treng Trayueng communes are situated close to the Kirirom National Park, known as one of the biodiversity hotspots in Cambodia (Phat 2015). Chambok commune possesses a natural bat cave surrounded by semi-evergreen and bamboo forests (Sin et al. 2020).

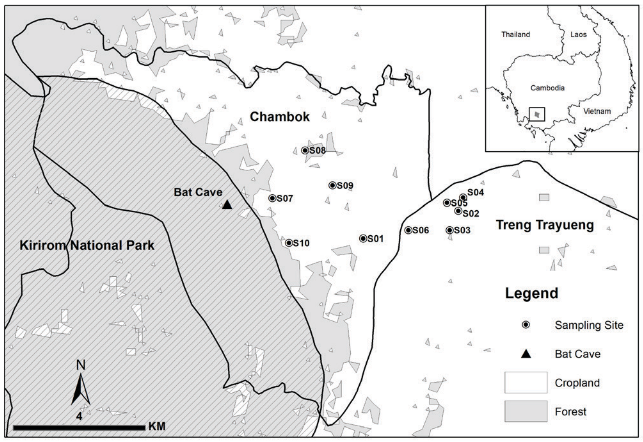

Fig. 1 - Study area with the ten sampling sites (S01–S10) of insectivorous bats in and around the mango orchards in Chambok and Treng Trayueng communes, Kampong Speu province, Cambodia.

The climate of Kampong Speu is characterised by a wet season, with heavy rainfall from May to October, humidity reaching 90% and temperatures ranging from 26 to 34 °C, a cool dry season from November to March, with temperatures ranging from 16 to 26 °C, and a hot dry season from March to May, with temperatures ranging from 25 to 35 °C (Heng 2014).

Field Sampling

Two field trips were conducted to capture insectivorous bats from 22 to 30 April during the dry season and from 25 May to 03 June 2023 during the wet season. Mist nets (7 × 2.5 m, 9 × 2.5 m and 12 × 2.5 m, denier 75/2, mesh 16 × 16 mm, five shelves; Ecotone, Inc., Poland) were employed for four hours after sunset from 18:00 to 22:00 hours for each night within ten randomly selected sites (Fig. 1 and SM Table 1) inside and around the mango orchards. All insectivorous bats captured in the nets were gently removed by hand with protected gloves and then placed in clean individual cloth bags overnight. Afterwards, we photographed and identified each captured bat to species level based on external morphology and standard measurements (Francis 2019), and were later released back to their natural habitats. We collected fresh bat faecal pellets from the cloth bags of the overnight captured bats using soft forceps and were then preserved in appropriately labelled vials containing 70% ethanol to be analysed in the laboratory (Weier et al. 2019, Sin et al. 2020). The used cloth bags were cleaned adequately before being reused.

Faecal analysis

We randomly selected 20 faecal pellets from each bat species for diet analysis following a protocol proposed by Whitaker et al. (1999). Faecal samples were analysed at the Zoological Museum of the Centre for Biodiversity

Conservation at the Royal University of Phnom Penh, Cambodia, by following the procedures highlighted in Whitaker et al. (2009) and Sin et al. (2020). Bats commonly chew their prey into small fragments and pass them into faces (Whitaker et al. 2004). However, those prey fragments were identifiable to order level following key identification guides (Whitaker et al. 2009, Pokhrel & Budha 2014, Ponmalar & Vanitharani 2014, Srilopan et al. 2018, Sin et al. 2020).

Data and statistical analyses

We estimated visually the percentage volume (PV) and percentage frequency (PF) of each insect order consumed by each bat species (Whitaker et al. 2009). The PV is calculated by dividing the total volume for a particular insect order between the total volume of samples and multiplied by 100. At the same time, the PF is calculated by dividing the number of pellets where a particular insect order occurred between the total number of pellets used for analysis, multiplied by 100. Non-parametric Kruskal-Wallis test and Dun's post hoc test were applied to compare diet variation within species using PV and PF. All statistical tests were performed using R software version 4.1.1 (R Core Team 2021). The $p \leq 0.05$ significant level was applied to test the differences between the compared variables.

RESULTS

Insectivorous bats in mango orchards

Within the two-time field collection, we captured a total of 80 individuals of insectivorous bats representing eight species from three families (Table 1 and Fig. 2). Three bat species that were considered the most common species in the mango orchards include Least horseshoe ba (*Rhinolophus pusillus)* (27.5%), Intermediate roundleaf bat (*Hipposideros* cf. *larvatus)* (25%), and Shamel's horseshoe bat (*R. shameli)* (23.75%), followed by Malayan horseshoe bat (*R. malayanus*) (11.25%). Asian whiskered myotis (*Myotis muricola*), Lesser Asian house bat (*Scotophilus kuhlii),* Large-eared roundleaf bat (*H. gentilis*), and Great Roundleaf bats (*H. armiger*) were least common species (≤ 5%) in our study.

Bat diet account

We obtained a total of 1,198 faecal pellets from the eight bat species (Table 1). Of which, 134 were analysed and quantified, consisting of 20 pellets for *R. pusillus*, *R. shameli, R. malayanus, H.* cf. *larvatus*, *M. muricola* and *S. kuhlii*, nine pellets for *H. gentilis* and five pellets for *H. armiger*. Identified prey fragments belonged to eight insect orders, including Coleoptera (beetles), Lepidoptera (moths), Hymenoptera (wasps), Hemiptera (true bugs), Homoptera (hoppers), Diptera (flies), Isoptera (termites), and Dermaptera (earwigs) (Fig. 3). In terms of PV, the dominant prey from all eight bat species diets combined were Coleoptera (49.2 ± 3.8%), Hymenoptera (19.7 ± 3.1%) and Lepidoptera (17.7 ± 2.6). All three insect orders were also recorded highest in terms of PF, Coleoptera constituted (72%), Lepidoptera (64%), and Hymenoptera (38%). Diet compositions for each insectivorous bat species were presented in Table 2 and Table 3.

Rhinolophus pusillus. We detected six insect orders, comprising of Lepidoptera, Coleoptera, Hymenoptera, Hemiptera, Homoptera, and Isoptera. We found a significant difference in the PV (*Kruskal-Wallis* test, $\chi^2 = 78.917$; df = 5; $p < 0.001$) and the PF ($\chi^2 = 62.78$; df = 5; $p < 0.001$) among all insect orders. Based on Dunn's post hoc test, Lepidoptera and Coleoptera were found to be higher in terms of both diet volume and frequency (all p values < 0.001) compared to Hymenoptera, Hemiptera, Homoptera, and Isoptera.

Rhinolophus shameli. Five insect orders were identified in the diet of *R. shameli*, which consisted of Coleoptera, Lepidoptera, Hemiptera, Homoptera, and Hymenoptera. We detected statistical differences in diet volume between the consumed insects ($\chi^2 = 77.43$; df = 4; $p < 0.001$) and the

Table 1 - Insectivorous bat species and faecal pellets collected in mango orchards in the Chambok and Treng Trayueng communes, Kampong Speu province, Cambodia.

Family/Species	Number of individuals	Percentage of individuals (%)	Weight (g)	Forearm (mm)	Number of pellets
Rhinolophidae					
Rhinolophus pusillus	22	27.5	4.4	35.7	365
Rhinolophus shameli	19	23.75	9.5	46.4	212
Rhinolophus malayanus	9	11.25	6.3	40.3	172
Hipposideridae					
Hipposideros cf. *larvatus*	20	25	17.6	58.5	255
Hipposideros gentilis	2	2.5	7	40.6	9
Hipposideros armiger	1	1.25	29	93	5
Verpertilionidae					
Myotis muricola	4	5	5.5	34.4	40
Scotophilus kuhlii	3	3.75	21.4	49.6	140
Total	**80**	**100**			**1,198**

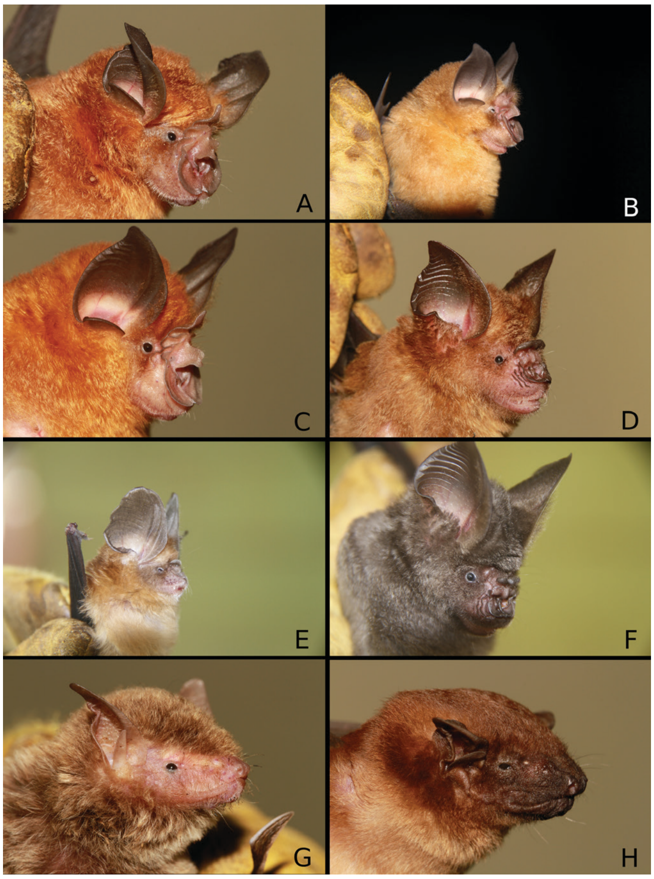

Fig. 2 - Eight insectivorous bat species were captured in the mango orchards, Chambok and Treng Trayueng communes, Kampong Speu province, Cambodia. **A)** *Rhinolophus pusillus*. **B)** *R. shameli*. **C)** *R. malayanus*. **D)** *Hipposideros* cf. *larvatus*. **E)** *H. gentilis*. **F)** *H. armiger*. **G)** *Myotis muricola*. **H)** *Scotophilus kuhlii*.

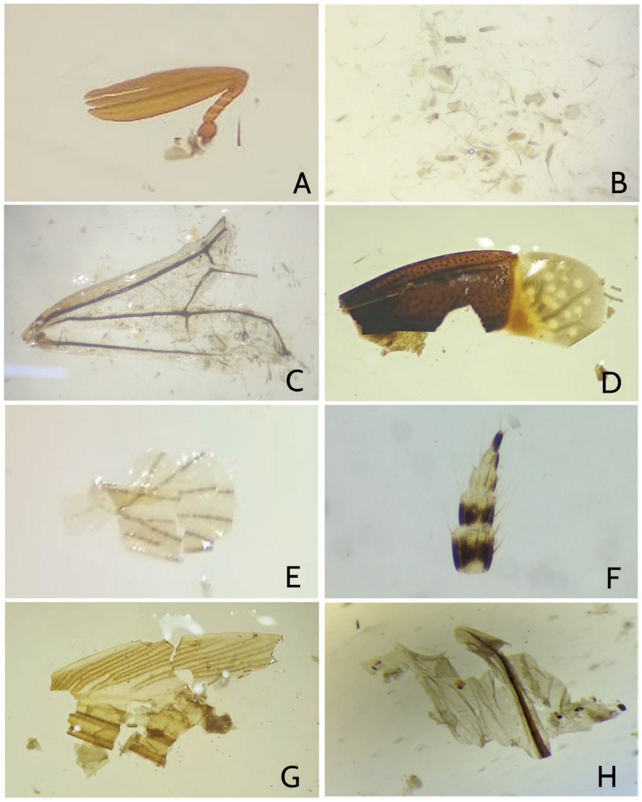

Fig. 3 - Prey fragments represent eight insect orders consumed by insectivorous bats in the mango orchards, Chambok and Treng Trayueng communes, Kampong Speu province, Cambodia. **A)** Coleoptera-antennae. **B)** Lepidoptera-wing scales. **C)** Hymenoptera-wing. **D)** Hemiptera-wing. **E)** Homoptera-wing. **F)** Diptera-abdomen. **G)** Isoptera-wing. **H)** Dermaptera-hind wing.

diet frequency (χ^2= 70.47; df = 4; $p < 0.001$). Coleoptera was more consumed (PV) compared to Lepidoptera ($p = 0.007$), Hemiptera, Homoptera and Hymenoptera (all p values < 0.001). However, Coleoptera was not significantly different in the PF, compared to Lepidoptera, but varied between other preys (all p values < 0.001).

Rhinolophus malayanus. A total of five insect orders were identified, including Hymenoptera, Lepidoptera, Isoptera, Coleoptera, and Homoptera. Among the five insect orders, there were significant differences in the PV (χ^2= 70.17; df = 4; $p < 0.001$) and PF (χ^2= 55.93; df = 4; $p < 0.001$). Hymenoptera was detected as the dominant group in the diet volume compared to Lepidoptera, Isoptera, Coleoptera, and Homoptera (all p values < 0.001). Regarding PF, Hymenoptera and Lepidoptera occurred in higher proportions compared with other prey (all p values < 0.009).

Hipposideros cf. *larvatus.* This species consumed all identified insect orders recorded in the study area except Dermaptera. A significant variation was determined among insect orders in the diet volume (χ^2= 75.53; df = 6; $p < 0.001$) and the diet frequency (χ^2= 65.24; df = 6; $p < 0.001$). Coleoptera higher proportions in the PV (all p values < 0.001) and the PF (all p values < 0.001) compared to other insect orders.

Hipposideros gentilis and *H. armiger. H. gentilis* preyed on similar proportions of Lepidoptera, Diptera and Dermaptera. Dermaptera was found only in the diet of *H. gentilis*. We found no significant differences among prey consumed by this bat. By analysing five faecal samples of *H. armiger*, we found that only Coleoptera occurred in the diet of this bat (PV = 100%; PF = 100%).

Myotis muricola. We found the diet of *M. muricola* comprised six insect orders, including Hymenoptera, Lepidoptera, Coleoptera, Hemiptera, Homptera, and Diptera. We found significant differences in the PV (χ^2= 72.435; df = 5; $p < 0.001$) and the PF (χ^2= 49.837; df = 5; $p < 0.001$) among proportions of the insect consumed. Hymenoptera was more commonly found in the diet volume, but no significant differences were found compared with the Lepidoptera ($p = 0.109$). However, Hymenoptera differed between Coleoptera, Hemiptera, Homoptera, and Diptera (all p values < 0.001). Lepidoptera was also considered an essential prey of *M. muricola*, and significantly differed from Coleoptera, Hemiptera, Homoptera, and Diptera (all p values < 0.014). Examining the diet frequency, Hymenoptera, Lepidoptera, Coleoptera, and Hemiptera had significantly higher proportions than Homoptera and Diptera (all p values < 0.01).

Scotophilus kuhlii. Coleoptera and Hemiptera were identified in its diet. Coleoptera was found in higher proportions in PV and PF (84.5%; 100%) than Hemiptera (15.5%; 80%). Statistical analysis showed a highly significant difference in the diet volume between the two insect orders ($p < 0.001$) and significant differences in diet frequency ($p = 0.039$).

Table 2 - Percentage volume (PV) (mean ± SE) of all insect orders consumed by bat species in mango orchards in Chambok and Treng Trayueng communes, Kampong Speu province. N= Number of faecal pellets, Col= Coleoptera, Lep= Lepidoptera, Hym= Hymenoptera, Hem= Hemiptera, Hom= Homoptera, Dip= Diptera, Iso= Isoptera, Der= Dermaptera.

Species	N	Col	Lep	Hym	Hem	Hom	Dip	Iso	Der
R. pusillus	20	28.7 ± 7.3	63.8 ± 7.2	2.7 ± 1.1	2.5 ± 1.2	2.0 ± 1.0	0	0.3 ± 0.3	0
R. shameli	20	86.2 ± 4.5	9.8 ± 4.1	0.2 ± 0.1	3.2 ± 2.5	0.6 ± 0.3	0	0	0
R. malayanus	20	1.5 ± 1.0	13.1 ± 4	77.2 ± 6.0	0	0.3 ± 0.3	0	8.0 ± 2.6	0
H. cf. *larvatus*	20	86.8 ± 6.7	0.2 ± 0.1	11.0 ± 6.8	0.6 ± 0.6	0.3 ± 0.3	0.7 ± 0.7	0.2 ± 0.2	0
H. gentilis	9	0	34.4 ± 16.4	0	0	0	32.8 ± 15.6	0	32.8 ± 15.6
H. armiger	5	100 ± 0	0	0	0	0	0	0	0
M. muricola	20	5.5 ± 1.5	20.7 ± 5.4	66.4 ± 5.0	4.1 ± 1.2	1.7 ± 0.7	1.5 ± 0.8	0	0
S. kuhlii	20	84.5 ± 4.5	0	0	15.5 ± 4.4	0	0	0	0

Table 3 - Percentage frequency (PF) (mean ± SE) of all insect orders consumed by bat species in mango orchards in Chambok and Treng Trayueng communes, Kampong Speu province. N= Number of faecal pellets, Col= Coleoptera, Lep= Lepidoptera, Hym= Hymenoptera, Hem= Hemiptera, Hom= Homoptera, Dip= Diptera, Iso= Isoptera, Der= Dermaptera.

Species	N	Col	Lep	Hym	Hem	Hom	Dip	Iso	Der
R. pusillus	20	90.0 ± 6.9	100 ± 0	25.0 ± 9.9	20.0 ± 9.2	25.0 ± 9.9	0	5.0 ± 5.0	0
R. shameli	20	100 ± 0	90.0 ± 6.9	5.0 ± 5.0	10.0 ± 6.9	15.0 ± 8.2	0	0	0
R. malayanus	20	20.0 ± 9.2	95.0 ± 5	100 ± 0	0	5.0 ± 5.0	0	45.0 ± 11.4	0
H. cf. *larvatus*	20	90.0 ± 6.9	25.0 ± 9.9	25.0 ± 9.9	5.0 ± 5.0	5.0 ± 5.0	5.0 ± 5.0	5.0 ± 5.0	0
H. gentilis	9	0	56.0 ± 17.6	0	0	0	44.0 ± 17.6	0	44.0 ±17.6
H. armiger	5	100 ± 0	0	0	0	0	0	0	0
M. muricola	20	60.0 ± 11.2	95.0 ± 5	100 ± 0	60.0 ± 11.2	25.0 ± 9.9	15.0 ± 8.2	0	0
S. kuhlii	20	100 ± 0	0	0	80.0 ± 9.2	0	0	0	0

DISCUSSION

Insectivorous bats in mango orchards

We captured eight insectivorous bat species representing three families that inhabit mango orchards in Chambok and Treng Trayueng communes, Kampong Speu province. Almost all bat species have been previously found roosting in caves and bamboo clumps, except *M. muricola* and *S. kuhlii* (Francis 2019). A former study of insectivorous bat diet captured five species, including *R. pusillus*, *R. shameli*, *H.* cf. *larvatus*, *H. gentilis*, and *Megaderma spasma* in the semi-evergreen forest mixed bamboo near the bat cave in Chambok (Sin et al. 2020). *Myotis muricola* roosts in the furled central banana leaves and vegetated areas near cave entrances. Similarly, *S. kuhlii* is found in various roosting sites, including house roofs, palm leaves and hallow trees (Francis 2019). Most bat species generally forage in similar habitats, including evergreen and semi-evergreen forests, open spaces and modified areas (i.e., agricultural areas) (Francis 2019). All insectivorous bat species recorded in this study are listed as Least Concern (LC) in the IUCN Red List (Francis 2019, IUCN 2023), and they are commonly found in cropland across the Southeast Asia region (Francis 2019). This suggests that these bats are flexible in terms of habitat use, as they are commonly found in human-modified habitats (i.e., mango orchards).

Diet preferences of insectivorous bats

Our study provides insight into the diet of the eight insectivorous bat species foraging in Cambodia's mango orchards in Kampong Speu province. The insectivorous bats' diet comprised Coleoptera, Lepidoptera, Hymenoptera, Diptera, and Dermaptera, followed by Hemiptera. These insect orders have been formerly identified as important food sources of insectivorous bats, except Dermaptera (Gonsalves et al. 2013, Waghiiwimbom et al. 2019, Alviola et al. 2023).

A previous study also revealed that Coleoptera and Lepidoptera are the primary food of insectivorous bats in Cambodia (Sin et al. 2020). These two insect orders are relatively large and produce noise; and are, therefore, quickly detected by most echolocating bats (Siemers & Güttinger 2006). The observed four large insectivorous bat species (i.e., *H. armiger*, *H.* cf. *larvatus*, *S. kuhlii*, and *R. shameli*) in this study have large bodies with large skulls, emit low call frequencies, and mainly consumed

Coleoptera (Pavey & Burwell 1997). Likewise, the four small bat species in our study, which are known to have small skulls and emitting high call frequencies from 65-126 kHz (Bogdanowicz et al. 1999, Weterings & Umponstira 2014, Ponmalar & Vanitharani 2014), consumed high proportions of Diptera and Lepidoptera. Our results suggest that different insectivorous bat species or groups forage on particular target insect groups as their primary diet.

Food consumption of insectivorous bats is determined by the percent volume and percent frequency (Srilopan et al. 2018). Percent frequency provides a reliable interpretation for small size and soft-bodies prey: Lepidoptera, Diptera, Odonata, Orthoptera, and Hymenoptera (Kaspari & Joern 1993, Lease & Wolf 2010, Srilopan et al. 2018, Sin et al. 2020). Insectivorous bats consumed a higher percentage frequency of small-size and soft-bodies insects compared to the percent volume (Whitaker et al. 2009, Srilopan et al. 2018, Sin et al. 2020), which is also in line with our findings. The consumption of small and soft-bodied insects is associated with a greater susceptibility of these prey to the processes involved in mastication and digestion (Rabinowitz & Tuttle 1982, Dickman & Huang 1988). Prey consumption of insectivorous bats may differ in proportions among bat species and depending on food availability, which can spatially and seasonally vary (Whitaker et al. 1996, Lee & McCracken 2005). Either with PV or the PF, diet compositions of these bats are strongly species-dependent and mostly depend on food availability at their foraging habitats (Zhu et al. 2024). The dietary analysis of *M. plicatus* foraging over water bodies showed a high proportion of Hemiptera and Diptera during the dry season in Thailand (Srilopan et al. 2018, Thongjued et al. 2021). In contrast, *M. plicatus* consumed more Coleoptera during the wet season in paddy fields (Srilopan et al. 2018). These previous studies and our own data support the hypothesis that the diet composition of the same bat species can vary significantly depending on the habitat and season (Kurta & Whitaker 1998).

Insectivorous bat diet account

In this study, *R. pusillus* consumed more Lepidoptera and Coleoptera. Similarly, *R. pusillus* has been reported to consume a high number of Lepidoptera, followed by Homoptera, Coleoptera, Heteroptera, Hymenoptera and Diptera during the wet season at mountainous gradients in Chambok (Sin et al. 2020). These findings suggest that *R. pusillus* is a predator of lepidopterans; however, this species can consume various insect groups in their foraging areas (Sin et al. 2020). In this investigation, we found that *R. shameli* heavily consumed Coleoptera, followed by Lepidoptera. Similar to a previous study, *R. shameli* highly consumed Lepidoptera, Coleoptera, and Hymenoptera, followed by Hemiptera in the wet season at mountainous gradients (Sin et al. 2020). The slight difference in diet compositions of this species might be affected by seasons (Leelapaibul et al. 2005, Zhang et al. 2005) and geographical structure variation (Kurta & Whitaker 1998). Another explanation could be due to the availability of certain insect groups in the mango orchards. Our results further suggest that *R. shameli* is a generalist predator (Waghiiwimbom et al. 2019) but might likely concentrate on Coleoptera. Interestingly, in this study *R. malayanus* preyed on Hymenoptera, followed by Lepidoptera. This bat species also preyed on Isoptera, Coleoptera, and Homoptera. This is the first report on the diet of *R. malayanus* in Cambodia. The higher proportions of Hymenoptera in the *R. malayanus* diet could be due to their capacity to emit relatively high call frequency (81.1–84.7kHz) (Schnitzler & Kalko 2001, Phauk et al. 2013). Bats that use higher call frequency can detect much smaller insects (e.g. Hymenoptera: Formicidae) (Houston et al. 2004, Jones 2005).

Hipposideros cf. *larvatus* constantly preyed upon Coleoptera. Similarly, Hemiptera and Coleoptera were found to be essential food sources of *H.* cf. *larvatus* in Chambok (Sin et al. 2020). Our results suggest that *H.* cf. *larvatus* is likely to concentrate on hard-bodied insects (i.e., Coleoptera and Hemiptera). *Hipposideros gentilis* had similar diet composition with Lepidoptera, Diptera, and Dermaptera. Hemiptera, Homoptera, and Lepidoptera were preferably consumed by *H. gentilis*, followed by Hymenoptera, Coleoptera, and Isoptera (Sin et al. 2020). Our data suggests that *H. gentilis* is rather opportunistic. On the other side *H. armiger* consumed only a single order (Coleoptera). In other studies, *H. armiger* consumed high concentrations of Hemiptera, Lepidoptera, and Coleoptera in north-western Thailand (Weterings et al. 2015). This could be due to the small sample size in this study (Whitaker et al. 1999). Therefore, larger samples of this species should be further investigated.

Myotis muricola mostly consumed Hymenoptera and Lepidoptera. The diet of this bat species is similar to *R. malayanus*. There is no previous report on the diet of *M. muricola* in Cambodia. It has been reported that bats of the genus *Myotis* consumed significantly small and soft-bodied insects (Best et al. 1997, Vesterinen et al. 2017). For instance, *M. lucifugus* and *M. keenii* mainly consumed Lepidoptera, Neuroptera and Diptera, followed by Hymenoptera (Burles et al. 2008). These findings provide a good indication that bats in the genus *Myotis* are generalist predators but concentrate on small and soft-bodied insects (Waghiiwimbom et al. 2019). On the other hand, *S. kuhlii* in our study consumed only Coleoptera and Hemiptera. Similar to our study, a study on the diet of this bat species demonstrated that Lepidoptera, Coleoptera and Hemiptera were important food sources at Hainan Island, in the South of China (Zhu et al. 2012). This bat produces relatively low-frequency calls, and regularly prey on large insects with exoskeleton (i.e., Coleoptera and Hemiptera) (Zhu et al. 2012, Weterings et al. 2015).

The captures of eight insectivorous bat species in this study suggest that mango orchards can be a foraging habitat for diverse bat species. Although *R. shameli*, *R. pusillus*, *H.* cf. *larvatus* and *H. gentilis* are not usually found in agriculture systems, they share some common foraging habitats. It is likely that some of these species could contribute to insect pest suppression in mango farming systems. The diet analyses of these bats showed that insectivorous bats consumed an estimated diet volume combined of up to 86.6% of Coleoptera, Hymenoptera and Lepidoptera (Pavey & Burwell 1997, Alviola et al. 2023). In this study, we identified insects at the order levels, representing a critical limitation in confirming whether these insects are insect pests (Maine

& Boyles 2015, Kolkert et al. 2020). DNA analyses of these insects should be carried out to identify them at the species level. Finally, we cannot confirm whether the identified insects are consumed from mango orchards or not, but we can partially assume that insectivorous bats could play roles as biological control agents in suppressing insect densities and pests through their food consumption.

CONCLUSION

Our study indicates that mango orchards could be a foraging habitat for diverse insectivorous bat species and highlights the significant role of insectivorous bats in agricultural systems. Our results show that certain insectivorous bat species consume several groups of insect orders, which include many insect pests, suggesting bats may play a significant role in the management of agricultural systems as biological control agents. This study also suggests that different bat species select specific insect groups positively depending on food availability and foraging behaviour. We, therefore, suggest that insectivorous bat diversity and diet composition should be expanded and further investigated in other main agricultural landscapes, particularly in paddy or maize fields.

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AUTHOR CONTRIBUTIONS

ST, SS and SM designed the study. SS, ST and CK collected data. SS and ST analysed the data. SS wrote the first draft of the manuscript. SS, SK, SS, OU and ST edited and revised the manuscript. All authors read, contributed to revision and approved the manuscript.

REFERENCES

ALVIOLA, P. A., ALVIOLA, M. S., TARAY, K. J., LUCAÑAS, C. C., DE GUIA, A. P. O., DUPO, A. L. B., CUEVAS, V. C., PAMPOLINA, N. M. & LIT JR, I. L. (2023). Dietary analysis of eight insectivorous bats (Chiroptera) from Puting Bato Cave Complex, Burdeos, Polillo Island, Philippines. *J Asia-Pacific Biodi*, 16(3): 291–299. https://doi.org/10.1016/j.japb.2023.05.003

BEST, T. L., MILAM, B. A., HAAS, T. D., CVILIKAS, W. S. & SAIDAK, L. R. (1997). Variation in diet of the gray bat (*Myotis grisescens*). *J Mammal,* 78(2): 569–83. https://doi.org/10.2307/1382909

BOGDANOWICZ, W., FENTON, M. B. & DALESZCZYK, K. (1999). The relationships between echolocation calls, morphology and diet in insectivorous bats. *J Zool,* 247: 381–393. https://doi.org/10.1111/j.1469-7998.1999.tb01001.x

BOYLES, J. G., CRYAN, P. M., MCCRACKEN, G. F. & KUNZ, T. H. (2011). Economic importance of bats in agriculture. *Science,* 332: 41–42. https://doi.org/10.1126/science.1201366

BURLES, D. W., BRIGHAM, R. M., RING, R. A. & REIMCHEN, T. E. (2008). Diet of two insectivorous bats, *Myotis lucifugus* and *Myotis keenii*, in relation to arthropod abundance in a temperate Pacific Northwest rainforest environment. *Canadian J Zool,* 86(12): 1367–75. https://doi.org/10.1139/Z08-125

CEDAR, H. (September 8, 2023). Bat basic information. https://www.cedarhilltx.com/2889/Bats.

CLEVELAND, C. J., BETKE, M., FEDERICO, P., FRANK, J. D., HALLAM, T. G., HORN, J., LÓPEZ JR, J. D., MCCRACKEN, G. F., MEDELLÍN, R. A., MORENO-VALDEZ, A. & SANSONE, C. G. (2006). Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. *Front Ecol Environ,* 4(5): 238–243. https://doi.org/10.1890/1540-9295(2006)004[0238:EVOTPC]2.0.CO;2

CSORBA, G. & FUREY, N. M. (2022). From greener times: a new species of Thick-thumbed Myotis from Phnom Penh, Cambodia. *Acta Zoologica Academiae Scientiarum Hungaricae,* 68(1): 85–97. https://doi.org/10.17109/AZH.68.1.85.2022

DICKMAN, C. R, & HUANG, C. (1988). The reliability of fecal analysis as a method for determining the diet of insectivorous mammals. *J Mammal*, 69: 108–113. https://doi.org/10.2307/1381753

DUNN, L., LATTY, T., VAN OGTROP, F. F. & TAN, D. K. (2023). Cambodian rice farmers' knowledge, attitudes, and practices (KAPs) regarding insect pest management and pesticide use. *International J Agri Sustaina,* 21(1):2178804. https://doi.org/10.1080/14735903.2023.2178804

FRANCIS, C. (2019). Field guide to the mammals of Southeast Asia (2nd Edtion). Bloomsbury Publishing, 409 pp.

FUREY, N.M., TU, V.T., HITCH, A.T., PIMSAI, A., KIMASHALEN, C., VUTHY, B., RAKSMEY, Y., SARAK, C., BORTHWICK, S.A., CH'NG, L. & SINLY, S. (2021). First records of seemingly rare bats (Mammalia: Chiroptera) in Cambodia, with a revised checklist of species for the country. *Acta Chiropterologica,* 23(2): 345–369. https://doi.org/10.3161/15081109ACC2021.23.2.005

GONSALVES, L., BICKNELL, B., LAW, B., WEBB, C. & MONAMY, V. (2013). Mosquito consumption by insectivorous bats: does size matter? *PLoS One,* 8(10): e77183. https://doi.org/10.1371/journal.pone.0077183

HEAN, V. (2003). Endemic and Quarantine pests of Mango Fruit of Cambodia. *Depart of Agro and Agric Land Impro (DAALI)*, Phnom Penh 1–3.

HENG, N. (2014). Background Information of Kampong Speu Province, Cambodia. *Graduate School International Development Nagoya University*, Overseas Fieldwork Report 1–6.

HOUSTON, R. D., BOONMAN, A. M. & JONES, G. (2004). Do echolocation signal parameters restrict bats' choice of prey? In "Echolocation in Bats and Dolphins" Ed by J Thomas, C Moss, M Vater, Chicago University Press, Chicago, pp 339–345.

THAVRY, H., CAPPELLE, J., BUMRUNGSRI, S., THONA, L. & FUREY, N. M. (2017). The Diet of the Cave Nectar Bat (*Eonycteris spelaea* Dobson) Suggests it Pollinates Economically and Ecologically Significant Plants in Southern Cambodia. *Zool stud,* 56: 1–7. https://doi.org/10.6620/ZS.2017.56-17

IUCN. (2023). The IUCN Red List of Threatened Species. https://www.iucnredlist.org. (Accessed on 12 June, 2023).

JONES, G. (2005). Echolocation. Current Biology 15:R484–R488.

KASPARI, M. & JOERN, A. (1993). Prey Choice by Three Insectivorous Grassland Birds: Reevaluating Opportunism. *Oikos,* 68(3): 414–430. https://doi.org/10.2307/3544909

KOLKERT, H., ANDREW, R., SMITH, R., RADER, R. & REID, N. (2020). Insectivorous bats selectively source moths and eat mostly pest insects on dryland and irrigated cotton farms. *Ecol and Evol,* 10(1):371–388. https://doi.org/10.1002/ece3.5901

KUNZ, T. H., BRAUN DE TORREZ, E., BAUER, D., LOBOVA, T. & FLEMING, T. H. (2011). Ecosystem services provided by bats. In: Ostfeld RS, Schlesinger WH, editors. Year in Ecology and Conservation Biology. Annals of the New York Academy of Sciences. 1223. Oxford: Blackwell Science Publ; 2011. p. 1–38. https://doi.org/10.1111/j.1749-6632.2011.06004.x

KURTA, A. & WHITAKER, J. J. O. (1998). Diet of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *The American midland naturalist,* 140(2): 280–286.

LEASE, H. M. & WOLF, B. O. (2010). Exoskeletal chitin scales isometrically with body size in terrestrial insects. *J Morpho,* 271(6): 759–768. https://doi.org/10.1002/jmor.10835

LEE, Y. F. & MCCRACKEN, G. F. (2005). Dietary Variation of Brazilian Free-Tailed Bats Links to Migratory Populations of Pest Insects. *J Mammal,* 86(1): 67–76. https://doi.org/10.1644/1545-1542(2005)086%3C0067:DVOBFB%3E2.0.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(1): 111–119. https://doi.org/10.3161/1733-5329(2005)7[111:DOWFBT]2.0.CO;2

MAFF. (2022). Yearly Report 2021 and Workplan 2022 of Agriculture Forestry and Fishery. *Ministry of Agriculture Forestry and Fishery*, Phnom Penh, 151 pp.

MAINE, J. J. & BOYLES, J. G. (2015). Bats initiate vital agroecological interactions in corn. *Proceedings of the National Academy of science,* 112(40): 12438–43. https://doi.org/10.1073/pnas.1505413112

PATHAK, M. D. & KHAN, Z. R. (1994). Insect Pest of Rice. *Inter Rice Res Insti*, Los Baños, 18–19.

PAVEY, C.R. & BURWELL, C. J. (1997). The diet of the diadem leaf-nosed bat *Hipposideros diadema*: confirmation of a morphologically-based prediction of carnivory. *J Zool,* 243(3): 295–303. https://doi.org/10.1111/j.1469-7998.1997.tb02783.x

PHAT, C. (2015). Willingness to Pay for the Conservation of Recreational Services in a National Park: A Case Study at Kirirom National Park, Cambodia. *Asian Institute of Technology School of Environment, Resource and Development,* 65 pp.

PHAUK, S., PHEN, S. & FUREY, N. M. (2013). Cambodian bat echolocation: a first description of assemblage call parameters and assessment of their utility for species identification. *Cambodian J Natur Hist,* 2013(1): 16–26.

POKHREL, S. & BUDHA, P. B. (2014). Key to identify insects from droppings of some insectivorous bats of Nepal. *J Institute of Science and Technology,* 19(1): 129–136. https://doi.org/10.3126/jist.v19i1.13838

PONMALAR, S. & VANITHARANI, J. (2014). Insect pest management by the horseshoe bats (Rhinolophus species) in the forest ecosystem of Kalakad Mundanthurai Tiger Reserve, India. *Scrut Internal Res J Biol and Environ Sci,* 1(5): 1–19.

R CORE TEAM (2021). R: A language and environment for statisticalcomputing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

RABINOWITZ, A. & TUTTLE, M. (1982). A test of the validity of two currently used methods of determining bat prey preferences. *Acta Theriol*, 27: 283–293. https://doi.org/10.4098/AT.arch.82-25

SCHNITZLER, H. & KALKO, E. K. V. (2001). Echolocation by insect-eating bats. *Bioscience,* 51(7): 557–569.

SIEMERS, M. B & GÜTTINGER, R. (2006). Prey conspicuousness can explain apparent prey selectivity. *Current Biol,* 16(5): 157–159.

SIMMONS, N. B. & CIRRANELLO, A. L. (August 25, 2023). Bat of the World: A taxonomic and geographic database. Version 1.4. https://batnames.org/

SIMMONS, N. B. (2005). Order Chiroptera. 1: 312–529. In: Wilson DE, Reeder DM. (eds.) Mammal Species of the World: A Taxonomic and Geographical Reference. Johns Hopkins University Press, Baltimore.

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 J Natur Hist,* 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. https://doi.org/10.3161/15081109ACC2018.20.1.016

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. https://doi.org/10.3161/15081109ACC2021.23.1.008

VENKATA, R. R. P., GUNDAPPA, B. & CHAKRAVARTHY, A. K. (2018). Pests of mango. *Pests and their management,* 415–440 pp. https://doi.org/10.1007/978-981-10-8687-8_12

VESTERINEN, E.J., RUOKOLAINEN, L., WAHLBERG, N., PEÑA, C., ROSLIN, T., LAINE, V.N., VASKO, V., SÄÄKSJÄRVI, I.E., NORRDAHL, K. & LILLEY, T.M. (2017). What you need is what you eat? Prey selection by the bat *Myotis daubentonii*. *Mol ecol,* 25(7): 1581–94. DOI: https://doi.org/10.1111/mec.13564

WAGHIIWIMBOM, M. D., MOISE, B. F., JULES, A.P. & TAMESSE, J. L. (2019). The diet composition of four vesper bats (Chiroptera: Vespertilionidae) from the Centre region of Cameroon (Central Africa). *Internal J Natur Res Ecol and Management,* 4(6): 153–63. DOI: https://doi.org/10.11648/j.ijnrem.20190406.11

WANGER, T. C., DARRAS, K., BUMRUNGSRI, S., TSCHARNTKE, T. & KLEIN, A. M. (2014). Bat pest control contributes to food security in Thailand. *Bio Cons*, 171, 220-223. https://doi.org/10.1016/j.biocon.2014.01.030

WEIER, S. M., MOODLEY, Y., FRASER, M. F., LINDEN, V. M., GRASS, I., TSCHARNTKE, T. & TAYLOR, P. J. (2019). Insect pest consumption by bats in macadamia orchards established by molecular diet analyses. *Glob Ecol and Cons*, 18:e00626. https://doi.org/10.1016/j.gecco.2019.e00626

WETERINGS, R. & UMPONSTIRA, C. (2014). Bodyweight-forearm ratio, cranial morphology and call frequency relate to prey selection in insectivorous bats. *Elec J Biol,* 10(1): 21–27.

WETERINGS, R., WARDENAAR, J., DUNN, S. & UMPONSTIRA, C. (2015). Dietary analysis of five insectivorous bat species from Kamphaeng Phet, Thailand. *Raffle bull zool,* 63: 91–96.

WHITAKER, J. O., DANNELLY, H. K. & PRENTICE, D. A. (2004). Chitinase in Insectivorous Bats. *J Mammal,* 85(1): 15–18. https://doi.org/10.1644/1545-1542(2004)085%3C0015:CIIB%3E2.0.CO;2

WHITAKER, J. O., NEEFUS, C. & KUNZ, T. H. (1996). Dietary Variation in the Mexican Free-tailed Bat (*Tadarida brasiliensis mexicana*). *J Mammal,* 77(3): 716–724. https://doi.org/10.2307/1382676

WHITAKER, J. O., ISSAC, S. S., MARIMUTHU, G. & KUNZ, T. H. (1999). Seasonal variation in the diet of the Indian pygmy bat, *Pipistrellus mimus*, in southern India. *J Mammal,* 80(1): 60–70. https://doi.org/10.2307/1383208

WHITAKER, J. O., MCCRACKEN, G. F. & SIEMERS, B. M. (2009). Food habits analysis of insectivorous bats. In: Kunz TH, Parsons S (eds) Ecological and Behavioural Methods for the Study of Bats, Second Edition. Pp 567–592.

WHITAKER, J. O. (1995). Food of the big brown bat, *Eptesicus fuscus*, from maternity colonies in Indiana and Illinois. *American Midland Naturalist,* 134: 346–360. https://doi.org/10.2307/2426304

WILLIG, M. R. (2001). Latitude, common trends within. In 'Encyclopedia of Biodiversity'. (Ed. S. A. Levin.): pp. 701–714. (Academic Press: San Diego.).

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. *J Mammal,* 86(1): 61–66. https://doi.org/10.1644/1545-1542(2005)086%3C0061:DOFBTP%3E2.0.CO;2

ZHU, D., LIU, Y., GONG, L., SI, M., WANG, Q., FENG, J. & JIANG, T. (2024). The Consumption and Diversity Variation Responses of Agricultural Pests and Their Dietary Niche Differentiation in Insectivorous Bat. *Animals*, 14(5): 815. https://doi.org/10.3390/ani14050815

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. https://doi.org/10.3161/150811012X654394