DNA Metabarcoding Reveals Insights into Diet Partitioning and Pest Suppression by Open Space Bats in Agricultural Landscapes

Authors: Srilopan, Supawan, Mata, Vanessa A., and Bumrungsri, Sara

Source: Acta Chiropterologica, 26(2) : 171-187

Published By: Museum and Institute of Zoology, Polish Academy of Sciences

URL: https://doi.org/10.3161/15081109ACC2024.26.2.003

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Acta-Chiropterologica on 22 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Acta Chiropterologica, 26(2): 171–187, 2024
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS
doi: 10.3161/15081109ACC2024.26.2.003

DNA metabarcoding reveals insights into diet partitioning and pest suppression by open space bats in agricultural landscapes

SUPAWAN SRILOPAN[1], VANESSA A. MATA[2], and SARA BUMRUNGSRI[1, 3]

[1]*Division of Biological Science, Prince of Songkla University, 90110, Hat Yai, Songkhla, Thailand*
[2]*CIBIO-InBIO, Research Center in Biodiversity and Genetic Resources, University of Porto, Vairão, Portugal*
[3]*Corresponding author: E-mail: sara.b@psu.ac.th*

Open-space bats are abundant and common in agricultural landscapes, and widely recognized for their effectiveness as natural suppressors of pest insects. However, there is currently a lack of comprehensive studies on the diets and diet partitioning of these bats, particularly in terms of ingested pest prey species. Here, we explored the diet and diet partitioning of open-space foraging bats using DNA metabarcoding. We hypothesized that open-space bats residing near intensive agricultural areas would primarily feed on pest insects. Additionally, considering their shared guild and foraging habitats, we anticipated the occurrence of diet partitioning as a mechanism of reducing competition. Our results demonstrate the effectiveness of DNA metabarcoding in bat diet analysis, revealing a high diet diversity and enabling prey species identification. The outcomes exposed 1,557 OTUs and at least 36 agricultural pest species were found in the diet of these aerial insectivorous bats, including *Nilaparvata lugens*, *Nysius graminicola*, *Piezodorus hybneri*, *Mythimna impura*, *Sesamia inferens*, and *Spodoptera frugiperda*, among others. This finding underscores the crucial role of the studied bat species in pest control across a variety of crops such as sugarcane, rice, and corn, among others. We also observed evidence of diet partitioning. *Mops plicatus* primarily preyed on Hemiptera (Pentatomidae and Delphacidae). *Taphozous theobaldi* predominantly fed on Lepidoptera (Noctuidae and Erebidae). *Taphozous melanopogon* primarily fed on Lepidoptera (Noctuidae, Erebidae, Crambidae, Pyralidae, Geometridae). *Scotophilus heathii* focused on Coleoptera (Hydrophilidae and Tenebrionidae). Niche overlap was high between *T. theobaldi* and *T. melanopogon*, while *T. theobaldi* also moderately overlapped with *M. plicatus*. *Mops plicatus* had lower degress of overlap with *T. melanopogon* and *S. heathii*. The lowest degrees of overlap were observed between *S. heathii* and *T. melanopogon*, as well as between *S. heathii* and *T. theobaldi*. Thus, these bats exhibited niche diet partitioning at the family level. Our study highlights the occurrence of diet overlap and partitioning among open-space bats, underscoring their crucial role as effective pest suppressors in Asian agricultural regions. Their widespread presence, sizable population, and consumption of key pests, including migratory species, emphasize their significance in pest suppression. Protecting these bats is essential for suppressing pest insects and aiding farmers in protecting their crop yields across the region.

Key words: migratory species, niche overlap, diet analysis, crops, competition

INTRODUCTION

Studying wildlife-crop interactions is crucial for agricultural productivity and for understanding wildlife biology in anthropogenic landscapes (Federico *et al*., 2008; Aizpurua *et al*., 2018). Globally, pest animals can cause losses in annual crop production of more than 25% (Oerke, 2006). However, conventional agricultural practices often overlook the ecosystem services provided by pest-regulating animals. Integrated pest management (IPM) emphasizes the significance of biological pest control, aiming to reduce the use of pesticides while mitigating monetary losses from agricultural pests (Ehler, 2006).

Bats are recognized as highly effective natural suppressors of pest insects in agricultural landscapes (Boyles *et al*., 2011; Kunz *et al*., 2011; Maas *et al*., 2013). They provide essential ecosystem services by foraging on airborne insects above farmland, particularly when including crop-associated arthropods in their diet (Leelapaibul *et al*., 2005; Wanger *et al*., 2014; Maine and Boyles, 2015; Aizpurua *et al*., 2018; Srilopan *et al*., 2018). Open-space foraging insectivorous bats dominate local bat communities in agricultural areas and serve as excellent bioindicators due to their high trophic position in food webs, making them sensitive to anthropogenic factors (Kalko *et al*., 2008; Jones *et al*., 2009). Open-space bats are not only important in agricultural landscapes due to their adaptability to habitat fragmentation but also for providing valuable ecosystem services to farmers by consuming pest insects worldwide (Boyles *et al*., 2011; Kunz *et al*., 2011; Ghanem and Voigt 2012; Williams-Guillén *et al*., 2016). These bats are known for their high-altitude flights, which are associated with the migration of pest insects at high altitudes (Leelapaibul *et al*., 2005; McCracken *et al*., 2008; Krauel *et al*., 2018*b*; Srilopan *et al*., 2018; Nguyen *et al*., 2019). These bats have been reported to reduce production costs to crops like rice, corn, cotton, sugar cane, coffee, and cocoa (Wanger *et al*., 2014; Maine and Boyles, 2015; Puig-Montserrat *et al*., 2015). As these crops are usually grown in large continuous areas, open-space bats navigate these landscapes effectively (Schnitzler *et al*., 2003; Denzinger and Schnitzler, 2013).

In agricultural landscapes of central Thailand, bat activity is dominated by open-space species such as *Mops plicatus*, *Taphozous melanopogon*, *T. theobaldi*, and *Scotophilus heathii* (Suksai and Bumrungsri, 2020). These species forage in open spaces for airborne prey, and share similar wing morphologies with high aspect ratios and wing loadings (Zhu *et al*., 2012; Suksai and Bumrungsri, 2020). Bat species belonging to the same guild, such as open-space foragers, often exhibit niche differentiation in order to reduce competition (Denzinger *et al*., 2016). Ecological niche differentiation contributes to stable coexistence in the presence of competition, as it reduces the degree of competition for limited resources (Chesson, 2000). Previous studies have shown that local insectivorous bat species, especially closely related taxa, may differentiate along various niche dimensions, such as diet, to facilitate coexistence and reduce competition (Hooper and Brown, 1968; Siemers and Swift, 2006; Ruadreo *et al*., 2018). Limited data on dietary niches within the same bat guilds hinder our understanding of bat community partitioning (Bumrungsri *et al*., 2007). Detailed studies on resource use, particularly those that take advantage of new molecular approaches are needed to reveal insights into community structuring.

The recent advances in DNA-based dietary analysis provide detailed information on bat diets, capable of identifying individual pest species (Williams-Guillén *et al*., 2016). Improved methods of diet analysis may provide a clearer understanding of trophic resource partitioning among coexisting bat species (Razgour *et al*., 2011). Conventional techniques have sometimes failed to identify resource partitioning in morphologically similar bat species, but finer-scale evaluations of diet analysis can reveal distinct dietary niches (Jacobs and Barclay, 2009; Schoeman and Jacobs, 2011). DNA metabarcoding of bat faecal pellets, using mini-barcoding PCRs and high-throughput sequencing (HTS), is an effective approach to assess arthropod diversity (Bohmann *et al*., 2011) and has been successfully applied to address various aspects of bat diets, such as predator-prey interactions and resource partitioning (Clare *et al*., 2009; Bohmann *et al*., 2011; Razgour *et al*., 2011; Dodd *et al*., 2012; Mata *et al*., 2016; Vesterinen *et al*., 2016). However, few studies have explored the prevalence of pest species in landscapes primarily dominated by diverse annual crops, such as those found in Asia, along with the diet partitioning of sympatric bats. This study aims to improve our understanding of the dietary habits of prevalent open-space bats that inhabit agricultural landscapes, specifically examining the presence of pest insect species using DNA metabarcoding. Our objective is to examine the extent of resource partitioning among these bat species, considering potential differences in resource utilization within their ecological niches.

We hypothesize that open-space bats residing in agricultural areas might consume both local pest insects and migratory pest insects owing to the nature of their habitat. Additionally, we posit that bats sharing the same foraging guild and habitat might display diet partitioning. This hypothesis is based on the premise that when multiple bat species coexist in overlapping habitats, they may partition their diets to reduce competition for resources (Siemers and Swift, 2006; Ruadreo *et al*., 2018). By testing these hypotheses, we aim to gain insights into the foraging behaviour and dietary habits of open-space bats in agricultural landscapes.

MATERIALS AND METHODS

Study Site and Species

This study was carried out in central Thailand (Lopburi and Ayutthaya provinces). Bats were captured using mist nets and hand nets as they returned to caves after foraging. The first roost, Khao Wong cave (15°02'N, 101°18'E), was inhabited by *Mops plicatus* and *Taphozous theobaldi*, while the second roost, Wat Tham Bot Yawat cave (15°03'N, 101°32'E), was a roosting site for *T. melanopogon*, located approximately 1.49 km away from the first cave. Additionally, a house-dwelling colony of *Scotophilus heathii* (14°18'N, 100°29'E) was found approximately 116 km away from both caves. The local landscape is dominated by sugarcane, corn, cassava plantations, and rice fields. Sugarcane is planted from October through February, taking 10–14 months to harvest (Manivong and Bourgois, 2017). Corn is planted in May–June and is harvested in 100–120 days, around September–October (Ekasingh *et al*., 2004). Cassava is planted March–May and harvested in January–March, 8–20 months after planting (Arthey *et al*., 2018). Rice is typically planted around May and harvested around December–January, depending on rainfall (Felkner *et al*., 2009). The region experiences three distinct seasons influenced by monsoon winds: dry, rainy, and cool dry. The dry season, from mid-February to mid-May, is dry and hot. The rainy season, lasting from mid-May to mid-October, brings abundant rainfall, especially in August and September. From mid-October to mid-February, the cool dry season prevails, characterized by cooler temperatures and dry weather (Ruadreo *et al*., 2018).

Open-space bats have narrow wings with high wing loading and aspect ratio for fast flight (Voigt *et al*., 2018). The wrinkle-lipped free-tailed bat (*M. plicatus*, Molossidae) is known for its foraging behaviour at high altitudes (Nguyen *et al*., 2019). This species typically forms large colonies in caves, ranging from 10,000 to several million individuals (Srilopan *et al*., 2018). Theobald's tomb bat (*T. theobaldi*, Emballonuridae) is known to roost in caves and forage above nearby forests. It has been observed foraging at altitudes of up to 800 m above ground (Roeleke *et al*., 2018). The black-bearded tomb bat (*T. melanopogon*, Emballonuridae) is typically found in hilly and forested areas, and this species roosts in caves, buildings, and temples, where they form sizable populations (Wei *et al*., 2008). The Greater Asiatic yellow house bat (*S. heathii*) is widespread and commonly found in various habitats, especially human settlements. It roosts in crevices, cracks in buildings, palm crowns, tree hollows, and among banana leaves, either alone or in colonies of up to 50 individuals (Shahbaz *et al*., 2014).

Sampling and Faecal Storage

We collected faeces from 70 individuals each of *M. plicatus*, *T. theobaldi*, and *T. melanopogon*. Additionally, we obtained 40 faecal samples from a roost of *S. heathii* by randomly collecting faces from bats in different spots within the roost. We ensured that the samples were collected from various locations to confidently ascertain that the pellets came from different individuals (Table 1). The bats were captured upon returning to the roost following foraging activities, ensuring prompt defecation. To prevent cross-contamination of samples, each bat was kept separately in a clean, single-use cotton bag for 15–20 minutes. They were then identified, sexed, and aged before being released. Faecal pellets were collected from the bags and stored in 1.5-ml collection tubes filled with silica gel granules and kept at room temperature (around 25°C) for up to 24 hours before being transferred to a freezer. All samples were kept dry and refrigerated (4–8°C) for 2 to 12 months until arrival at the laboratory. The experimental procedures and protocols received approval from the 'Standard of Animal Research, Research and Development' office, Prince of Songkla University (project license number: U1-06459-2560, protocol code: 2564-01-026).

Laboratory Procedures

DNA was extracted from one dropping per study individual. The numbers of individuals and pellets analysed were carefully chosen to balance accuracy in diet estimation and cost considerations (Mata *et al*., 2019). A previous study has shown that pooling samples can provide poor estimates of diet diversity and frequency of occurrence. Mata *et al*. (2019) suggests that most variation in diet composition is associated with differences among individual bats, followed by the number of pellets per individual, and PCRs per pellet. Therefore, we chose to collect one sample from each individual rather than five samples from one individual to capture more individual variation and provided a more comprehensive understanding of the diet diversity within the population, despite the limited budget. We randomly selected a complete pellet that was not broken, ensuring it was of average size.

The extraction protocol followed methods described by Gonçalves *et al*. (2024), which involved an initial incubation period using a lysis buffer composed of 0.1 M Tris-HCl, 0.1 M EDTA, 0.01 M NaCl, 1% N-lauroylsarcosine, pH 7.5–8.0 (Maudet *et al*., 2002). Cell lysis, DNA precipitation, and washing steps were performed using E.Z.N.A. Tissue Kits (Omega Bio-Tek, Norcross, Georgia, USA). For each extraction, one faecal pellet was added to 650 µL of the lysis buffer. The samples were homogenized with a spatula, vortexed, and incubated in a dry bath at 70ºC for 30 minutes. Following incubation, the samples were briefly centrifuged, and up to 500 µL of the supernatant was transferred to a new tube containing 25 µL of OB Protease. The remaining steps of the extraction protocol followed the recommendations provided with the E.Z.N.A. Tissue Kits, except that the DNA was eluted twice in separate 50-µL elutions. The DNA extraction process was carried out in batches, with each batch consisting of 23 samples and one negative control (without a faecal pellet). All extracted DNA was distributed across 96-well plates, with the final well in each plate designated for the PCR negative control.

The prey DNA was amplified using the FwhF2-R2n COI primer set (Vamos *et al*., 2017), which were modified to include Illumina adaptors. The Fwh2 primer was originally designed for amplifying freshwater invertebrates but has been shown to be effective in amplifying a wide range of terrestrial arthropods, including moths, ants, beetles, true bugs, spiders, and even springtails (Mata *et al*., 2021). PCR reactions consisted of 5 µL of Qiagen Multiplex Master Mix, 0.3 µL of each 10 nM primer (forward and reverse), 2.4 µL of water, and 1 µL of DNA

TABLE 1. Number of samples collected from each bat species during each season

Date	Season	*M. plicatus* (# bats)	*T. theobaldi* (# bats)	*T. melanopogon* (# bats)	*S. heathii* (# pellets)
March 2021	Dry	14	14	14	–
May 2021	Rainy	14	14	14	–
September 2021	Rainy	14	14	14	–
November 2021	Cool dry	14	14	14	–
January 2022	Cool dry	14	14	14	40

extract. The cycling conditions started with an initial denaturation at 95ºC for 15 minutes, followed by 40 cycles of denaturation at 95ºC for 30 seconds, annealing at 50ºC for 30 seconds, and extension at 72ºC for 30 seconds. A final extension step was carried out at 60ºC for 10 minutes. PCR products were diluted 1:3 with water and subjected to a second PCR reaction to incorporate 7 bp identification tags and Illumina P5 and P7 adaptors. The second PCR reactions and cycling conditions were similar to the first PCR, with the exception that KAPA HiFi HotStart ReadyMix (Rocher, KAPA Biosystems, Basel, Switzerland) was used, and only nine cycles of denaturation, annealing, and extension were performed, with an annealing temperature of 55ºC. The PCR products were purified using Agencourt AMPure XP beads (Beckman Coulter, Brea, California, USA) and quantified using Nanodrop. They were then diluted to a concentration of 15 nM. The purified and normalized PCR products were pooled. The library was quantified using qPCR (KAPA Library Quant Kit qPCR Mix, Rocher) and diluted to a concentration of 4 nM. Sequencing was performed on a MiSeq platform using a v2 kit (500 cycles), targeting a coverage of 30k reads per PCR product. The target coverage was determined based on the taxa amplified by the marker. It is important to note that Fwh2 amplifies not only insects but also some fungi and vertebrates like bats, which may result in the loss of some reads to non-dietary items (Mata *et al*., 2021).

Bioinformatic Analysis

We aligned pairs of sequences using Obitools, then eliminated primer sequences. Sample information was added to each assembled read using the ‘ngsfilter’ command from OBITools (Boyer *et al*., 2016). Next, the reads were de-replicated into unique sequences using the ‘obiuniq’ command and merged into a single fasta file. Afterward, we employed VSEARCH (Rognes *et al*., 2016) to denoise the dataset, remove chimeric sequences, cluster sequences into Operating Taxonomic Units (OTUs) with 99% similarity, and map raw reads with the resulting OTUs. Further refinement of the obtained OTU table and sequences was performed using the R package LULU (Frøslev *et al*., 2017) to remove potential mtDNA nuclear copies and persisting PCR and sequencing errors. OTUs were taxonomically assigned using BOLDigger (Buchner and Leese, 2020), and the outcomes were subsequently scrutinized and refined through manual assessment. In scenarios where achieving species-level assignments was unattainable using BOLD, we performed supplementary manual BLAST searches on NCBI to ensure precise identification. Sequences displaying fewer than 90% similarity were categorized at the class level. Those with similarities ranging from 90% to 95% were assigned to the family level, while sequences with over 95% similarity were allocated to species or genus level. In cases where sequences matched multiple species within the same genus, the OTU was designated at the genus level (Collins and Cruickshank, 2013; Wray *et al*., 2018). When encountering matches with multiple genera or species, OTUs were assigned based on species records in Thailand. Each OTU was classified as either ‘diet’ (representing most arthropods) or ‘not diet’ (including fungi and internal and external parasites) based on its taxonomic identification. Samples with fewer than 100 reads attributed to dietary items were considered unsuccessful and excluded from further analysis. To minimize potential false interactions related to cross-talk (Edgar, 2016) and secondary predation (Deagle *et al*., 2019), taxa representing fewer than 1% of the total number of dietary reads in each sample were removed. After this filtering step, the remaining samples were used for subsequent analysis.

Statistical Analysis

For statistical analysis, presence/absence matrices were constructed for each sample at three identification levels: species, family, and order. Additionally, we calculated the frequency of occurrence for each prey taxon at the species, family, and order levels for each bat species. The frequency of occurrence was determined by dividing the number of faecal samples in which a specific species, family, or order was detected by the total number of samples collected for each bat species.

All analyses were performed with R (version 4.2.2) and R Studio. We tested for differences in prey richness, niche width, and prey composition among bat species diet, as well as overall niche overlap among bats. To test for differences in prey average richness between bat species, we conducted a generalized linear mixed model with a Poisson error distribution using the ‘glm’ function from the R package ‘lme4’. The variable ‘season’ was included as a random factor to account for potential temporal effects. The significance of the generalized linear mixed model was assessed using the ‘Anova’ function from the ‘car’ package. We compared the niche breadth of the four bat species at the species, family, and order levels by estimating richness values using Hill numbers base on twice the number of samples of the species with the smallest sample size. This analysis was conducted using the 'iNEXT' function from the R package ‘iNEXT’. Differences between estimates were deemed significant if the 95% confidence intervals (CIs) around the richness estimates did not overlap. To examine the influence of bat species on the diversity of prey species composition within each sample, we performed a permutational multivariate analysis of variance (PERMANOVA) based on presence/absence data and the Jaccard index. Significance was assessed using 9,999 random permutations (Anderson, 2001). To identify the most distinct prey items, we conducted a SIMPER analysis by calculating the percentage similarities within samples attributed to bat species that contributed to these similarities. This analysis was based on Jaccard’s similarities, using the frequency of prey occurrences in samples as a measure of abundance. To assess trophic niche overlap among the four bat species, we calculated dietary niche similarity using Pianka’s index, which is based on the frequency of occurrence of prey insects. This index ranges from 0 to 1, with a value of 1 indicating complete overlap in dietary niche among the bat species. The interaction network between each bat species and insect family was constructed and analysed using the R package ‘bipartite’. The strength of interactions was assessed based on the number of samples in which each insect family was detected.

Analysis of Agricultural Pest Insects

We assessed the pest status of prey taxa identified to species level or as a species complex (i.e., when two or three species of the same genus were equally matched) with high support (> 99% identity). We focused on agricultural insect pests based on a comprehensive literature survey (Sukonthaphirom Na Phatthalung *et al*., 2021; http://ippc.acfs.go.th/pest; http://www.ricethailand.go.th/rkb3/Insect.htm; https://www.si.edu/spotlight/buginfo/diseases). We also evaluated the pest status of migratory insect prey based on a comprehensive review of the literature (Fox, 1978; Farrow and McDonald, 1987; Riley *et al*., 1987, 1995; Chapman *et al*., 2002; Song, 2005; Wood *et al*., 2009; Margam *et al*., 2011; Fu *et al*., 2015; Longbottom *et al*., 2017; Huang *et al*., 2020; Shen *et al*., 2020; Zeng *et al*., 2020; Chen *et al*., 2022; Wang *et al*., 2022; Atieli *et al*., 2023; Chatterjee *et al*., 2023; Huang *et al*., 2023).

RESULTS

A total of 1,557 operational taxonomic units (OTUs) were obtained from all samples. Arthropods considered to be diet constituted a significant proportion of the OTUs (49.45% — 770). In contrast, Chiroptera OTUs, not part of the diet, contributed to a smaller fraction, approximately 0.83% (13). The remaining OTUs were either fungi, parasites, or other non-dietary items. Among the studied bat species, *M. plicatus* exhibited a remarkably diverse diet, consuming 216 OTUs from 67 families and 11 orders. The primary prey items were predominantly from the order Hemiptera (28.6%), specifically, the families Pentatomidae (9.1%), and Delphacidae (7.7%). The order Diptera (16.8%) was primarily composed of the families Limoniidae (5.5%) and Culicidae (2.5%). The order Lepidoptera (14.3%) consisted of the families Noctuidae (3.2%) and Erebidae (2.3%). Additionally, the order Blattodea (12.1%) was primarily attributed to the family Termitidae (10.9%). The order Coleoptera (11.1%) was mostly comprised of the families Tenebrionidae (3%) and Carabidae (1.4%). These orders served as the primary contributors to the diet of *M. plicatus* (Fig. 1).

The diet of *T. theobaldi* included 110 OTUs across 42 families and 11 orders. The primary prey items were predominantly derived from the order Lepidoptera (40.3%), with notable contributions from the families Noctuidae (16.6%) and Erebidae (12.8%). Another significant order was Orthoptera (29.7%), primarily comprising the families Gryllidae (11.0%), Gryllotalpidae (6.9%), and Tettigoniidae (5.5%). The order Blattodea (11.7%), was represented mainly by the family Termitidae (10.7%). The order Diptera (5.5%) had the family Chironomidae (3.1%) as the main contributor. Additionally, the order Coleoptera (4.5%), was comprised largely by the family Bostrichidae (1.7%) (Fig. 1).

Taphozous melanopogon consumed a total of 137 OTUs from 34 families and eight orders. The main prey order observed was Lepidoptera (58%), accounting for a significant proportion of the diet. The most common lepidopteran families were Noctuidae (25.6%), followed by Erebidae (13.9%), Crambidae (6.8%), Pyralidae (3.2%), and Geometridae (2.1%). Another significant order in the diet was Orthoptera (30.3%), represented by the families Gryllotalpidae (9.6%), Gryllidae (9.3%), Tettigoniidae (6.1%), and Acrididae (3.6%). The order Diptera (3.9%), was primarily represented by the family Limoniidae (1.8%) (Fig. 1).

The diet of *S. heathii* included a total of 126 OTUs across 47 families and 12 orders. The primary order observed was Coleoptera (44.8%) which was represented mostly by the families Hydrophilidae (11.2%) and Tenebrionidae (9.4%). The order Hemiptera (18.8%) also played a substantial role in the diet, with the families Pentatomidae (8.0%) and Notonectidae (2.2%) being the most abundant. The OTUs in the order Lepidoptera (10.8%) were primarily within the families Gelechiidae (4.0%) and Tortricidae (1.4%). Additionally, the order Diptera (9.4%) was represented by the families Chironomidae (2.2%) and Culicidae (1.8%) while the order Psocodea (5.1%) was primarily represented by the family Liposcelididae (4.7%) (Fig. 1).

Rarefaction curves indicated that the dietary items of *M. plicatus* and *T. melanopogon*, approached saturation, while those of *T. theobaldi* and *S. heathii* did not seem to be saturated. Predicted family richness estimates indicated that more samples were needed for the latter species. At the family level, *M. plicatus* and *S. heathii* showed the widest niches, while *T. theobaldi* and *T. melanopogon* exhibited the lowest (Fig. 2). Confidence intervals (95%) indicated significant differences in niche width between *M. plicatus* and both *Taphozous* species, as well as between *S. heathii* and *T. melanopogon*. Analysis of prey richness per sample indicated significant differences among certain bat species. Specifically, *T. melanopogon* and *T. theobaldi* exhibited significantly lower prey richness compared to *M. plicatus* ($P < 0.001$), while *S. heatii* showed no significant difference ($P = 0.235$).

The bat species in this study showed different levels of dietary overlap. *Taphozous theobaldi* and *T. melanopogon* had the highest overlap (0.75), indicating similar food preferences. *Taphozous theobaldi* also had moderate overlap with *M. plicatus* (0.41). *Mops plicatus* had lower overlap values with *T. melanopogon* (0.25) and *S. heathii* (0.24). The lowest degrees of overlap were observed between *S. heathii* and *T. melanopogon* (0.07) and *S. heathii* and *T. theobaldi* (0.1) (Fig. 3).

Diet composition at the family level displayed significant differences between bat species, where the species factor showed a significant effect on the composition (F-value = 9.401, $d.f. = 3$, $R^2 = 0.112$,

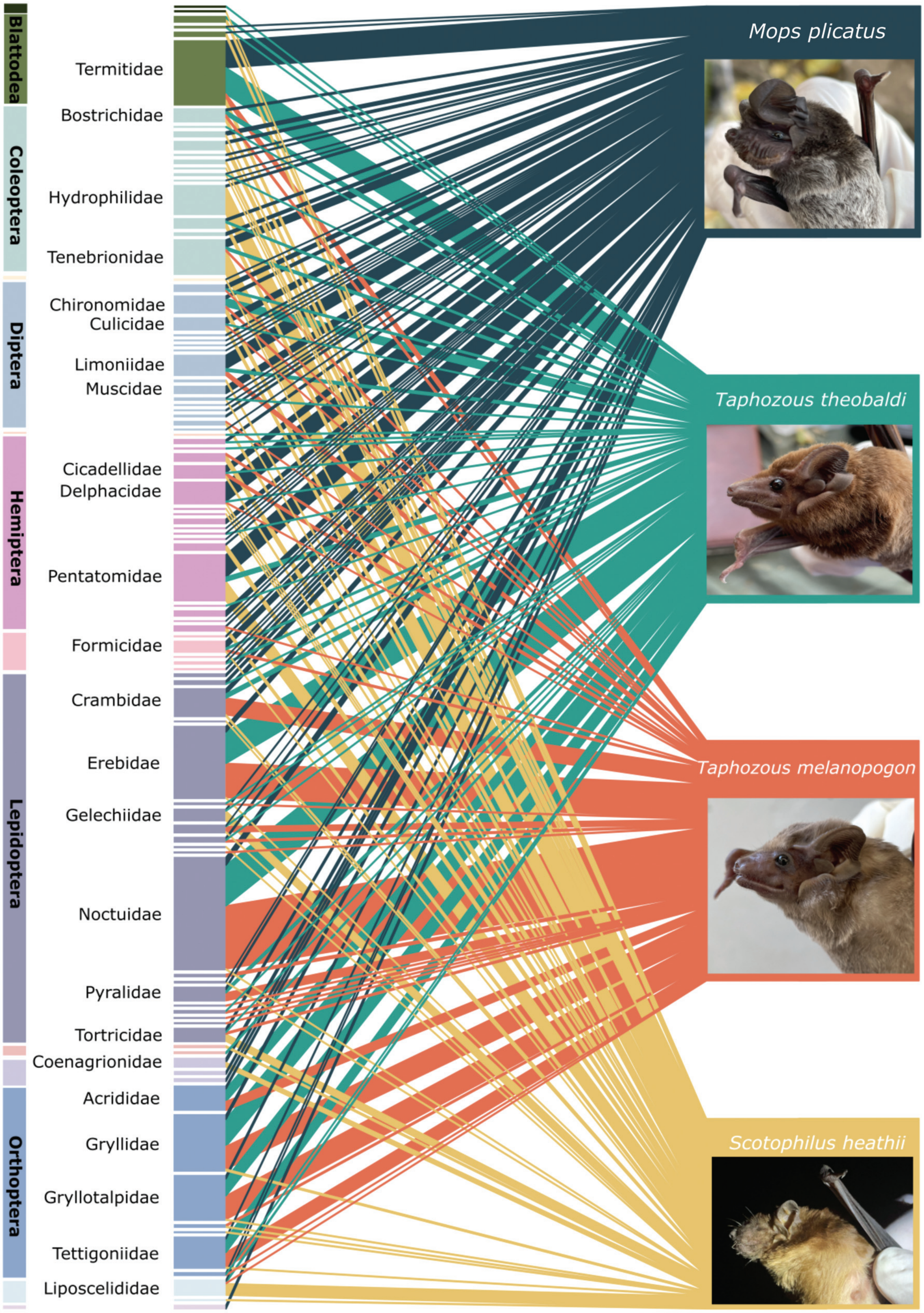

FIG. 1. Interaction network showing the dietary niches of the four open-space bat species studied in central Thailand. Link width represents the percent frequency of occurrence of each prey family/order detected in each bat sample

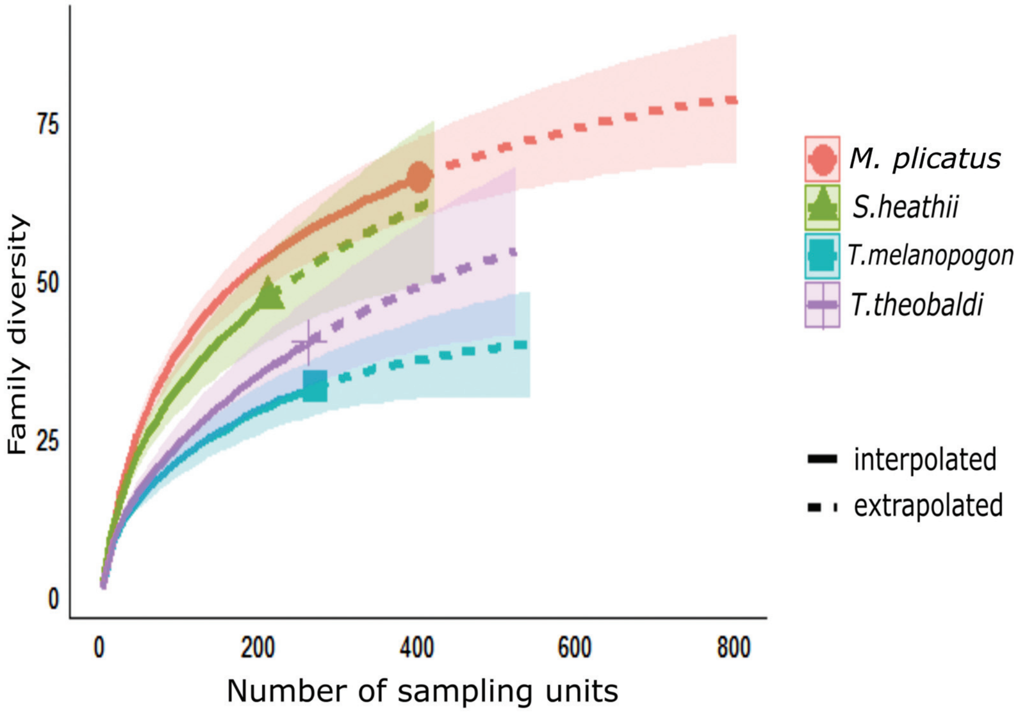

FIG. 2. Rarefaction and extrapolation curves of prey richness for the studied bat species: *M. plicatus*, *S. heathii*, *T. melanopogon*, and *T. theobaldi*

P = 0.001). SIMPER tests revealed that *M. plicatus* and *S. heathii* exhibited differences across 27 families. For instance, *M. plicatus* consumed more Cicadellidae, Delphacidae, and Pentatomidae from the order Hemiptera, while *S. heathii* consumed more Cerambycidae, Hydrophilidae, and Tenebrionidae from the order Coleoptera. *Mops plicatus* displayed differences in diet composition across 35 families compared to *T. melanopogon*, and across 34 families compared to *T. theobaldi*. For example, *M. plicatus* consumed higher amounts of Chrysomelidae and Staphylinidae from the order Coleoptera, along with Limoniidae and Muscidae from the order Diptera, and Delphacidae and Lygaeidae from the order Hemiptera. On the other hand, *T. melanopogon* had a greater intake of Crambidae and Noctuidae from the order Lepidoptera. Similarly, *S. heathii* showed differences across 25 families compared to *T. melanopogon*, and across 24 families compared to *T. theobaldi*. As an example, *S. heathii* consumed larger quantities of Hydrophilidae, Tenebrionidae, and Cerambycidae from the order Coleoptera, along with Micropezidae from the order Diptera, and Belostomatidae, Notonectidae, and Flatidae from the order Hemiptera. In contrast, *T. melanopogon* exhibited a higher consumption of Noctuidae from the order Lepidoptera and Gryllotalpidae from the order Orthoptera. Additionally, there were differences in diet composition across 22 families between *T. melanopogon* and *T. theobaldi*. For instance, *T. melanopogon* showed greater consumption of Erebidae, Noctuidae, and Pyralidae from the order Lepidoptera, as well as Gryllotalpidae and Tettigoniidae from the order Orthoptera. Conversely, *T. theobaldi* exhibited higher consumption of Baetidae from the order Ephemeroptera, along with

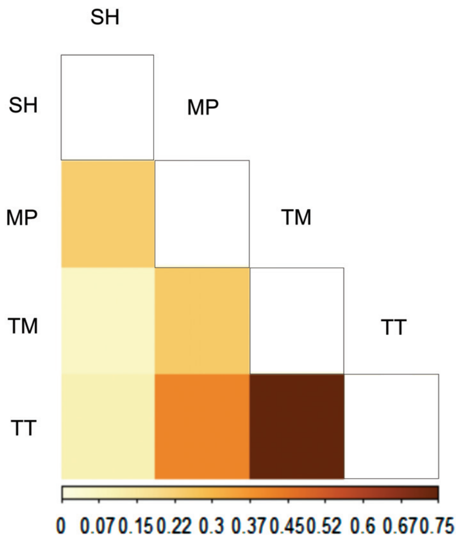

FIG. 3. Niche overlap among open-space bats in central Thailand, with overlap values ranging from 0–1. SH — *S. heathi*, MP — *M. plicatus*, TM — *T. melanopogon*, TT — *T. theobaldi*

Aphididae and Psyllidae from the order Hemiptera, and Mantidae from the order Mantodea (Fig. 1 and the Appendix).

We found at least 36 agricultural pest species in the diet of these open-space bats (Table 2). *Mops plicatus* and *T. melanopogon* consumed the highest number of pests (20), followed by *T. theobaldi* (18), and *S. heathii* (6). Additionally, these bats were observed foraging on at least 22 species of migratory insect pests, including: *Culex tritaeniorhynchus*, *Nephotettix virescens*, *Nilaparvata lugens*, *Sogatella furcifera*, *Nezara viridula*, *Cnaphalocrocis patnalis*, *C. poeyalis*, *Maruca vitrata*, *Ostrinia furnacalis*, *Scirpophaga incertulas*, *Achaea janata*, *Anomis flava*, *Mythimna formosana*, *M. impura*, *Sesamia inferens*, *Spodoptera exigua*, *S. frugiperda*, *S. litura*, *S. mauritia*, *Plutella xylostella*, *Cyrtacanthacris tatarica*, and *Locusta migratoria* — Table 2). Certain migratory pest insects were consumed by all four sympatric open-space bat species, including the pests, e.g., *M. impura*, *S. inferens*, and *S. frugiperda* (Table 2).

The family Termitidae (notably, *Macrotermes annandalei*, *Odontotermes* sp. 1, and *Odontotermes* sp. 2) was consumed at a high frequency of occurrence by most of the bat species. Additionally, in the diet of *M. plicatus*, the family Delphacidae (notably, *N. lugens* and *S. furcifera*) was found to be consumed frequently. On the other hand, *T. theobaldi* and *T. melanopogon* primarily consumed prey from the family Noctuidae (notably, *M. impura*, *S. inferens*, *S. frugiperda*, and *S. litura*) (Table 2).

DISCUSSION

Insectivorous bats are well-known as important predators of arthropod pests (Aizpurua *et al*., 2018). Our DNA metabarcoding results showed that the open-space bats, *M. plicatus*, *S. heathii*, *T. melanopogon*, and *T. theobaldi*, have diverse diets that include economically damaging insect pests that harm crops and serve as disease vectors. We identified at least 36 insect species known to damage agricultural crops and carry human diseases. These pests are known to affect a variety of crops, including sugarcane (e.g., *Macrotermes annandalei*, *Chilo tumidicostalis*), rice (e.g., *N. lugens*, *S. furcifera*), and corn (e.g., *S. frugiperda*, *M. impura*), as well as other plants such as cotton, mung beans, grapes, okra, dendrobium, asparagus, yard-long beans, cruciferous vegetables, sunflowers, sorg-hum, soybeans, sesame, castor beans, groundnuts or peanuts, chili, garden peas, tomatoes, and mangosteen (Sukonthaphirom Na Phatthalung *et al*., 2021). Additionally, these bats also consumed *Culex tritaeniorhynchus* and *Culex vishnui*, which are known to be the primary vectors of Japanese encephalitis (Karthika *et al*., 2018).

In accordance with previous research, *M. plicatus* was found to primarily feed on rice insect pests, including *N. lugens*, *S. furcifera*, *N. virescens*, and *S. incertulas*, as well as disease vectors such as *Culex gelicus*, *C. tritaeniorhynchus*, and *C. vishnui* (Leelapaibul *et al*., 2005; Srilopan *et al*., 2018; Thongjued, 2019). In contrast, there have been no previous reports of insect pests in the diets of *T. theobaldi*, *T. melanopogon*, and *S. heathii*. However, our study revealed that these three species consume various insect pests, including *Mythimna formosana*, *M. impura*, *S. inferens*, *C. tumidicostalis*, *Cnaphalocrocis exigua*, *C. patnalis*, and *S. frugiperda*, among others. These findings suggest that these bat species might also play important roles in pest suppression within agricultural landscapes, similar to *M. plicatus*.

Our results demonstrate the effectiveness of DNA metabarcoding in bat diet analysis, revealing substantially high prey diversity compared to previous studies conducted in Thailand (Leelapaibul *et al*., 2005; Weterings *et al*., 2015; Ruadreo *et al*., 2018; Srilopan *et al*., 2018; Thongjued, 2019). *Mops plicatus* exhibited the most diverse diet, consuming 216 OTUs from 67 families and 11 orders. The diet primarily consisted of prey items from the order Hemiptera, followed by Diptera and Lepidoptera. This finding corresponds to the results of previous studies, including those that identified prey from faecal pellets via microscopic analysis, which identified Hemiptera, Coleoptera, Lepidoptera, and Diptera as the main components within the diet of *M. plicatus* (Leelapaibul *et al*., 2005; Srilopan *et al*., 2018). In contrast, research conducted by Ruadreo and colleagues (2018) and Thongjued (2019) reported Diptera as the primary prey, followed by Hemiptera, Lepidoptera, and Coleoptera. Thongjued (2019) used direct PCR-DGGE and found that while Diptera constituted the primary diet, Hemiptera also made up a substantial proportion, with minimal differences between them. Ruadreo and colleagues (2018) used stable isotopes for diet analysis. However, this method is more suitable for providing a broad overview of the ecological niche rather than detailed dietary information (Roswag *et al*., 2018). The observed differences in results are likely due in part to the different methods employed. Additionally, our results showed that *M. plicatus*

TABLE 2. List of arthropod pest species preyed upon by open-space bats in central Thailand (*M. plicatus* — MP, *T. melanopogon* — TM, *T. theobaldi* — TT, and *S. heathii* — SH), along with the crops or hosts affected by each species and the frequency of occurrence in the diet of each bat species (* = migratory pest). Please also note that *Culex tritaeniorhynchus* and *C. vishnui* are arbovirus vectors

Family/Species	Crop or host	Frequency of occurrence (%)			
		MP	TT	TM	SH
Termitidae					
Macrotermes annandalei	sugarcane	18.0	20.3	6.1	2.7
Odontotermes sp.1	sugarcane	23.0	15.6	1.5	–
Odontotermes sp. 2	sugarcane	1.6	1.6	1.5	–
Culicidae					
*Culex tritaeniorhynchus**	humans	4.9	1.6	–	–
Culex vishnui	humans	1.6	–	1.5	8.1
Alydidae					
Leptocorisa oratoria	rice	–	–	–	2.7
Riptortus serripes	soybean	4.9	1.6	–	–
Cicadellidae					
*Nephotettix virescens**	rice	4.9	–	–	–
Delphacidae					
*Nilaparvata lugens**	rice	29.5	1.6	–	–
*Sogatella furcifera**	rice	4.9	–	1.5	–
Lygaeidae					
Nysius graminicola	sunflower, sesame, rice	11.5	–	–	–
Nysius plebeius	sunflower, sesame	1.6	–	–	–
Pentatomidae					
*Nezara viridula**	sunflower, sesame, sorghum, soybean, mung bean	4.9	1.6	–	–
Piezodorus hybneri	sunflower, mung bean, soybean	16.4	1.6	–	2.7
Crambidae					
Chilo tumidicostalis	sugarcane	–	–	–	2.7
Cnaphalocrocis exigua	rice	3.3	–	3.0	–
*Cnaphalocrocis patnalis**	rice			3.0	–
*Cnaphalocrocis poeyalis**	rice			1.5	–
*Maruca vitrata**	mung bean			1.5	–
*Ostrinia furnacalis**	corn		1.6		–
*Scirpophaga incertulas**	rice	4.9		3.0	–
Erebidae					
*Achaea janata**	castor bean			3.0	–
*Anomis flava**	cotton		3.1	1.5	–
Anomis leucolopha	cotton, rice		3.1		–
Gelechiidae					
Aproaerema simplexella	groundnut or peanut, soybean	3.3	–	–	–
Noctuidae					
*Mythimna formosana**	sorghum, corn, rice	–	–	1.5	–
*Mythimna impura**	sorghum, corn, rice	4.9	17.2	–	–
*Sesamia inferens**	rice, sugarcane	1.6	9.4	–	–
*Spodoptera exigua**	corn, cotton, mung bean, grape, okra, dendrobium, asparagus, yard-long bean, cruciferous	–	–	1.5	–
*Spodoptera frugiperda**	corn	1.6	6.2	10.6	–
*Spodoptera litura**	soybean, mung bean, groundnut or peanut, chili, cruciferous, yard-long bean, garden pea, tomato, asparagus	3.1	3.0	–	–
*Spodoptera mauritia**	rice	–	3.1	3.0	–
Stictoptera cucullioides	mangosteen	–	1.6	1.5	–
Plutellidae					
*Plutella xylostella**	cruciferous	–	1.6	–	2.7
Acrididae					
*Cyrtacanthacris tatarica**	rice	–	–	1.5	–
*Locusta migratoria**	corn, sugarcane, rice	–	1.6	–	–

feeds mainly on insects in Hemiptera, whereas *Tadarida brasiliensis* primarily consumes Lepidoptera, despite both being molossid bats with similar behaviour. This difference may be due to the distinct regions and main crops each species inhabits (Krauel *et al*., 2018*a*). In Thailand, Hemipterans are the main pests of rice, which is widely cultivated in central Thailand (Srilopan *et al*., 2018). Nevertheless, previous studies have consistently shown that *M. plicatus* primarily consumes migratory pest insects, such as *N. lugens* and *S. furcifera*, despite variations in methodology (Leelapaibul *et al*., 2005; Srilopan *et al*., 2018; Thongjued, 2019). Similarly, *T. brasiliensis*, which preys on migratory insects (Krauel *et al*., 2018*a*). This high-flying bat provides potential for investigating the flows of migratory insects across the landscape in Texas (Krauel *et al*., 2018*a*).

Our dietary analysis also revealed that the congeners *T. theobaldi* and *T. melanopogon* have similar diets. *Taphozous theobaldi* consumed 110 OTUs from 42 families and 11 orders. Similarly, the diet of *T. melanopogon* comprised 137 OTUs from 34 families and eight orders. Their primary prey items were predominantly from the order Lepidoptera, followed by Orthoptera, Blattodea, and Diptera. This is also supported by previous studies examining the diets of *T. melanopogon* and *T. longimanus*, where Lepidoptera was the primary prey, followed by Coleoptera, Diptera, and Orthoptera (Srinivasulu and Srinivasulu, 2005; Wei *et al*., 2008). Additionally, *T. theobaldi*, known for high-altitude foraging (Roeleke *et al*., 2018), exhibited a preference for Lepidoptera, especially the Noctuidae family, in every sampling period. We assume from their diets that both species primarily feed on migratory insects such as Noctuidae at high altitudes. This behaviour may be similar to that of *T. brasiliensis*, an open-space bat known for consuming migratory noctuid moths (Krauel *et al*., 2018*b*). In contrast, a previous study conducted in our study area that use stable isotopes reported that *T. theobaldi* primarily consumed Diptera and Lepidoptera during the dry season and shifted to a Diptera dominant diet in the wet season, while *T. melanopogon* mainly consumed Diptera in both seasons (Ruadreo *et al*., 2018). However, the observed variations in the diets of *T. theobaldi* and *T. melanopogon* between our study and prior research could be attributed to several factors, such as the time of data collection, which may impact the availability of insects, and differences in the methods used (Dai *et al*., 2023).

Dietary analysis of *S. heathii* revealed the consumption of 126 OTUs from 47 families and 12 orders. The primary order observed was Coleoptera, followed by Hemiptera, Lepidoptera, and Diptera. This finding is consistent with a previous study in India, where Coleoptera were predominantly found in the guano of *S. heathii* (Misra and Elangovan, 2016). Additionally, Coleoptera, Hemiptera, Diptera, and Lepidoptera were recorded in the diet of a smaller congener, S. kuhlii (Srinivasulu *et al*., 2010; Zhu and Zhang, 2012; Misra and Elangovan, 2016).

The dietary analysis of these four bat species, reveals varying patterns of dietary breadth and specialization. *Mops plicatus* exhibits the broadest dietary breadth, with a primary focus on Hemiptera but also including Diptera and Lepidoptera. In contrast, *T. theobaldi* and *T. melanopogon* show degrees of specialization towards Lepidoptera, along with other orders such as Orthoptera, Blattodea, and Diptera, albeit with fewer total OTUs and narrower taxonomic ranges compared to *M. plicatus*. *Scotophilus heathii*, demonstrates a moderate dietary breadth with a primary focus on Coleoptera, supplemented by Hemiptera, Lepidoptera, and Diptera. These findings suggest that while some species like *M. plicatus* maintain a broader dietary spectrum encompassing multiple prey types, others like *T. theobaldi* and *T. melanopogon* exhibit more specialized feeding behaviours, possibly influenced by habitat preferences and available prey resources (Dai *et al*., 2023), indicating niche partitioning among these bat species.

Regarding dietary niche partitioning of these four sympatric insectivorous bats, our observations revealed a varying degree of diet overlap and partition. Specifically, we observed notable instances of diet overlap, such as all four bat species consuming *M. annandalei*, a termite known to swarm abundantly during the night time a few days before or after rainfall (Peppuy *et al*., 2004). This finding suggests that these bats may share a preference for this termite, which becomes readily available during specific weather conditions. In the analysis of each bat pair, *T. theobaldi* and *T. melanopogon* exhibited a substantial overlap in insect prey at the family level, and thus a preference for similar food items. This may be notable as they are sibling species and co-occur throughout their distributions (Arrizabalaga-Escudero *et al*., 2018). We observed that the dietary niche width and composition of both species were remarkably similar, characterized by the consumption of Noctuidae and Erebidae from the order Lepidoptera. Noctuidae and Erebidae are well-documented as common agricultural pests (Crabo *et al*., 2013; Rakkasikorn *et al*., 2019; Sukonthaphirom Na Phatthalung *et al*., 2021). These bats may share agricultural migratory pest insects, particularly moths that migrate at high altitudes (Lee and McCracken, 2005; Müller *et al*., 2012), as evidenced by the presence of such pests in their diets. However, differences in diet composition across 22 families were observed. *Taphozous melanopogon* showed greater consumption of Noctuidae (Lepidoptera) and Gryllotalpidae (Orthoptera), while *T. theobaldi* showed higher consumption of Baetidae (Ephemeroptera), Aphididae, and Psyllidae (Hemiptera). Our study suggests specific prey differences might contribute to the partitioning of their diet. This is supported by previous research showing that, even though their prey belong to the same orders of Arthropoda, the exact species of insects available to the bats likely varies (Rolfe *et al*., 2014). When migratory insect pests are not abundant, these bats may focus on different prey while foraging in distinct habitats. Previous research aligns with our findings, illustrating varied habitat preferences. Bats often exploit different habitats and are consequently exposed to various species of insects while foraging (Rolfe *et al*., 2014). *Taphozous melanopogon* tends to forage more in agricultural areas and edge forests where Noctuidae and Gryllotalpidae are widespread, while *T. theobaldi* seems to prefer settlements and water bodies where Baetidae are prevalent (Zahoor *et al*., 2003; Kubendran *et al*., 2017; Suksai and Bumrungsri, 2020; Holusa and Kalab, 2023).

Our findings revealed moderate dietary overlap between *T. theobaldi* and *M. plicatus*, possibly due to their shared characteristics as high-altitude aerial insectivores that forage in open spaces, coexist in sympatric areas, and share roosts in the same cave (Ruadreo *et al*., 2018; Kemp *et al*., 2019). However, despite this overlap, our study clearly identified diet partitioning between them. For example, *T. theobaldi* exhibited a preference for pest insects from the order Lepidoptera, while *M. plicatus* primarily targeted those from the order Hemiptera (Leelapaibul *et al*., 2005; Srinivasulu and Srinivasulu, 2005; Wei *et al*., 2008; Srilopan *et al*., 2018). This distinction may be linked to the size difference between the bats, as *T. theobaldi*, being larger than *M. plicatus* (Ruadreo *et al*., 2018), shows a preference for larger moths over smaller planthoppers.

Moreover, *M. plicatus* exhibited lower overlap with *T. melanopogon* and *S. heathii*, indicating differences in their diet compositions. *Mops plicatus* mainly consumed pest insects from the order Hemiptera, *T. melanopogon* primarily targeted pest insects from the order Lepidoptera, and *S. heathii* predominantly consumed insects from the order Coleoptera (Leelapaibul *et al*., 2005; Srinivasulu and Srinivasulu, 2005; Wei *et al*., 2008; Misra and Elangovan, 2016; Srilopan *et al*., 2018). Previous studies have suggested that *Mops plicatus* flies at different altitudes compared to *T. melanopogon* and *S. heathii* (Roeleke *et al*., 2018; Nguyen *et al*., 2019). This variation in flight altitude may correspond to the insects targeted by each bat during foraging (Nguyen *et al*., 2019), leading to distinct diets, a phenomenon referred to as resource partitioning.

Scotophilus heathii has relatively low overlap with other open space bat. The diet of *S. heathii* exhibited lower diversity in pest insects compared to other species. However, *Culex vishnui* appeared notably frequently in its diet, particularly compared to other pest insects. This trend could be attributed to its habit of roosting in human houses within urban areas, reflecting its foraging preferences in such environments.

We acknowledge several limitations that are worthy of discussion. First, the collection of bat faeces from the house-dwelling colony of *S. heathii* posed challenges, restricting us to a single collection event. The obtained faeces were not fresh, potentially influencing prey species detection. Second, the house-dwelling colony of *S. heathii* was geographically distant from the other sampled roosts, with bats potentially exposed to distinct habitats and environmental factors. Third, we faced constraints in collecting and analysing insects in their natural habitat to serve as reference for dietary analysis. The cost associated with DNA metabarcoding, while continuing to become more affordable, remain a limiting factor in undertaking comprehensive insect analysis.

Dietary analysis of four insectivorous bats, *M. plicatus*, *T. theobaldi*, *T. melanopogon*, and *S. heathii*, emphasizing their crucial role in agricultural landscapes through the consumption of numerous pest insects, including migratory species that threaten crops. Our results indicate dietary partitioning among these sympatric species: *M. plicatus* primarily consumes Hemipterans, *T. theobaldi* and *T. melanopogon* favor lepidopterans, while *S. heathii* prefers coleopterans. This partitioning is essential for their coexistence and highlights their collective importance in pest suppression. While our study focused on the family level, a more detailed analysis at the species level could reveal even greater dietary distinctions. Future research should delve deeper into the specific diets of these bats and quantify the ecosystem services they offer. These findings underscore the significant ecosystem services provided by insectivorous bats. Communicating these insights to stakeholders involved in bat conservation is crucial to protect these species and the benefits they provide to agriculture.

ACKNOWLEDGEMENTS

This research project is supported by National Research Council of Thailand (NRCT): NRCT5-RGJ63019-162. We thank Phongsin Inpaen, Kamonporn Srilopan, Tusita Srilopan, and Sunet Nalisa for help during the field work. We also thank CTM Team, CIBIO/InBIO for their assistance in the laboratory. We extend our special thanks to Alyssa Stewart for her valuable comments on the manuscript. We thank Christian Voigt, Jennifer Krauel and the members of the Small Mammal, Bird and Spider Research Unit who helped develop ideas. Additionally, we appreciate the support of the Faculty of Science, Prince of Songkla University and CIBIO-InBIO, Faculty of Sciences, University of Porto. VAM was funded by Fundação para Ciência e a Tecnologia (FCT) through an individual research contract (doi: 10.54499/2020.02547.CEECIND/CP1601/CP1649/CT0004).

AUTHOR CONTRIBUTION STATEMENT

SB: research concept and design, critical revision and final approval of the article; VAM: research concept and design, data analysis and interpretation, critical revision and final approval of the article; SS: research concept and design, collection and/or assembly of data, data analysis and interpretation, writing the article and its final approval.

LITERATURE CITED

AIZPURUA, O., I. BUDINSKI, P. GEORGIAKAKIS, S. GOPALAKRISHNAN, C. IBAÑEZ, V. MATA, H. REBELO, D. RUSSO, F. SZODORAY-PARÁDI, V. ZHELYAZKOVA, *et al*. 2018. Agriculture shapes the trophic niche of a bat preying on multiple pest arthropods across Europe: evidence from DNA metabarcoding. Molecular Ecology, 27: 815–825.

ANDERSON, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral ecology, 26: 32–46.

ARRIZABALAGA-ESCUDERO, A., E. L. CLARE, E. SALSAMENDI, A. ALBERDI, I. GARIN, J. AIHARTZA, and U. GOITI. 2018. Assessing niche partitioning of co-occurring sibling bat species by DNA metabarcoding. Molecular Ecology, 27: 1273–1283.

ARTHEY, T., O. SRISOMPUN, and Y. ZIMMER. 2018. Cassava production and processing in Thailand. Agri Benchmark. Braunschweig, Germany. [Online] Available at: http://www.agribenchmark.org/fileadmin/Dateiablage/B-Cash-Crop/Reports/CassavaReportFinal-181030.pdf.

ATIELI, H. E., G. ZHOU, D. ZHONG, X. WANG, M. C. LEE, A. S. YARO, M. DIALLO, J. GITHURE, J. KAZURA, T. LEHMANN, *et al*. 2023. Wind-assisted high-altitude dispersal of mosquitoes and other insects in East Africa. Journal of Medical Entomology, 60: 698–707.

BOHMANN, K., A. MONADJEM, C. L. NOER, M. RASMUSSEN, M. R. K. ZEALE, E. CLARE, G. JONES, E. WILLERSLEV, and M. T. P. GILBERT. 2011. Molecular diet analysis of two African free-tailed bats (Molossidae) using high throughput sequencing. PLoS ONE, 6: e21441.

BOYER, F., C. MERCIER, A. BONIN, Y. LE BRAS, P. TABERLET, and E. COISSAC. 2016. Obitools: a unix-inspired software package for DNA metabarcoding. Molecular Ecology Resources, 16: 176–182.

BOYLES, J. G., P. M. CRYAN, G. F. MCCRACKEN, and T. H. KUNZ. 2011. Economic importance of bats in agriculture. Science, 332: 41–42.

BUCHNER, D., and F. LEESE. 2020. BOLDigger – a Python package to identify and organise sequences with the Barcode of Life Data systems. Metabarcoding and Metagenomics, 4: e53535.

BUMRUNGSRI, S., W. LEELAPAIBUL, and P. A. RACEY. 2007. Resource partitioning in sympatric Cynopterus bats in lowland tropical rain forest, Thailand. Biotropica, 39: 241–248.

CHAPMAN, J. W., D. R. REYNOLDS, A. D. SMITH, J. R. RILEY, D. E. PEDGLEY, and I. P. WOIWOD. 2002. High-altitude migration of the diamondback moth *Plutella xylostella* to the UK: a study using radar, aerial netting, and ground trapping. Ecological Entomology, 27: 641–650.

CHATTERJEE, M., N. CHAUDHURI, S. PAL, and J. GHOSH. 2023. Species composition, occurrence pattern and seasonal incidence of rice leaf folder (*Cnaphalocrocis* spp.) on kharif rice under Terai agro-ecological conditions of Northern Parts of West Bengal. Journal of Entomological Research, 47: 386–392.

CHEN, H., Y. WANG, L. HUANG, C. F. XU, J. H. LI, F. Y. WANG, W. CHENG, B. Y. GAO, J. W. CHAPMAN, and G. HU. 2022. Flight capability and the low temperature threshold of a Chinese field population of the fall armyworm *Spodoptera frugiperda*. Insects, 13: 422.

CHESSON, P. 2000. Mechanism of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics, 31: 343–366.

CLARE, E. L., E. E. FRASER, H. E. BRAID, M. B. FENTON, and P. D. N. HEBERT. 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: 2532–2542.

COLLINS, R. A., and R. H. CRUICKSHANK. 2013. The seven deadly sins of DNA barcoding. Molecular Ecology Resources, 13: 969–975.

CRABO, L. G., M. DAVIS, P. HAMMOND, T. MUSTELIN, and J. SHEPARD. 2013. Five new species and three new subspecies of Erebidae and Noctuidae (Insecta, Lepidoptera) from northwestern North America, with notes on *Chytolita* Grote (Erebidae) and *Hydraecia* Guenée (Noctuidae). ZooKeys, 264: 85–123.

DAI, W., A. LI, Y. CHANG, T. LIU, L. ZHANG, J. LI, H. LENG, Z. LI, L. JIN, K. SUN, *et al*. 2023. Diet composition, niche overlap and partitioning of five sympatric rhinolophid bats in Southwestern China during summer. Frontiers in Ecology and Evolution, 11: 1108514.

DEAGLE, B. E., A. C. THOMAS, J. C. MCINNES, L. J. CLARKE, E. J. VESTERINEN, E. L. CLARE, T. R. KARTZINEL, and J. P. EVESON. 2019. Counting with DNA in metabarcoding studies: how should we convert sequence reads to dietary data? Molecular Ecology, 28: 391–406.

DENZINGER, A., and H.-U. SCHNITZLER. 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. Frontiers in Physiology, 4: 164.

Denzinger, A., E. K. Kalko, M. Tschapka, A. D. Grinnell, and H.-U. Schnitzler. 2016. Guild structure and niche differentiation in echolocating bats. Pp. 141–166, *in* Bat bioacoustics (M. B. Fenton, A. D. Grinnell, A. N. Popper, and R. R. Fay, eds.). Springer, New York, NY, 304 pp.

Dodd, L. E., E. G. Chapman, J. D. Harwood, M. J. Lacki, and L. K. Rieske. 2012. Identification of prey of *Myotis septentrionalis* using DNA-based techniques. Journal of Mammalogy, 93: 1119–1128.

Edgar, R. C. 2016. UNCROSS: filtering of high-frequency cross-talk in 16S amplicon reads. BioRxiv, 088666.

Ehler, L. E. 2006. Integrated pest management (IPM): Definition, historical development, and implementation, and the other IPM. Pest Management Science, 62: 787–789.

Ekasingh, B., P. Gypmantasiri, K. Thong Ngam, and P. Krudloyma. 2004. Maize in Thailand: production systems, constraints, and research priorities. CIMMYT, Mexico, D.F., viii + 36 pp.

Farrow, R. A., and G. McDonald. 1987. Migration strategies and outbreaks of noctuid pests in Australia. International Journal of Tropical Insect Science, 8: 531–542.

Federico, P., T. G. Hallam, G. F. McCracken, S. T. Purucker, W. E. Grant, A. N. Correa-Sandoval, J. K. Westbrook, R. A. Medellín, C. J. Cleveland, C. G. Sansone, *et al*. 2008. Brazilian free-tailed bats as insect pest regulators in transgenic and conventional cotton crops. Ecological Applications, 18: 826–837.

Felkner, J., K. Tazhibayeva, and R. Townsend. 2009. Impact of climate change on rice production in Thailand. American Economic Review, 99: 205–210.

Fox, K. J. 1978. The transoceanic migration of Lepidoptera to New Zealand — a history and a hypothesis on colonisation. New Zealand Entomologist, 6: 368–380.

Frøslev, T. G., R. Kjøller, H. H. Bruun, R. Ejrnæs, A. K. Brunbjerg, C. Pietroni, and A. J. Hansen. 2017. Algorithm for post-clustering curation of DNA amplicon data yields reliable biodiversity estimates. Nature Communications, 8: 1188.

Fu, X., X. Zhao, B. Xie, A. Ali, and K. Wu. 2015. Seasonal pattern of *Spodoptera litura* (Lepidoptera: Noctuidae) migration across the Bohai Strait in northern China. Journal of Economic Entomology, 108: 525–538.

Ghanem, S. J., and C. C. Voigt. 2012. Increasing awareness of ecosystem services provided by bats. Pp. 279–302, *in* Advances in the study of behaviour. Volume 44 (H. J. Brockmann, T. J. Roper, M. Naguib, J. C. Mitani, and L. W. Simmons, eds). Academic Press, San Diego, CA, 358 pp.

Gonçalves, A., E. K. Nóbrega, H. Rebelo, V. A. Mata, and R. Rocha. 2024. A metabarcoding assessment of the diet of the insectivorous bats of Madeira Island, Macaronesia. Journal of Mammalogy, 105: 524–533.

Holusa, J., and O. Kalab. 2023. The habitat-suitability models of the European mole cricket (*Gryllotalpa gryllotalpa*) as information tool for conservation and pest management. Heliyon, 9: e14826.

Hooper, E. T., and J. H. Brown. 1968. Foraging and breeding in two sympatric species of Neotropical bats, genus *Noctilio*. Journal of Mammalogy, 49: 310–312.

Huang, J., G. Li, H. Lei, C. Fan, C. Tian, Q. Chen, B. Huang, H. Li, Z. Lu, and H. Feng. 2020. Low-temperature derived temporal change in the vertical distribution of Sesamia inferens larvae in winter, with links to its latitudinal distribution. PLoS ONE, 15: e0236174.

Huang, X., Q. Du, L. Wang, and B. Chen. 2023. Impacts of oxygen deficiency on embryo life-history traits of migratory locust *Locusta migratoria* from low and high altitudes. Insect Science, 30: 867–879.

Jacobs, D. S., and R. M. Barclay. 2009. Niche differentiation in two sympatric sibling bat species, *Scotophilus dinganii* and *Scotophilus mhlanganii*. Journal of Mammalogy, 90: 879–887.

Jones, G., D. S. Jacobs, T. H. Kunz, M. R. Willig, and P. A. Racey. 2009. Carpe noctem: the importance of bats as bioindicators. Endangered species research, 8: 93–115.

Kalko, E. K. V., S. Estrada Villegas., M. Schmidt, M. Wegmann., and C. F. J. Meyer. 2008. Flying high — assessing the use of the aerosphere by bats. Integrative and Comparative Biology, 48: 60–73.

Karthika, P., C. Vadivalagan, D. Thirumurugan, R. R. Kumar, K. Murugan, A. Canale, and G. Benelli. 2018. DNA barcoding of five Japanese encephalitis mosquito vectors (*Culex fuscocephala*, *Culex gelidus*, *Culex tritaeniorhynchus*, *Culex pseudovishnui* and *Culex vishnui*). Acta Tropica, 183: 84–91.

Kemp, J., A. López-Baucells, R. Rocha, O. S. Wangensteen, Z. Andriatafika, A. Nair, and M. Cabeza. 2019. Bats as potential suppressors of multiple agricultural pests: a case study from Madagascar. Agriculture, Ecosystems & Environment, 269: 88–96.

Krauel, J. J., V. A., Brown, J. K. Westbrook, and G. F. McCracken. 2018*a*. Predator-prey interaction reveals local effects of high-altitude insect migration. Oecologia, 186, 49–58.

Krauel, J. J., J. M. Ratcliffe, J. K. Westbrook, and G. F. McCracken. 2018*b*. Brazilian free-tailed bats (*Tadarida brasiliensis*) adjust foraging behaviour in response to migratory moths. Canadian Journal of Zoology, 96: 513–520.

Kubendran, T., C. Selvakumar, A. K. Sidhu, S. M. Krishnan, and A. Nair. 2017. Diversity and distribution of Baetidae (Insecta: Ephemeroptera) larvae of streams and rivers of the southern Western Ghats, India. Journal of Entomology and Zoology Studies, 5: 613–625.

Kunz, T. H., E. B. de Torrez, D. Bauer, T. Lobova, and T. H. Fleming. 2011. Ecosystem services provided by bats. Annals of the New York Academy of Sciences, 1223: 1–38.

Lee, Y.-F., and G. F. McCracken. 2005. Dietary variation of Brazilian free-tailed bats links to migratory populations of pest insects. Journal of Mammalogy, 86: 67–76.

Leelapaibul, W., S. Bumrungsri, and A. Pattanawiboon. 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.

Longbottom, J., A. J. Browne, D. M. Pigott, M. E. Sinka, N. Golding, S. I. Hay, C. L. Moyes, and F. M. Shearer. 2017. Mapping the spatial distribution of the Japanese encephalitis vector, *Culex tritaeniorhynchus* Giles, 1901 (Diptera: Culicidae) within areas of Japanese encephalitis risk. Parasites & Vectors, 10: 148.

Maas, B., Y. Clough, and T. Tscharntke. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. Ecology Letters, 16: 1480–1487.

Maine, J. J., and J. G. Boyles. 2015. Bats initiate vital agroecological interactions in corn. Proceedings of the National Academy of Sciences of the USA, 112: 12438–12443.

Manivong, P., and E. Bourgois. 2017. Thai sugarcane sector and sustainability. FairAgora, 46 pp. Available at: https://www.bonsucro.com/white-paper-thai-sugarcane-industry-sustainability-released. Accessed 15 June 2024.

Margam, V. M., B. S. Coates, M. N. Ba, W. Sun, C. L. Binso-Dabire, I. Baoua, M. F. Ishiyaku, J. T. Shukle, R. L. Hellmich, F. G. Covas, *et al*. 2011. Geographic distribution of phylogenetically-distinct legume pod borer, *Maruca vitrata* (Lepidoptera: Pyraloidea: Crambidae). Molecular Biology Reports, 38: 893–903.

Mata, V. A., F. Amorim, M. F. V. Corley, G. F. McCracken, H. Rebelo, and P. Beja. 2016. Female dietary bias towards large migratory moths in the European free-tailed bat (*Tadarida teniotis*). Biology Letters, 12: 20150988.

Mata, V. A., H. Rebelo, F. Amorim, G. F. McCracken, S. Jarman, and P. Beja. 2019. How much is enough? Effects of technical and biological replication on metabarcoding dietary analysis. Molecular Ecology, 28: 165–175.

Mata, V. A., L. P. da Silva, J. Veríssimo, P. Horta, H. Raposeira, G. F. McCracken, H. Rebelo, and P. Beja. 2021. Combining DNA metabarcoding and ecological networks to inform conservation biocontrol by small vertebrate predators. Ecological Applications, 31: e02457.

Maudet, C., C. Miller, B. Bassano, C. Breitenmoser-Würsten, D. Gauthier, G. Obexer-Ruff, J. Michallet, P. Taberlet, and G. Luikart. 2002. Microsatellite DNA and recent statistical methods in wildlife conservation management: applications in Alpine ibex [*Capra ibex* (*ibex*)]. Molecular Ecology, 11: 421–436.

McCracken, G. F., E. H. Gillam, J. K. Westbrook, Y.-F. Lee, M. L. Jensen, and B. B. Balsley. 2008. Brazilian free-tailed bats (*Tadarida brasiliensis*: Molossidae, Chiroptera) at high altitude: links to migratory insect populations. Integrative and Comparative Biology, 48: 107–118.

Misra, P. K., and V. Elangovan. 2016. Light and scanning electron microscopic studies on food habit analysis of insectivorous bats. Advances in Life Sciences, 5: 3649–3654.

Müller, J., M. Mehr, C. Bässler, M. B. Fenton, T. Hothorn, H. Pretzsch, H. J. Klemmt, and R. Brandl. 2012. Aggregative response in bats: prey abundance versus habitat. Oecologia, 169: 673–684.

Nguyen, T. N., A. Ruangwiset, and S. Bumrungsri. 2019. Vertical stratification in foraging activity of *Chaerephon plicatus* (Molossidae, Chiroptera) in central Thailand. Mammalian Biology, 96: 1–6.

Oerke, E.-C. 2006. Crop losses to pests. The Journal of Agricultural Science, 144: 31–43.

Peppuy, A., A. Robert, and C. Bordereau. 2004. Species-specific sex pheromones secreted from new sexual glands in two sympatric fungus-growing termites from northern Vietnam, *Macrotermes annandalei* and *M. barneyi*. Insectes Sociaux, 51: 91–98.

Puig-Montserrat, X., I. Torre, A. López-Baucells, E. Guerrieri, M. M. Monti, R. Ràfols-Garcia, X. Ferrer, D. Gisbert, and C. Flaquer. 2015. Pest control service provided by bats in Mediterranean rice paddies: linking agroecosystems structure to ecological functions. Mammalian Biology, 80: 237–245.

Rakkasikorn, A., S. Chaowalit, D. Chaireeukonkaew, A. Phongmee, K. Boonsanga, and J. Chaiyawong. 2019. Morphological differences of economically important Spodoptera moths (Lepidoptera: Noctuidae) in Thailand. Pp. 1–15, *in* Proceedings of the 14th National Plant Pathology Conference, at Dusit Thani, Hua Hin District, Cha-am, Phetchaburi Province, Thailand, November 12–14, 2019.

Razgour, O., E. L. Clare, M. R. K. Zeale, J. Hanmer, I. B. Schnell, M. Rasmussen, T. P. Gilbert, and G. Jones. 2011. High-throughput sequencing offers insight into mechanisms of resource partitioning in cryptic bat species. Ecology and Evolution, 1: 556–570.

Riley, J. R., D. R. Reynolds, and R. A. Farrow. 1987. The migration of *Nilaparvata lugens* (Stål) (Delphacidae) and other Hemiptera associated with rice during the dry season in the Philippines: a study using radar, visual observations, aerial netting and ground trapping. Bulletin of Entomological Research, 77: 145–169.

Riley, J. R., D. R. Reynolds, A. D. Smith, A. S. Edwards, X.-X. Zhang, X.-N. Cheng, H.-K. Wang, J.-Y. Cheng, and B.-P. Zhai. 1995. Observations of the autumn migration of the rice leaf roller *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae) and other moths in eastern China. Bulletin of Entomological Research, 85: 397–414.

Roeleke, M., S. Bumrungsri, and C. C. Voigt. 2018. Bats probe the aerosphere during landscape-guided altitudinal flights. Mammal Review, 48: 7–11.

Rognes, T., T. Flouri, B. Nichols, C. Quince, and F. Mahé. 2016. VSEARCH: a versatile open source tool for metagenomics. PeerJ, 4: e2584.

Rolfe, A. K., A. Kurta, and D. L. Clemans. 2014. Species-level analysis of diets of two mormoopid bats from Puerto Rico. Journal of Mammalogy, 95: 587–596.

Roswag, A., N. I. Becker, and J. A. Encarnção. 2018. Isotopic and dietary niches as indicators for resource partitioning in the gleaner bats *Myotis bechsteinii*, *M. nattereri*, and *Plecotus auritus*. Mammalian Biology, 89, 62–70.

Ruadreo, N., C. C. Voigt, and S. Bumrungsri. 2018. Large dietary niche overlap of sympatric open-space foraging bats revealed by carbon and nitrogen stable isotopes. Acta Chiropterologica, 20: 329–341.

Schnitzler, H.-U., C. F. Moss, and A. Denzinger. 2003. From spatial orientation to food acquisition in echolocating bats. Trends in Ecology & Evolution, 18: 386–394.

Schoeman, M. C., and D. S. Jacobs. 2011. The relative influence of competition and prey defences on the trophic structure of animalivorous bat ensembles. Oecologia, 166: 493–506.

Shahbaz, M., A. Javid, M. Mahmood-ul-Hassan, S. M. Hussain, S. Ashraf, and M. Idnan. 2014. Recent record of *Scotophilus heathii* from wheat-rice based agroecosystem of Punjab. Pakistan Journal of Zoology, 46: 1175–1179.

Shen, X., X. Fu, Y. Huang, J. Guo, Q. Wu, L. He, X. Yang, and K. Wu. 2020. Seasonal migration patterns of *Ostrinia furnacalis* (Lepidoptera: Crambidae) across the Bohai strait in northern China. Journal of economic entomology, 113: 194–202.

Siemers, B. M., and S. M. Swift. 2006. Differences in sensory ecology contribute to resource partitioning in the bats *Myotis bechsteinii* and *Myotis nattereri* (Chiroptera: Vespertilionidae). Behavioral Ecology and Sociobiology, 59: 373–380.

Song, H. 2005. Phylogenetic perspectives on the evolution of locust phase polyphenism. Journal of Orthoptera Research, 14: 235–245.

Srilopan, S., S. Bumrungsri, and S. Jantarit. 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: 207–219.

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

Srinivasulu, B., C. Srinivasulu, and P. Venkateshwarlu. 2010. First record of lesser yellow house bat *Scotophilus kuhlii* Leach, 1821 from Secunderabad, Andhra Pradesh, India with a note on its diet. Journal of Threatened Taxa, 2: 1234–1236.

Sukonthaphirom Na Phatthalung, S., P. Punwattho, S. Phonphunsak, and S. Srijantra. 2021. Guidelines for safe pest and insect management. Plant Pest Management Division/Entomology Group, Office of Crop Research and Development, Department of Agriculture, Bangkok, Thailand, 280 pp. [In Thai].

Suksai, P., and S. Bumrungsri. 2020. Water bodies are a critical foraging habitat for insectivorous bats in tropical agricultural landscapes of central Thailand. Songklanakarin Journal of Science and Technology, 42: 521–532.

Thongjued, K. 2019. Diet analysis of wrinkle-lipped free-tailed bat (*Chaerephon plicatus* Buchannan, 1800) using direct-PCR DGGE technique. M.Sc. Thesis, Prince of Songkla University , Songkhla, Thailand, 118 pp.

Vamos, E. E., V. Elbrecht, and F. Leese. 2017. Short COI markers for freshwater macroinvertebrate metabarcoding. Metabarcoding and Metagenomics 1: e14625. https://doi.org/10.3897/mbmg.1.14625.

Vesterinen, E. J., L. Ruokolainen, N. Wahlberg, C. Peña, T. Roslin, V. N. Laine, V. Vasko, I. E. Sääksjärvi, K. Norrdahl, and T. M. Lilley. 2016. What you need is what you eat? Prey selection by the bat *Myotis daubentonii* Molecular Ecology, 25: 1581–1594.

Voigt, C. C., S. E. Currie, M. Fritze, M. Roeleke, and O. Lindecke. 2018. Conservation strategies for bats flying at high altitudes. BioScience, 68: 427–435.

Wang, X., X. Yang, L. Zhou, K. A. G. Wyckhuys, S. Jiang, N. Van Liem, L. X. Vi, A. Ali, and K. Wu. 2022. Population genetics unveils large-scale migration dynamics and population turnover of *Spodoptera exigua*. Pest Management Science, 78: 612–625.

Wanger, T. C., K. Darras, S. Bumringsri, T. Tscharntke, and A. M. Klein. 2014. Bat pest control contributes to food security in Thailand. Biological Conservation, 171: 220–223.

Wei, L., N. Han, L. Zhang, K. M. Helgen, S. Parsons, S. Zhou, and S. Zhang. 2008. Wing morphology, echolocation calls, diet and emergence time of black-bearded tomb bats (*Taphozous melanopogon*, Emballonuridae) from southwest China. Acta Chiropterologica, 10: 51–59.

Weterings, R., J. Wardenaar, S. Dunn, and C. Umponstira. 2015. Dietary analysis of five insectivorous bat species from Kamphaeng Phet, Thailand. Raffles Bulletin of Zoology, 63: 91–96.

Williams-Guillén, K., E. Olimpi, B. Maas, P. J. Taylor, and R. Arlettaz. 2016. Bats in the anthropogenic matrix: challenges and opportunities for the conservation of Chiroptera and their ecosystem services in agricultural landscapes. Pp. 151–186, *in* Bats in the Anthropocene: conservation of bats in a changing World (C. C. Voigt and T. Kingston, eds.). Springer, Cham, 606 pp.

Wood, C. R., D. R. Reynolds, P. M. Wells, J. F. Barlow, I. P. Woiwod, and J. W. Chapman. 2009. Flight periodicity and the vertical distribution of high-altitude moth migration over southern Britain. Bulletin of Entomological Research, 99: 525–535.

Wray, A. K., M. A. Jusino, M. T. Banik, J. M. Palmer, H. Kaarakka, J. P. White, D. L. Lindner, C. Gratton, and M. Z. Peery. 2018. Incidence and taxonomic richness of mosquitoes in the diets of little brown and big brown bats. Journal of Mammalogy, 99: 668–674.

Zahoor, M. K., A. Suhail, J. Iqbal, Z. Zulfaqar, and M. Anwar. 2003. Biodiversity of Noctuidae (Lepidoptera) in Agro-forest area of Faisalabad. International Journal of Agriculture & Biology, 4: 560–563.

Zeng, J., Y. Liu, H. Zhang, J. Liu, Y. Jiang, K. A. G. Wyckhuys, and K. Wu. 2020. Global warming modifies long-distance migration of an agricultural insect pest. Journal of Pest Science, 93: 569–581.

Zhu, G., A. Chmura, and L. Zhang. 2012. Morphology, echolocation calls and diet of *Scotophilus kuhlii* (Chiroptera: Vespertilionidae) on Hainan Island, south China. Acta Chiropterologica, 14: 175–181.

Received 04 April 2024, accepted 05 September 2024

Associate Editor: Wiesław Bogdanowicz

APPENDIX

Statistically significant differences in prey items at the family level from 14 prey orders among aerial insectivorous bat species' diets. Abbreviations for the bat species; MP — *M. plicatus*, SH — *S. heathii*, TM — *T. melanopogon*, TB — *T. theobaldi*. Different colors in the table represented statistically significant differences: ■ $P < 0.001$, ▩ $P < 0.01$, ▨ $P < 0.05$, ░ $P < 0.1$, □ non-significant

Order	Family	MP-SH	MP-TM	MP-TB	SH-TM	SH-TB	TM-TB
Araneae	Ochyroceratidae						TM<TB
	Theridiidae				SH>TM	SH>TB	
Blattodea	Blaberidae				SH>TM	SH>TB	
	Blattidae						
	Ectobiidae	MP<SH	0	0	0	0	0
	Termitidae	0	MP>TM	MP>TB	0	0	TM<TB
Coleoptera	Bostrichidae	MP<SH	0	0	SH>TM	SH>TB	0
	Buprestidae	0	0	0	0	0	0
	Carabidae	MP>SH	MP>TM	MP>TB	0	0	0
	Cerambycidae	MP<SH	0	0	SH>TM	SH>TB	0
	Chrysomelidae	0	MP>TM	MP>TB	0	0	0
	Curculionidae	MP<SH	0	0	SH>TM	SH>TB	0
	Dermestidae	0	0	0	SH>TM	SH>TB	0
	Dytiscidae	0	0	0	0	0	0
	Heteroceridae	0	MP>TM	MP>TB	0	0	0
	Hydrophilidae	MP<SH	0	0	SH>TM	SH>TB	0
	Scarabaeidae	MP<SH	0	0	SH>TM	SH>TB	0
	Staphylinidae	MP>SH	MP>TM	MP>TB	0	0	0
	Tenebrionidae	MP<SH	0	0	SH>TM	SH>TB	0
Dermaptera	Labiduridae	0	0	0	0	0	0
Diptera	Calliphoridae	0	MP>TM	MP>TB	0	0	0
	Chironomidae	0	0	0	0	SH<TB	0
	Culicidae	MP>SH	0	MP>TB	0	0	0
	Dolichopodidae	0	MP>TM	MP>TB	0	0	0
	Drosophilidae	0	MP>TM	MP>TB	0	0	0
	Ephydridae	0	MP>TM	MP>TB	0	0	0
	Lauxaniidae	0	MP>TM	MP> TB	0	0	0
	Limoniidae	0	MP>TM	MP>TB	0	0	0
	Micropezidae	MP<SH	0	0	SH>TM	SH>TB	0
	Muscidae	MP>SH	MP>TM	MP>TB	0	0	
	Sciomyzidae	0	0	0	0	0	0
	Sphaeroceridae	0	MP>TM	MP>TB	0	0	0
	Stratiomyidae	0	MP>TM	MP>TB	0	0	0
	Tabanidae	0	MP>TM	MP>TB	0	0	0
	Tachinidae	MP<SH	0	0	0	SH>TB	0
	Tipulidae	0	MP>TM	MP>TB	0	0	0
Ephemeroptera	Baetidae	0	0	0	0	0	TM<TB
Hemiptera	Alydidae	0	0	0	0	0	0
	Aphididae	0	0	0	0	0	TM<TB
	Belostomatidae	MP<SH	0	0	SH>TM	SH>TB	0
	Cicadellidae	MP>SH	MP>TM	MP>TB	0	0	0
	Delphacidae	MP>SH	MP>TM	MP>TB	0	0	0
	Flatidae	0	0	0	SH>TM	SH>TB	0
	Gerridae	0	0	0	SH>TM	SH>TB	0
	Lygaeidae	MP>SH	MP>TM	MP>TB	0	0	0

Appendix. Continued

Order	Family	MP-SH	MP-TM	MP-TB	SH-TM	SH-TB	TM-TB
	Meenoplidae	0	MP>TM	MP>TB	0	0	0
	Membracidae	0	0	0	0	0	0
	Miridae	0	0	MP>TB	0	0	0
	Notonectidae	MP<SH	0	0	SH>TM	SH>TB	0
	Pentatomidae	MP>SH	MP>TM	MP>TB	SH>TM	SH>TB	0
	Psyllidae	0	0	0	0	0	TM<TB
	Pyrrhocoridae	MP>SH	MP>TM	MP>TB	0	0	0
	Reduviidae	0	0	0	0	0	0
	Rhyparochromidae	MP<SH	0	0	0	0	0
Hymenoptera	Apidae	0	MP>TM	MP>TB	0	0	0
	Formicidae	0	MP>TM	MP>TB	0	0	0
	Halictidae	0	MP>TM	MP>TB	0	0	0
	Ichneumonidae	0	0	0	0	0	0
	Megachilidae	0	MP>TM		0	0	0
Lepidoptera	Blastobasidae	0	MP>TM	MP>TB	0	0	0
	Cosmopterigidae	0	MP>TM	MP>TB	0	0	0
	Crambidae	0	MP<TM	0	0	0	TM>TB
	Depressariidae	0	0	0	SH>TM	SH>TB	0
	Erebidae	0	0	0	0	0	TM>TB
	Euteliidae	0	0	0	0	0	TM>TB
	Gelechiidae	MP<SH	0	0	SH>TM	SH>TB	0
	Geometridae	0	0	0	0	0	TM>TB
	Hyblaeidae	0	MP>TM	0	0	0	0
	Limacodidae	0	0	0	SH>TM	0	0
	Lycaenidae	0	0	0	0	0	TM>TB
	Noctuidae	0	MP<TM	0	SH<TM	0	TM>TB
	Nolidae	0	0	0	0	0	TM>TB
	Plutellidae	0	0	0	0	0	0
	Pyralidae	0	0	0	0	0	TM>TB
	Saturniidae	0	0	0	0	0	TM>TB
	Sphingidae	0	0	0	0	0	TM>TB
	Thyrididae	0	0	0	0	0	TM>TB
	Tineodidae	0	0	0	0	0	TM>TB
	Tortricidae	MP<SH	0	0	SH>TM	0	0
Mantodea	Hymenopodidae	MP<SH	0	0	0	0	0
	Mantidae	0	0	0	0	0	TM<TB
Odonata	Coenagrionidae	MP>SH	MP>TM	MP>TB	0	0	0
	Lestidae	0	MP>TM	MP>TB	0	0	0
	Libellulidae	0	MP>TM	MP>TB	0	0	0
Orthoptera	Acrididae	0	0	0	0	0	TM<TB
	Gryllidae	0	0	0	0	0	TM<TB
	Gryllotalpidae	0	0	0	SH<TM	0	TM>TB
	Pyrgomorphidae	0	0	0	0	0	0
	Tetrigidae	0	0	0	SH>TM	0	0
	Tettigoniidae	0	0	0	0	0	TM>TB
	Trigonidiidae	0	0	0	0	0	0
Psocodea	Liposcelididae	MP<SH	0	0	SH>TM	0	0
	Trogiidae	0	0	0	SH>TM	0	0
Trichoptera	Hydropsychidae	MP>SH	MP>TM	MP>TB	0	0	0