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Cover: Parts of *Vachellia nilotica*, medium - watercolours. © P Kritika



Metabarcoding-based diet characterization of the Kolar Roundleaf Bat *Hipposideros hypophyllus* Kock & Bhat, 1994 (Chiroptera: Hipposideridae) and its peninsular Indian congeners

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Abstract: We used faecal DNA metabarcoding to analyse the diets of the Kolar Roundleaf Bat *Hipposideros hypophyllus*, and its three congeners (*H. durgadasi*, *H. fulvus*, & *H. speoris*) cohabiting a roost in Kolar District (Karnataka, India). We collected faecal pellets of these bats returning to the roost after the first feeding bout over three seasons between 2021 and 2022. The whole diet of all these species consisted of 7,309 Operational Taxonomic Units (OTU) belonging to phylum Arthropoda. Although no significant difference among the whole diets of the four species was found, *H. hypophyllus* consumed the most amount of insect taxa (4,114 species) compared to others. The core diets consisted of 48 taxa belonging to 10 orders, 37 families, and 46 genera. A significant difference was found between the core diets, with *H. hypophyllus* and *H. speoris* feeding on more diverse insects; diets did not overlap, hinting that the study species are diet specialists. Prey species belonging to orders Lepidoptera and Diptera were abundant in the diet of all four species of bats. The core diet of the Kolar Roundleaf Bat varied significantly between the seasons, with ≥70% intake of lepidopterans in the monsoon and winter seasons. All four species fed on medically and agriculturally significant insect pests as well, indicating their role as bio-controllers in this ecosystem. This study, the first of its kind in India, is an initial exploration of the use of non-invasive diet characterisation for enhancing our knowledge of the ecological interactions of endemic and threatened bat species in sensitive and diverse ecosystems.

Keywords: Biocontrollers, core diet, endemic and threatened, faecal analysis, *Hipposideros durgadasi*, *Hipposideros fulvus*, *Hipposideros hypophyllus*, *Hipposideros speoris*, insect pest, leaf-nosed bat, whole diet.

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INTRODUCTION

Comprising more than 1,500 species worldwide, bats constitute 22% of global mammalian diversity (Upham et al. 2024). The majority of bat species are insectivorous, consuming invertebrates up to 70–80% of their body weight during their numerous feeding bouts each night (Kurta et al. 1989; Kalka et al. 2008; Kunz et al. 2011). Much research has highlighted the beneficial effects of bats and their ecosystem services, especially as biocontrollers of pest insects (Leelapaibul et al. 2005; Cleveland et al. 2006; Boyles et al. 2011; Kunz et al. 2011; Wanger et al. 2014; Puig-Montserrat et al. 2015; Taylor et al. 2018; Kemp et al. 2019; Linden et al. 2019). Despite this diversity and ecological significance, there exists a shortfall in the knowledge of diets of most insectivorous bats (Adams & Sandbrook 2013; Tuneu-Corral et al. 2023).

Effective conservation prerequisites an understanding of the ecological interactions of any species (Adams & Sandbrook 2013), and the diet of an animal is a vital interaction to understand (Whitaker Jr. 1988; Racey et al. 2003; Clare 2014; Groom et al. 2017; Cravens et al. 2018) as the quality and quantity of food resources available for an animal are crucial both for individual- and population-level survival (Eeva et al. 1997; Vickery et al. 2001; Taylor & Schultz 2008; Sorensen et al. 2009; Johnsen et al. 2017; Serrano-Davies & Sanz 2017). Due to their diverse diets and varied foraging ranges, bats consume diverse insect species, and the ecosystem services that they provide cannot be compensated by predators such as birds; the loss of such services leads to increased insect pest abundance, reduced crop production, increased use of pesticides, and deleterious effects on the health of the habitat, ecosystem, and humans (Maas et al. 2013; Maslo et al. 2017; Scholz & Voigt 2022). Additionally, bats provide value to the ecosystems as primary, secondary, and tertiary consumers sustaining both unmodified natural and human-dominated landscapes (Kunz et al. 2011). They help maintain diversity of the forests by seed dispersal, introduce novel plant species, maintain genetic diversity of flowering plants (especially those that bloom exclusively at night), and redistribute nutrients through their guano (Kunz et al. 2011).

However, identifying and analysing the diet of bats is complicated due to their highly mobile nature (Painter et al. 2009). The most widely used approach to assessing bat diets is through the analysis of faeces, either through ‘classical’ methods such as manual dissection of faeces, or more modern approaches including molecular analysis of DNA: bat faeces contain the DNA of the species that

produced them as well as the remains (and consequently the DNA) of prey insects (Reed et al. 1997). As classical methods usually result in relatively coarse family- or even order-level identification of remains (with many unidentifiable fragments), DNA-based methods are increasingly used (Zeale et al. 2011; Clare et al. 2014; Krüger et al. 2014; Foo et al. 2017; Krauel et al. 2018; Scholz & Voigt 2022) mainly due to the higher taxonomic resolution and detection rates of rare or overlooked prey taxa (Clare et al. 2009, 2011; Ashrafi et al. 2011; Razgour et al. 2011; Krüger et al. 2012; Clare 2014; Vesterinen et al. 2013; Vesterinen et al. 2016; De Sousa et al. 2019; Gordon et al. 2019; Hayes et al. 2019).

Of the 153 species of bats extant in South Asia (Srinivasulu et al. 2025), only the Kolar Roundleaf Bat *Hipposideros hypophyllus* has been assessed to be ‘Critically Endangered’ by the IUCN Red List (Chakravarty et al. 2015). Its only known roost is a single subterranean cave on a granite hill in the vicinity of Hanumanhalli Village in the Kolar District of Karnataka, southern India, and the population has been estimated to be around 200 individuals (Srinivasulu et al. 2014). Since its ‘rediscovery’ in 2014, significant steps have been taken for its conservation, including the designation of the roost and its environs as a conservation reserve, and the inclusion of the species in the Indian Wildlife (Protection) Amendment Act, 2022, granting it the highest legal protection by the Government of India. It shares its roost with Durga Das’ Roundleaf Bat *Hipposideros durgadasi* (VU; Mishra & Dookia 2016), the Fulvous Roundleaf Bat *Hipposideros fulvus* (LC; Srinivasulu & Srinivasulu 2018), and Schneider’s Roundleaf Bat *Hipposideros speoris* (LC; Srinivasulu & Srinivasulu 2019). This study explores the diets and variations therein of the highly threatened Kolar Roundleaf Bat and congeners in its only known roost. It is an initial exploration of the potential dietary niche of this sensitive and endangered species alongside its congeners, aiming to provide a vital foundation for future conservation management and policymaking to ensure the continued survival of this species and the health of this multispecies colony and its surrounding ecosystem.

MATERIALS AND METHODS

Study area

The study site, Hanumanahalli Betta (near Hanumanhalli Village, Kolar District, Karnataka, India; 13.16° N, 78.29° E) is a monolithic granite hill with a single narrow subterranean cave housing the only

known population of the 'Critically Endangered' Kolar Roundleaf Bat *Hipposideros hypophyllus* (Srinivasulu et al. 2014). The general habitat surrounding the hill is comprised of scrublands with scattered boulders and hills, agricultural lands, and patches of reserve forest dominated by tropical dry deciduous and tropical thorny forest vegetation (Champion & Seth 1968; Srinivasulu et al. 2014), with small rain-fed waterbodies located just beside the hill and scattered in the study area.

Fecal sample collection

Between April 2021 and March 2022, individuals of each of the four study species (*Hipposideros hypophyllus* (Image 1), *H. durgadasi* (Image 2), *H. fulvus* (Image 3), & *H. speoris*) (Image 4) were captured from the cave using mist-nets and were handled strictly according to the ethical and responsible handling practices outlined in the American Society of Mammalogists guidelines (Sikes & American Society of Mammalogists 2016—importantly including double-layered gloves and masks) to ensure minimal stress and exposure. All collections and surveys were conducted under express permission from the Karnataka State Forest Department (No. PCCF(WL)/E2/CR/2016-17, dated 19.i.2022 vide Government Order No. FEE 404 FWL 2014, dated 20.i.2015), Government of Karnataka. The experimental protocols and procedures were reviewed and approved (59A/CBCS/OU/2021-22) by the Research Committee of Centre for Biodiversity and Conservation Studies, Osmania University, Hyderabad. The study is reported in accordance with ARRIVE guidelines.

Mist-nets were erected after the bats had completed their emergence and were returning from their feeding bouts. Bat emergence times were initially determined based on Srinivasulu et al. (2014) and confirmed based on active echolocation call analysis. Echo Meter Touch 2 Pro (Wildlife Acoustics Inc., USA) and u384 USB ultrasound microphone (Pettersson Elektronik, AB, Uppsala, Sweden) ultrasound detectors were used at the entrance/exit points to determine bat species identity based on call frequencies, corroborated by published data (Srinivasulu et al. 2016). We captured four individuals of each species, which were safely held in clean cloth bags for 30 minutes or until they voided 3–5 faecal pellets each, and were then released back near the roosting site. The pellets were pooled by species (and by season for *Hipposideros hypophyllus*) and placed in vials filled with RNAlater stabilization solution (Invitrogen) for DNA extraction.

DNA extraction

DNA was extracted from bat faecal samples using Qiagen QIAamp fast DNA stool mini kit. The method of DNA extraction involved bead-beating, use of QIAamp fast DNA Stool Mini Kit and RNase treatment. From the collected faecal samples, an aliquot of the stool sample (500 µl) was pipetted into a micro-centrifuge tube using a cut tip. About 3.1 ml of InhibitEX buffer was added to each stool sample and vortexed continuously for one minute until thoroughly homogenized and sample was incubated at 70°C for 10 minutes. The samples were treated with 200 µl of lysozyme (10 mg/ml) and incubated at 37°C for 30 minutes. Around 4–5 stainless steel beads were added, and bead-beating was performed for five cycles (Vortex at maximum speed for one minute, resting time 5 minutes). The tubes were allowed to cool on ice for 2–3 minutes and centrifuged at 16,000 xg for 5 minutes at 4°C. The supernatant was transferred to a fresh 2 ml Eppendorf tube. To the cell pellet 200 µl of lysozyme was added, followed by incubation at 37°C for 30 minutes. The bead-beating step was repeated for three cycles in the following scheme: vortex at maximum speed for one minute, resting time five minutes. The Eppendorf tube was centrifuged at 16,000 xg for 5 minutes at 4°C and the supernatant was transferred to a fresh 2 ml Eppendorf tube. The supernatant obtained from the earlier steps was pooled, and 20 µl proteinase K and 200 µl buffer AL was added, the tubes vortexed for 15 seconds and incubated at 56°C for 2 h. The supernatant was treated with 30 µl of RNase A and incubated at 65°C for 30 minutes. The lysate was thoroughly mixed with half volume of absolute ethanol and loaded into a QIAamp spin column placed in a 2 ml collection tube. The collection tube was then centrifuged at ≥ 6,000 xg for one minute and the flow-through was discarded. To the column, 500 µl Buffer AW1 was added and centrifuged for one minute at ≥ 6,000 xg and the flow-through was discarded. 500 µl of Buffer AW2 was added and centrifuged for one minute at 20,000 xg and the flow-through was discarded. This step was repeated twice. The QIAamp spin column was placed in a new 2 ml collection tube, and a dry spin was performed by centrifuging at 20,000 xg for one minute. The QIAamp spin column was then transferred into a new labelled 1.5 ml microcentrifuge tube, and the DNA was eluted by adding pre-warmed 30–50 µl 10 mM Tris HCl (pH 8.0), directly on the QIAamp membrane and incubated at room temperature (25°C) for 5 min. The microcentrifuge tube was centrifuged at 20,000 xg for one minute, and the DNA pellet was retained. The concentration and purity of genomic DNA was quantified using a nanodrop



Image 1. *Hipposideros hypophyllus*.



Image 2. *Hipposideros durgadasi*.



Image 3. *Hipposideros fulvus*.



Image 4. *Hipposideros speoris*.

spectrophotometer. The integrity of DNA in the sample was confirmed using gel electrophoresis and the DNA concentration was quantified using a Qubit dsDNA HS assay kit.

Library Preparation

Genomic DNA was amplified for COI gene using ANML LCO1490 and COI-CFMRa primers with KAPA HiFi

HotStart PCR Master Mix (KAPA Biosystems, USA). The forward and reverse primer concentrations were kept at 5 µM each. A 25 µl PCR was setup using 12.5 µl of the 2X KAPA HiFi HotStart Ready mix, 10.5 µl of the genomic DNA and nuclease-free water and one µl each of the forward and reverse primers using a two-step protocol: 94°C for one minute for initial denaturation, followed by 94°C for one minute, 45°C for one minute 45 seconds and 72°C for one minute and 15 seconds for five cycles; 94°C for one minute, 51°C for 30 seconds, 72°C for one minute and 15 seconds for 35 cycles followed by a final extension step of 72°C for 5 minutes. The amplicons were visualized on 1.2% agarose gel and purified using Sera-Mag™ Select beads (Cytiva). Sequencing libraries were prepared with Illumina-compatible NEXTflex Rapid DNA sequencing Bundle (BIOO Scientific, USA) at Genotypic Technology (Bangalore, India). 100 ng of Qubit quantified purified amplicons were end-repaired, adenylated, and ligated to Illumina multiplex barcode adaptors as per NEXTflex Rapid DNA sequencing bundle kit protocol. Illumina universal adapters used in the study were: 5'-AATGATACGGCGACCACCGAGATCTACACTCTTTCCCTACACGACGCTCTTCCGATCT-3' and index adapter: 5'-GATCGGAAGAGCACACGTCTGAACTCCAGTCAC [INDEX] ATCTCGTATGCCGTCTTCTGCTTG-3'.

Adapter-ligated fragments were purified using Sera-Mag™ select beads (Cytiva). Resultant fragments were amplified for six cycles of PCR using Illumina-compatible primers provided in the NEXTflex Rapid DNA sequencing Bundle. Final PCR products (sequencing library) were purified with Cytiva beads followed by library quality control. Sequencing libraries were quantified by qubit fluorometer (ThermoFisher Scientific, USA) and the fragment size distribution was analysed on Agilent 2200 TapeStation. The libraries were paired-end sequenced on Illumina HiSeq X Ten sequencer (Illumina, USA) for 150 cycles following the manufacturer's instructions. The raw sequencing data was demultiplexed using bcl2fastq software v2.20 (Illumina, USA). The sequencing quality (base call accuracy and adapter contamination) was assessed using FastQC v0.11.8 software (Andrews 2010). The adapter sequences were trimmed using TrimGalore (Felix 2015) and bases above Q30 were considered for downstream analysis. The high-quality processed reads were stitched using Fastq-join (Aronesty 2013).

The centrifuge tool (Kim et al. 2016) was used to align the trimmed reads against centrifuge-NT database. This database is designed to facilitate the classification and identification of sequences in metagenomic and microbiome datasets. It contains reference sequences from a wide range of organisms, including bacteria,

archaea, viruses, and eukaryotes, classifying from kingdom to higher taxonomic ranks. Centrifuge is a very rapid and memory-efficient system which uses a novel indexing scheme based on the Burrows-Wheeler transform (BWT) and the Ferragina-Manzini (FM) index, optimized specifically for the metagenomic classification. Pavian (Breitwieser & Salzberg 2020) was later used to estimate and interactively explore the taxonomic content. Only matches with a similarity level of 95% or higher were considered significant and retained during the alignment process. The sequences generated in this study are deposited in NCBI database (BioProject accession number PRJNA1281322).

From the classified report, OTU IDs were assigned using kraken-biom Python tools. kraken-biom parses the k-reports, counts for each operational taxonomic unit (OTU), and includes lineage information. The extracted OTU from the kraken-report is then stored in a BIOM (Biological Observation Matrix) table, linking each count to the respective sample and OTU. The final obtained OTU-specific read abundance was used for further analysis. The frequency of occurrence of each OTU (or taxa) in the diet of each bat species studied was calculated as percent relative abundance (i.e., each OTU's read abundance divided by total read abundance of each bat species multiplied by 100).

Niche overlap and niche breadth

Pianka's niche overlap and Levins' niche breadth were calculated using spaa package in R (Zhang & Ma 2014). The values of the niche breadth obtained were standardised to get values between zero and one using the Levins' index equation ($B_A = B-1/n-1$; (Levins 2020)). We performed a non-parametric analysis of variance of relative prey-item read abundance (number of reads for a prey species divided by total number of reads) grouped by bat species (for both whole and core diets) to investigate if the dietary composition differed between the four species of bats, and diversity indices (for both whole and core diets) to investigate the diet breadth of each species in PAST statistical software (Hammer et al. 2001). We used RAWGraphs 2.0 (Mauri et al. 2017) to visualize the whole diet and the core diets of the four species of hipposiderid bats across three seasons (summer, monsoon, & winter).

RESULTS

Of the 18,483,216 raw reads generated, only those with a taxonomic identity match percentage of > 95%

were retained, resulting in 17,360,540 reads post-processing. The final processed reads were further checked against the records available from India on the public data portal of the BOLD and GenBank databases. We obtained 17,179 records corresponding to 4,177 species (combined data from BOLD and GenBank databases), which were further filtered to obtain a final 7,309 OTUs (Supplementary Tables 1,2).

Dietary analysis

The final dataset of whole diets of the four hipposiderid species revealed that our samples of *Hipposideros hypophyllus* comprised the most insect diversity (4,114 species), followed by *H. durgadasi* (2,410 species), *H. fulvus* (1,945 species), and *H. speoris* (1,160 species). No significant difference among the diets of the four species of bats was found (Kruskal-Wallis H[2] = 5.407; $p > 0.05$).

From the whole diet dataset, we filtered out frequently consumed prey-items ($\geq 1\%$ frequency of

Table 1. Niche overlap (Pianka's overlap index – 0 indicates no overlap, 1 indicates full overlap; top right values represent the whole diet; bottom left values represent the core diet) of the four *Hipposideros* bat species in the study.

Species	<i>H. hypophyllus</i>	<i>H. durgadasi</i>	<i>H. fulvus</i>	<i>H. speoris</i>
<i>H. hypophyllus</i>	-	0.03183	0.02088	0.00086
<i>H. durgadasi</i>	0.02586	-	0.00012	0.00110
<i>H. fulvus</i>	0.01580	0.0	-	0.00116
<i>H. speoris</i>	0.0	0.0	0.0	-

occurrence); this was classified as the core diets of the four species of hipposiderid bats. In the core diets of the four species, we identified 48 taxa belonging to 10 orders, 37 families, 46 genera, and 48 species. A significant difference was found among the core diets of the four hipposiderid species (Kruskal-Wallis H[2] = 22.81; $p < 0.05$). Variation between the core diets of the four study species accounted for 22.8% of the total



Image 5. Prey taxonomic diversity in the core diet of *Hipposideros hypophyllus*. The circles represent taxonomic ranks (Order, Family, Genus).

variation, while the rest (77.2%) was due to within-group variance. *Hipposideros hypophyllus* and *H. speoris* consumed 17 taxa each, while *H. durgadasi* consumed eight taxa, and *H. fulvus* consumed six taxa of insects. Pairwise comparisons using Dunn's test highlighted a significant difference ($p < 0.05$) between the diet of *Hipposideros speoris* and that of *H. hypophyllus* and *H. fulvus*. There was no overlap in the whole and core diets between the four study species (Table 1), and all four species showed a high degree of specialization in the dietary items they consumed in both whole and core diets (Table 2).

Core diets

In the core diets of all four hipposiderid bat species, prey belonging to orders Lepidoptera and Diptera were consumed to a greater extent in comparison to other insect orders which is common for any bat species (Ingala et al. 2021). The core diet of *Hipposideros hypophyllus* consisted of four insect orders with lepidopterans figuring majorly in its diet with six families followed by

the three other insect orders (Image 5). The core diet of *Hipposideros durgadasi* consisted of taxa exclusively belonging to the orders Lepidoptera (4 families) and Diptera (1 family) (Image 6). *H. fulvus* fed on five insect orders including two families of lepidopterans and the other insect orders in equal measure (Image 7). While the core diet of *H. speoris* was very diverse and comprised eight insect orders lepidopterans were fed upon more in comparison to the rest of the insect orders (Image 8).

Amongst the lepidopteran families consumed by these four species of hipposiderid bats, the most consumed was the family Noctuidae, followed by Pyralidae, Gelechiidae, Geometridae, Papilionidae, and Elachistidae. The least consumed families were Tineidae and Nolidae (Image 9). *Hipposideros hypophyllus* preferred prey items belonging to the family Noctuidae (30.90%), followed by Papilionidae (7.89%), Elachistidae (6.70%), Pyralidae (5.03%). Prey items belonging to families Geometridae and Nolidae combined contributed to 3.59% of the diet of this species. *H. durgadasi*



Image 6. Prey taxonomic diversity in the core diet of *Hipposideros durgadasi*. The circles represent taxonomic ranks (Order, Family, Genus).

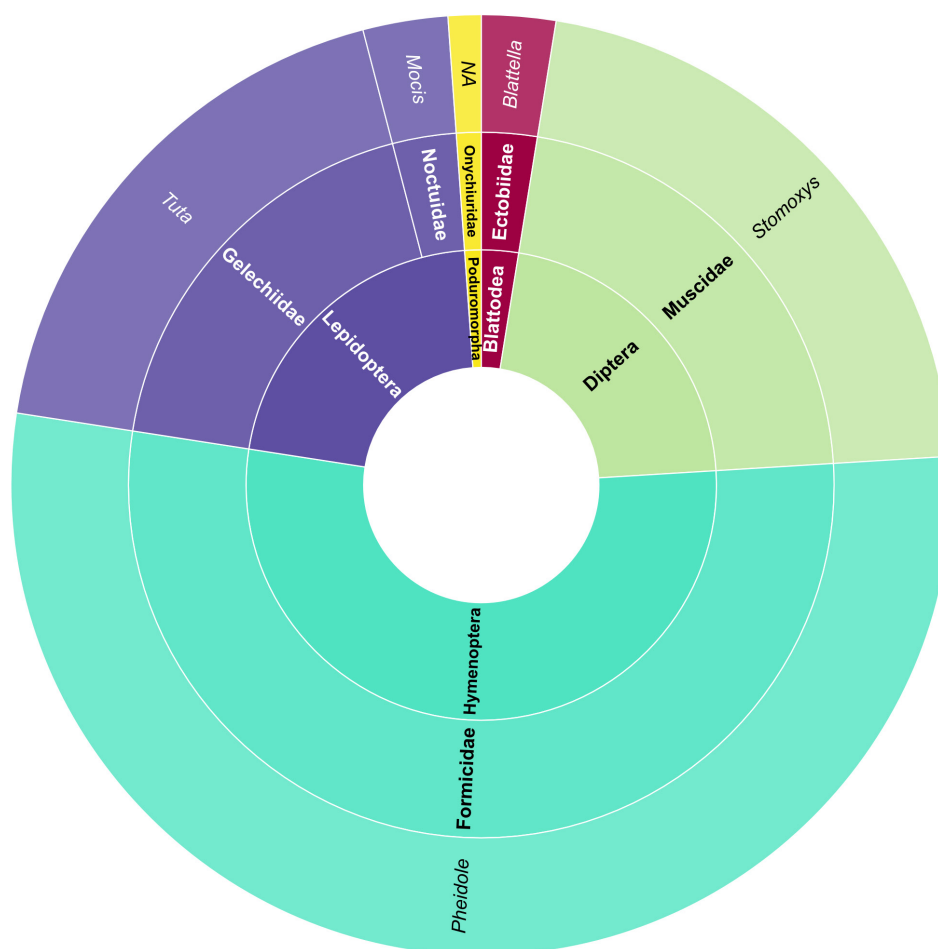


Image 7. Prey taxonomic diversity in the core diet of *Hipposideros fulvus*. The circles represent taxonomic ranks (Order, Family, Genus).

consumed prey items belonging to the family Pyralidae (43.9%), followed by Noctuidae (25.85%), Geometridae (10.58%), and Tineidae (1.65%). *H. fulvus* consumed prey items belonging to the family Gelechiidae (16.95%), followed by Noctuidae (2.67%). The least consumption of lepidopteran prey was by *H. speoris* with the family Pyralidae (3.39%), Gelechiidae (1.78%), and Noctuidae and an unclassified family (combined amounting to 2.05%).

Among the dipteran families, these hipposiderid bat species consumed families Chironomidae, Muscidae, Culicidae, Asilidae, Calliphoridae, Sciaridae, and Tabanidae (Image 10). *Hipposideros hypophyllus* consumed the family Chironomidae (16.20%), followed by Asilidae (2.88%), and Sciaridae (1.35%). *H. durgadasi* consumed the least number of dipterans and fed only on the family Calliphoridae (2.30%). Similarly, *H. fulvus* fed only on the family Muscidae (19.68%), while *H. speoris* fed on Culicidae (5.86%), Chironomidae (3.94%), and Tabanidae (1.10%).

Table 2. Niche breadth (Levins' index – 0 indicates specialism, 1 indicates generalism; top row represents the whole diet, bottom row represents the core diet) of the four *Hipposideros* bat species in the study.

Species	<i>H. hypophyllus</i>	<i>H. durgadasi</i>	<i>H. fulvus</i>	<i>H. speoris</i>
Whole diet	0.00237	0.00134	0.00115	0.00448
Core diet	0.42540	0.25349	0.28695	0.21752

Diversity indices

The degree to which a species influences other species in the community (or makes up most of the biomass) is quantified by the dominance index (D_i), where $D_i \leq 0.50$ indicates no species dominates, 0.50–0.75 indicates moderate dominance of a given species, and 0.75–1 indicates high dominance. None of the study species were found to be dominant in their whole diet [D_i (*H. fulvus*) = 0.31; (*H. durgadasi*) = 0.23; (*H. speoris*) = 0.16; (*H. hypophyllus*) = 0.09]. Diet species diversity



Image 8. Prey taxonomic diversity in the core diet of *Hipposideros speoris*. The circles represent taxonomic ranks (Order, Family, Genus).

is quantified by Simpson's diversity index, where an index of ≤ 0.50 indicates low diversity, between 0.50–0.75 indicates moderate diversity, and between 0.75–1 indicates high diversity. Simpson's diversity index for the whole diet showed a high diversity of diet in *Hipposideros hypophyllus* (0.91), followed by *H. speoris* (0.84), and *H. durgadasi* (0.76). However, the diet of *H. fulvus* was relatively less diverse (0.69). Shannon's H index of species diversity ranges between 1.5 and 3.5 and rarely exceeds 4.5; the Shannon index of the prey species in the four study species' whole diets shows that *Hipposideros hypophyllus* ($H = 3.05$) fed on highly diverse dietary items, followed by *H. speoris* ($H = 2.75$), *H. durgadasi* ($H = 2.38$), and *H. fulvus* ($H = 1.75$).

In the core diets of the four study species, the dominance index (Di) showed no dominant species [Di (*H. fulvus*) = 0.37; (*H. durgadasi*) = 0.33; (*H. speoris*) = 0.21; (*H. hypophyllus*) = 0.12]. Simpson's diversity index showed a high diversity in the core diets of *H. hypophyllus* (0.87) and *H. speoris* (0.79), and moderate diversity in *H.*

durgadasi (0.67) and *H. fulvus* (0.63). Shannon's H index showed that *H. hypophyllus* ($H = 2.39$) and *H. speoris* ($H = 2.05$) had a diverse diet, while *H. durgadasi* ($H = 1.44$) and *H. fulvus* ($H = 1.22$) had a relatively low diversity of insect species in their core diets. The core diets of *H. hypophyllus* and *H. speoris* included six species of pest insects each, while that of *H. durgadasi* and *H. fulvus* included three insect pest species each (Supplementary Table 3).

Seasonal variations in *Hipposideros hypophyllus* diet

The whole diet of our sampled *H. hypophyllus* individuals ($N = 4$) over summer, monsoon, and winter seasons showed no significant difference (Welch F-test: $F = 2.79$, $p > 0.05$). In the summer season, the diet was dominated by lepidopteran prey species (35.81%), followed by the orders Diptera (31.80%), Blattodea (20.72%), Coleoptera (2.96%), Mantodea (2.52%), followed by other insect orders. The monsoon diet was dominated by Lepidoptera (92.80%), followed by Diptera (1.5%) and other insect orders. The winter

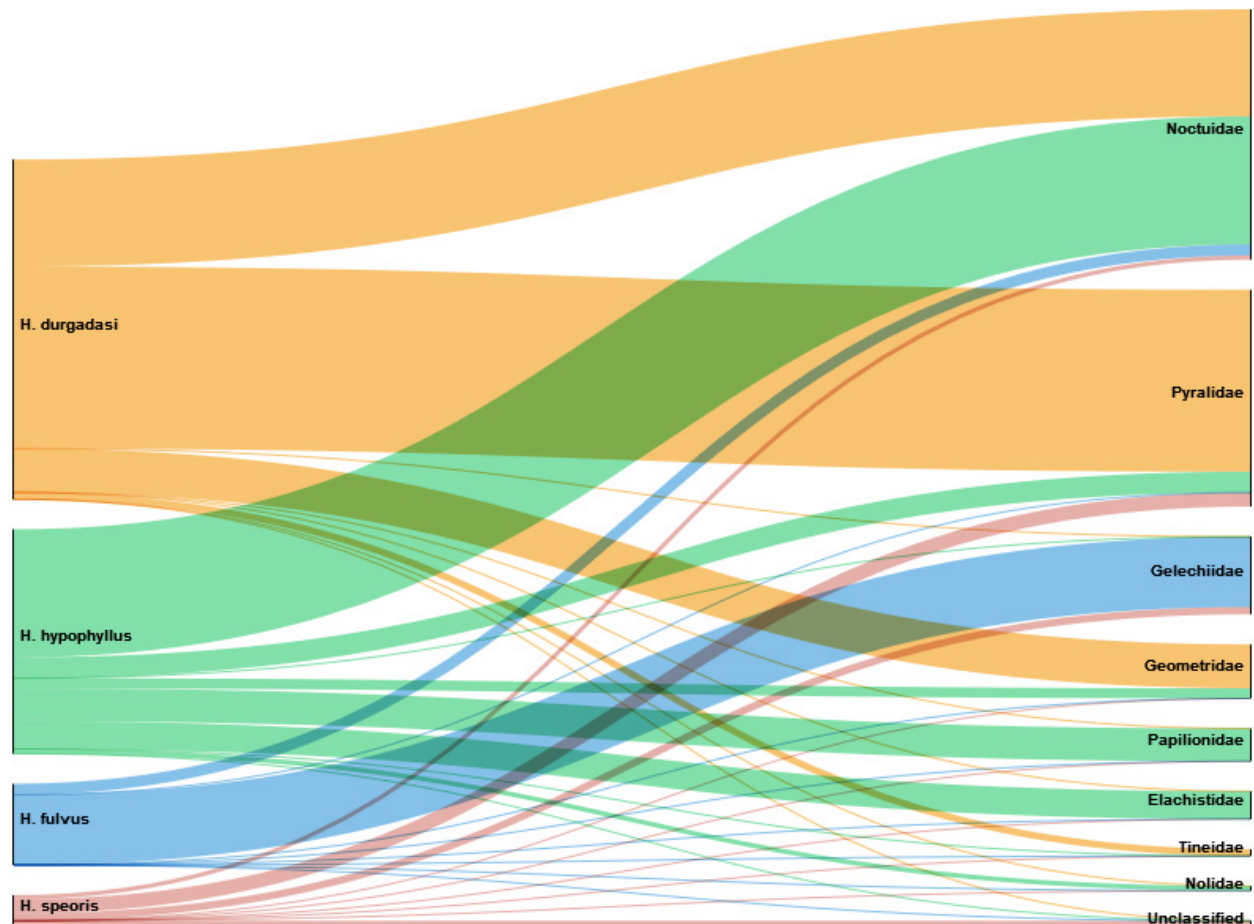


Image 9. Associations between bats (left) and lepidopteran insect prey taxa summarized at the taxonomic level of family (right). The connecting bar width represents the relative read abundance of each insect family between each bat and each dietary item.

diet was similarly dominated by the order Lepidoptera (85.82%), followed by Diptera (12.86%) and other insect orders (Image 11). The core diet of *H. hypophyllus* over the three seasons showed a significant difference (Welch F-test: $F = 3.99$, $p = 0.05$). The summer diet of *H. hypophyllus* sampled in the study period was dominated by the order Lepidoptera (32.70%), followed by Diptera (29.37%), Blattodea (20.72%), and Coleoptera (2.12%). In the monsoon, the diet was comprised mostly by lepidopteran prey (74%), while in the winter it consisted of orders Lepidoptera (82.68%) and Diptera (12.58%) (Image 12).

DISCUSSION

Despite the diversity of insectivorous bats in southern Asia (Srinivasulu et al. 2025), studies on insectivorous bat diets are sporadic and scattered, often employing either gut content analysis (Advani 1981) or faecal pellet

dissection (Whitaker Jr. 1988), which is more common due to its non-invasive nature (Kunz & Whitaker Jr. 1983; Dickman & Huang 1988; Whitaker Jr. 1988). Studies conducted on the faecal pellets or echolocation of some roundleaf bats in southern Asia have provided a broad understanding of their diets. For instance, studies based on the flight behaviour and echolocation calls of *H. fulvus* mentioned that it may prefer feeding on cockroaches and beetles, and on insects of intermediate size to avoid competition with other sympatric species such as *H. ater* and *H. speoris* (Madhavan et al. 1978; Jones et al. 1994). Khajuria (1980) states that the diet of *H. durgadasi* is similar to *H. fulvus*, and they likely feed on small insects such as beetles and small crickets. *H. speoris* was observed to feed on mosquitoes and flies (Brosset 1962), and beetles and other low-flying insects, especially termites (Phillips 1980). Jones et al. (1994) predicted it to feed on large-bodied insects based on its echolocation. There have been no studies yet on the diet of the Kolar Roundleaf Bat, however, Kock & Bhat (1994)

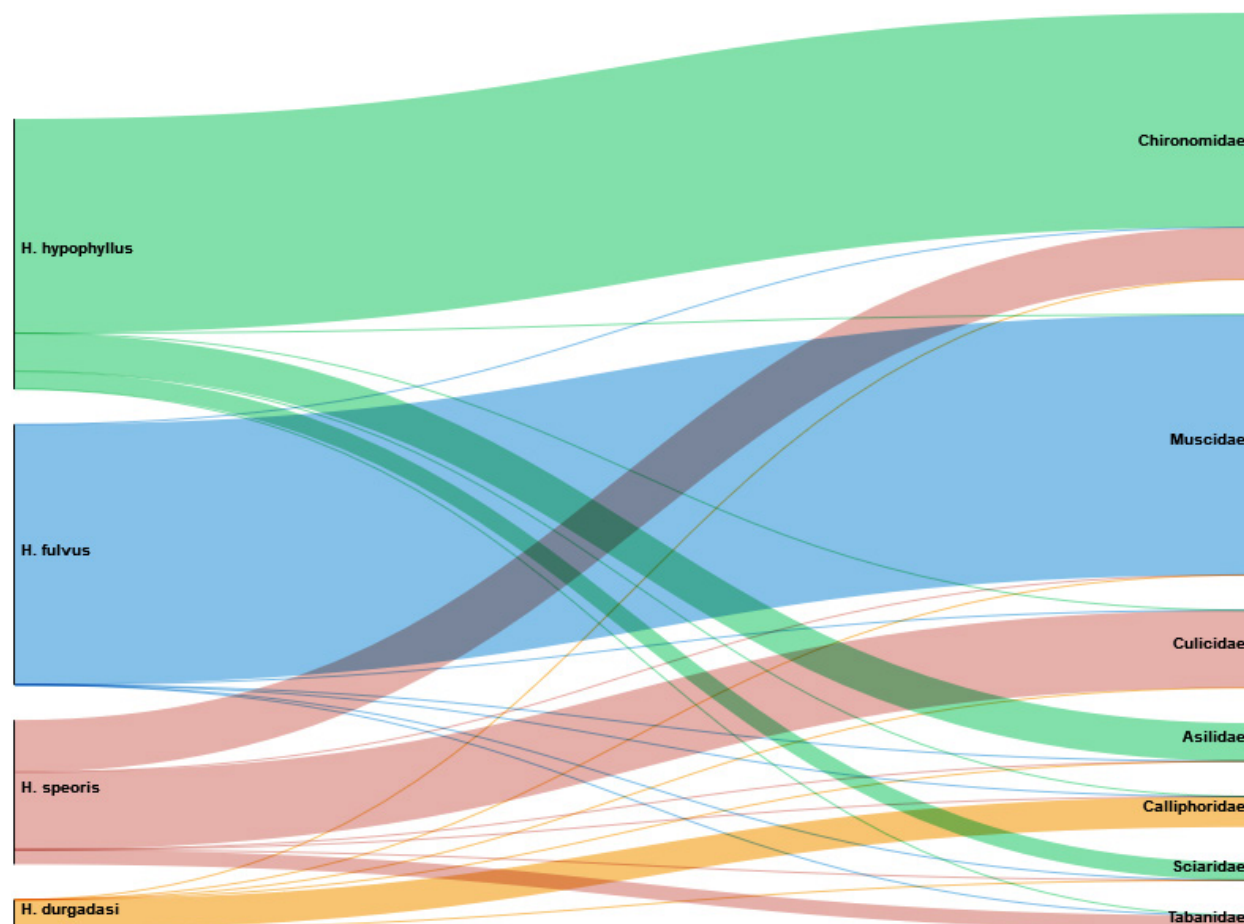


Image 10. Associations between bats (left) and dipteran insect prey taxa summarized at the taxonomic level of family (right). The connecting bar width represents the relative read abundance of each insect family between each bat and each dietary item.

mention that they observed fat deposits at the base of the tail of the species between the months of November and February.

The number of identifiable insect taxa is limited in a microscopic examination of faecal pellets due to the level of fragmentation of insect parts, making it rarely possible to identify insect remnants beyond order and, at times, family level (Hubancheva et al. 2023). DNA metabarcoding of bat guano provides higher-resolution appraisal of diet, often up to species level (Hubancheva et al. 2023; Liu et al. 2023; Ling et al. 2025). This has resulted in faecal DNA analysis becoming increasingly common in ecological, dietary, spatial, and phylogenetic studies (Thuvo et al. 2019; Ando et al. 2020; Guan et al. 2020; Ingala et al. 2021; Hubancheva et al. 2023; Liu et al. 2023; Treloar et al. 2023; Ling et al. 2025), emphasising its effectiveness in helping to make informed conservation decisions. However, metabarcoding studies are not without limitations. Metabarcoding analyses of diet are still in the nascent stages in southern Asia, and none

yet have been conducted on Indian bats. This technique is limited by resource and equipment costs, human resource expenditure, and computational limitations due to the need to effectively analyse many gigabytes of data – these costs are significantly lower in physical faecal dissection-based diet analyses. However, with the advent of more accessible and portable technologies (e.g., nanopore sequencing), this suite of techniques may grow more methodologically and economically feasible in southern Asia in the near future.

Our exploration of the diets of some individuals of the Kolar Roundleaf Bat *Hipposideros hypophyllus* and its congeners, the Fulvous Roundleaf Bat *H. fulvus*, Khajuria's Roundleaf Bat *H. durgadasi*, and Schneider's Roundleaf Bat *H. speoris* revealed highly similar whole diets, likely due to sharing a colony and therefore a resource space, but significant differences between the core diets (i.e., the most frequent prey items) in *H. hypophyllus* & *H. speoris* and *H. speoris* & *H. fulvus*. Further, no species dominated in terms of prey abundance, and Simpson's

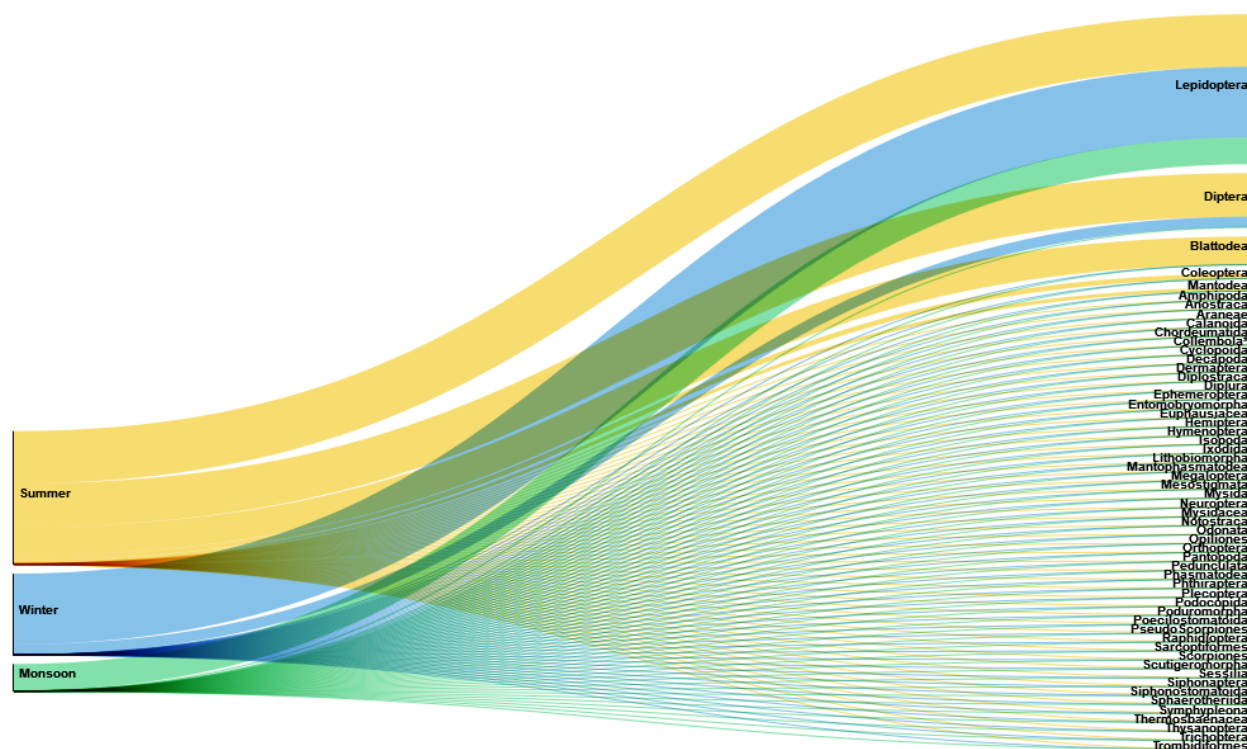


Image 11. Representation of the prey taxonomic diversity in the whole diet *Hipposideros hypophyllus* over three seasons and insect prey taxa summarized at the taxonomic level of order (right). The connecting bar width represents the relative read abundance of each insect order consumed over the seasons.

and Shannon's diversity indices of prey species in core diets indicated that the Kolar Roundleaf Bat likely preys on a wide diversity of invertebrate species. The core diet of the Kolar Roundleaf Bat also varied significantly between the three seasons (Summer, monsoon, & winter) sampled across one year, but in all seasons was dominated by lepidopteran prey.

Interestingly, there were some medically and agriculturally significant pests seen in the prey diversity of the four study species. For instance, all species were seen to feed on mosquitoes of *Aedes*, *Anopheles*, and *Culex* genera, known to carry various significant diseases (Achee et al. 2015; Choo & Blackwood 2017; Wilkman et al. 2023; Lim et al. 2025). *Hipposideros durgadasi* was the biggest suppressor of *Tetranychus urticae* (Trombidiformes: Tetranychidae), a mite that infests many vegetable crops and *Withania somnifera*, a medicinal plant (Mason 2001). Cockroaches, vectors of many viral and bacterial diseases (Donkor 2020), were majorly fed upon by *H. hypophyllus* and *H. fulvus*. *Hishimonus phycitis* (Hemiptera: Cicadellidae), a major hemipteran pest of citrus and brinjal (EFSA Panel on Plant Health et al. 2017), was suppressed mostly by *H. speoris*. Finally, the tomato leafminer *Tuta absoluta* (Lepidoptera: Gelechiidae), a highly invasive tomato pest

(Biondi et al. 2018), was majorly predated upon by *H. fulvus* and *H. hypophyllus*. However, natural predators of pests were also fed upon by our study species, including predatory mosquitoes *Lutzia fuscana* (Diptera: Culicidae; Surendran et al. 2013; Mudi et al. 2025), hatchet wasps *Prosevania* sp. (Hymenoptera: Evaniidae) which are predators and parasites of cockroaches (Tee & Lee 2017), Ichneumonid wasps of the genus *Leptobatopsis* (Hymenoptera: Ichneumonidae; Quicke et al. 2023), and *Megastigmus viggianii* (Hymenoptera: Megastigmidae), a natural suppressor of the Eucalyptus gall wasp *Leptocybe invasa* (Mendel et al. 2017). However, the bats sampled were seen to suppress pests much more effectively than their insect predators.

It is important to note that this study is only an initial exploration of the diets of these four species, limited to a small sample of four individuals per species per season, and three seasons over one cycle in one site – such a small sample size inherently leads to potential biases in prey species detectability through primer bias, and the diversity reported in our study may not represent the entire dietary breadth of our study species. Given the nascent state of DNA metabarcoding as a method for non-invasive assessment of biodiversity in southern Asia, a limited sample size also hampers the generalisability of

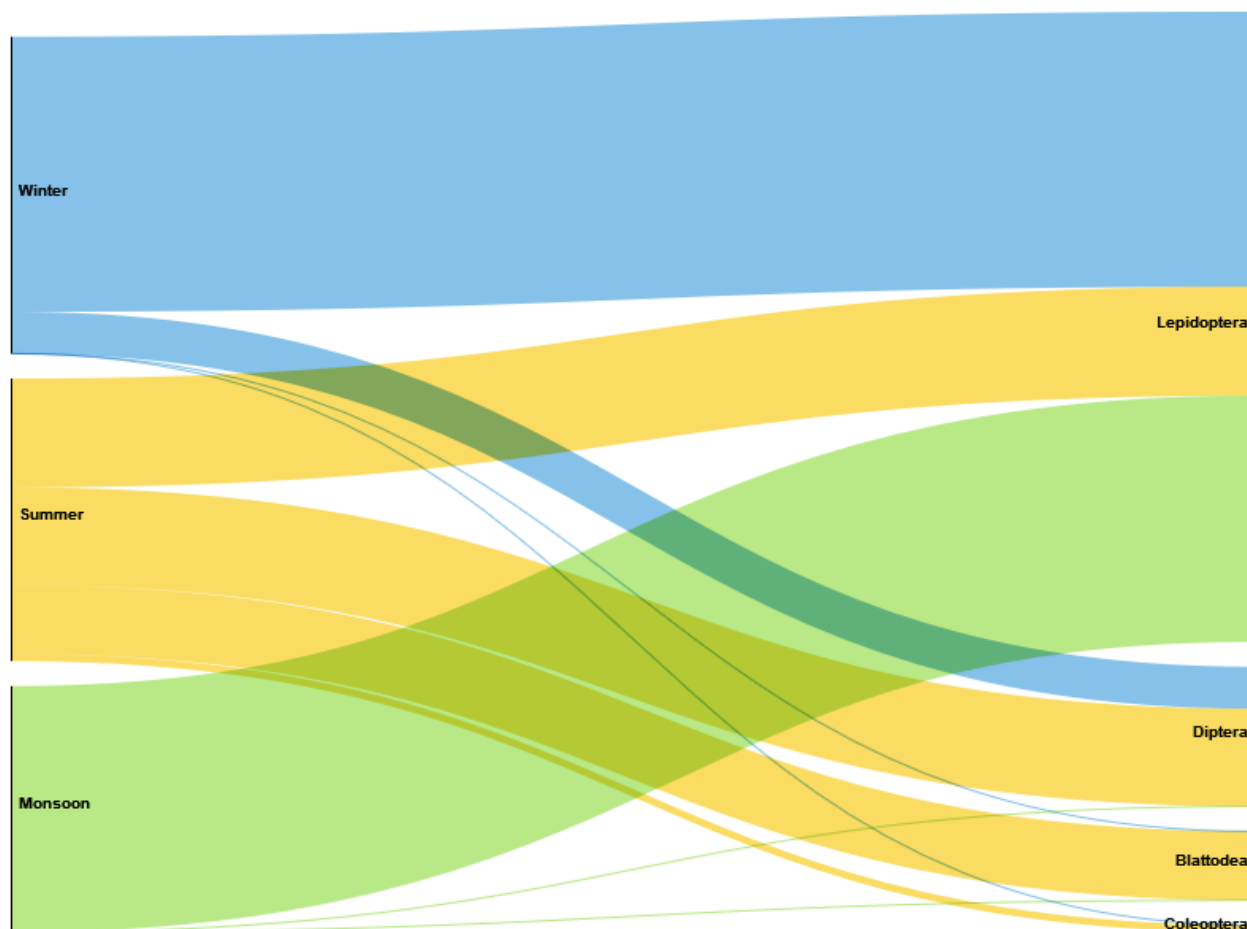


Image 12. Representation of the prey taxonomic diversity in the core diet *Hipposideros hypophyllus* over three seasons and insect prey taxa summarized at the taxonomic level of order (right). The connecting bar width represents the relative read abundance of each insect order consumed over the seasons.

this study, which insofar may only serve as a foundational piece of research on bat diets using genetic techniques. Further research using DNA metabarcoding is needed to clarify and confirm prey diversity patterns and seasonal variations in these and other bat species, and replicated metabarcoding studies are required across peninsular India and southern Asia as a whole to establish standard practices for these techniques. Our study explores the diets of these four roundleaf bats, identifying their importance as suppressors of medical and agricultural pests, and emphasising the effectiveness and importance of non-invasive assessment of bat diets in helping to guide future conservation research and planning. In the case of such sensitive roosts as Hanumanhalli Betta and threatened species such as the Kolar Roundleaf Bat and Durga Das' Roundleaf Bat, a non-invasive approach towards understanding their ecological interactions, appraising their ecosystem services (especially pest suppression in the case of insectivorous bats), and

assessing these against the threats they face is vital for effective conservation, ensuring the long-term survival of these irreplaceable species.

Data availability statement

All relevant data are within the manuscript and its Supporting Information files. The BioProject accession number is PRJNA1281322

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