

Seasonal variations in the diet of Greater Asiatic Yellow House bat, *Scotophilus heathii* (Horsfield, 1831)

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Abstract

Understanding the dietary composition of insectivorous bats is essential for evaluating the ecological role of bats. We investigated the diet of *Scotophilus heathii* across three roosting sites in Uttar Pradesh, India, using the food remnants. A total of 432 prey remains were recovered, of which 369 (85.4%) were identified, representing 12 insect orders. Coleoptera (27.8%) and Hemiptera (26.9%) dominated the diet, followed by Orthoptera (12.7%), whereas the remaining insect orders occurred in lower proportions. Dietary diversity was assessed using prey-order richness, Shannon diversity, Simpson diversity, and Pielou's evenness. Linear mixed-effects models showed that roosting site significantly influenced Shannon diversity, with Khairabad exhibiting higher diversity than Amausi, however seasonal differences in dietary diversity were not significant. In contrast, *Permanova* revealed significant differences in seasonal prey composition, while differences among roosting sites were not significant. Pairwise comparisons indicated that post-monsoon prey composition differed significantly from both summer and monsoon, and *permdisp* confirmed that these differences were not attributable to variation within-group dispersion. Overall, *S. heathii* exhibited a broad diet range, highlighting its potential ecological importance as a natural predator of nocturnal insect.

Keywords: Chiroptera, pest control, dietary composition, insectivorous, seasonal variation

Introduction

Insectivorous bats are important nocturnal predators of insects and other arthropods and play a key role in terrestrial food webs. Because flying, maintaining body temperature, and reproduction require a lot of energy, many insectivorous bats consume large amounts of prey each night, sometimes eating up to 80-95% of their body mass [1, 2]. Through these feeding activities, bats contribute significantly to ecosystem functioning by suppressing insect populations, including numerous agricultural and forestry pests, thereby providing valuable ecosystem services [3, 6]. Consequently, understanding dietary composition is fundamental for evaluating trophic ecology, prey selection, habitat use, and the ecological services provided by insectivorous bats [5, 7]. Dietary information is also essential for assessing the contribution of bats to natural pest suppression and for developing effective conservation and management strategies in rapidly changing landscapes [5, 8].

Several approaches have been employed to investigate the diet of insectivorous bats, including direct observation of foraging behaviour, stomach-content analysis, microscopic examination of guano, stable isotope analysis, and, more recently, DNA metabarcoding [7, 9, 10]. Among these methods, microscopic analysis of guano remains one of the most widely used cost effective non-invasive methods because it enables dietary assessment without capturing or sacrificing animals and permits identification of indigestible prey remains such as wings, legs, antennae, elytra, and other chitinous fragments [7, 11, 12]. Although this approach generally provides taxonomic resolution only to higher taxonomic levels and may underestimate soft-bodied prey owing to differential digestion, it remains a practical, reliable, and cost-effective method for evaluating dietary composition across broad spatial and temporal scales [13, 14].

Consequently, microscopic fecal analysis continues to be widely applied in ecological studies investigating dietary composition, seasonal variation, and trophic ecology of insectivorous bats [15, 16].

Previous studies have demonstrated that insectivorous bats consume a wide range of arthropod prey, with Coleoptera, Lepidoptera, Diptera, Hemiptera, Hymenoptera, and Orthoptera consistently representing the principal dietary components across diverse geographic regions [6, 15, 20]. However, dietary composition is highly dynamic and is influenced by prey availability, habitat characteristics, seasonal fluctuations in insect abundance, and local environmental conditions [21, 23]. In India, dietary studies have substantially improved our understanding of the feeding ecology of several insectivorous bats [16, 17, 24].

Scotophilus heathii Horsfield, 1831 [Chiroptera: Vespertilionidae], commonly known as the greater Asiatic yellow house bat, is a medium-sized insectivorous bat widely distributed throughout South and Southeast Asia, including India [25]. It is a predominantly nocturnal aerial hawker that forages in open habitats and along habitat edges and commonly roosts in buildings, abandoned structures, roofs, tree hollows, and other man-made structures [5]. According to the International Union for Conservation of Nature (IUCN), *S. heathii* is currently classified as Least Concern because of its wide distribution and presumed large population [26]. Despite its broad distribution and ecological importance as an insectivorous predator, information on its trophic ecology remains extremely limited. To date, a limited study has been carried out on the diet of *S. heathii* using microscopic analysis of guano, providing only a preliminary description of its prey composition [24, 27]. Consequently, seasonal variation in its diet and the influence of habitat on prey selection remain poorly understood.

Nevertheless, comparable information on the dietary ecology of the *S. heathii*, particularly across different seasons and habitat types, remains scarce. Therefore, the present study investigated the seasonal dietary composition of *S. heathii* in Uttar Pradesh, India, using microscopic analysis of guano. Specifically, we compared dietary composition among three roosting sites and across seasons to determine whether the diet of *S. heathii* varied spatially and temporally. We hypothesized that dietary composition would differ significantly among roosting sites and seasons, reflecting variation in prey availability and habitat characteristics. By providing the first comprehensive assessment of the seasonal diet of *S. heathii* in northern India, this study contributes to a better understanding of the trophic ecology of the species and its potential ecological role of *S. heathii*.

Materials and Methods

Study area and sites

The study was conducted at three roost sites located in Lucknow (Amausi, Qaiser Bagh) and Sitapur (Khairabad)

districts, Uttar Pradesh, India (Table 1; Figure 1). The study area lies within the central Indo-Gangetic Plain, one of the most densely populated and agriculturally productive regions of northern India. Geographic coordinates of each roost were recorded in decimal degrees (DD) using Google Earth Pro. The region experiences a subtropical monsoon climate characterized by hot summers, a humid rainy season, and cool winters.

According to the India Meteorological Department (IMD), four distinct seasons occur annually: summer (March-May), monsoon (June-September), post-monsoon (October-November), and winter (December-February). Three roosts representing different habitat types were selected for the study: Amausi (industrial habitat), where bats roosted in mature palm trees; Qaiser Bagh (urban habitat), where bats occupied an abandoned building within a densely built-up area; and Khairabad (peri-urban habitat), where bats roosted in an abandoned building surrounded by agricultural land, scattered vegetation, and human settlements.

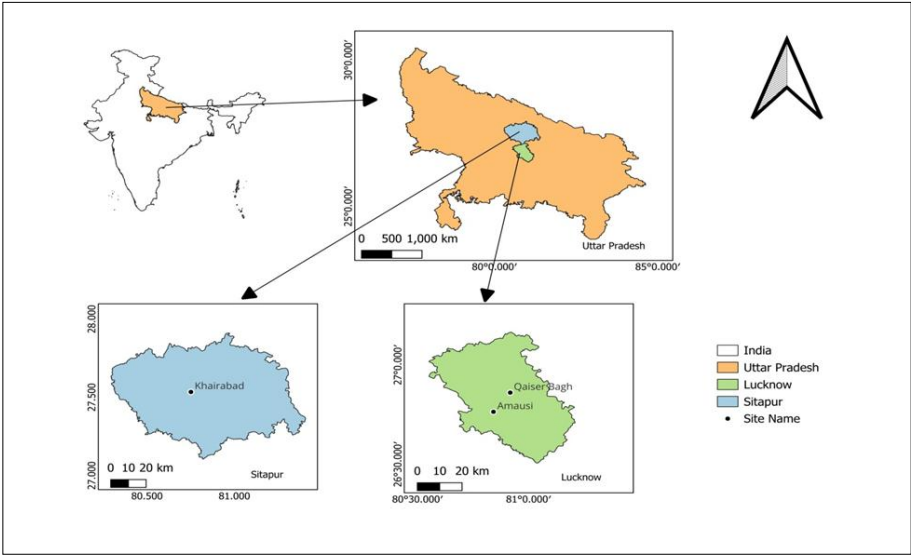


Fig 1: Study area map showing the geographic location of *Scotophilus heathii* roost sites in Sitapur and Lucknow, Uttar Pradesh, India.

Table 1: Roost sites details and geographic coordinates (latitude and longitude in decimal degrees, DD).

District	Roosting site	Habitat type	Roost type	Latitude (DD)	Longitude (DD)
Lucknow	Amausi	Industrial	Palm trees	26.76389	80.84167
Lucknow	Qaiser Bagh	Urban	Abandoned building	26.86028	80.91722
Sitapur	Khairabad	Peri-urban	Abandoned building	27.53861	81.75139

Guano collection

Fresh guano pellets were collected every month from March to November 2024. Winter (Dec-Feb) sampling was not conducted because bats were in hibernation during this period. At each sampling event, a clean polythene sheet (2 × 2 m) was placed beneath the bat roost prior to evening emergence (17:00–18:00 h) to collect freshly deposited fecal pellets following [16, 17]. The following morning (07:00–08:00 h), freshly deposited guano pellets were aseptically collected using sterile forceps. A total of 50 pellets were collected from each study site during every month, resulting in 1,350 pellets across all sites and sampling months (50 pellets × 3 sites × 9 months). The collected pellets were immediately transferred into pre-labelled sterile 50 ml tubes

containing 70% ethanol and transported to the laboratory [20].

Pellet analysis and prey identification

Thirty guano pellets were randomly selected from each study site during each month, resulting in a total of 810 pellets (30 pellets × 3 sites × 9 months). A sample was defined as all freshly collected pellets obtained from a single roost during one sampling event. Individual pellets were softened by soaking in 70% ethanol containing a few drops of glycerol for 30-45 min to facilitate disaggregation [7]. Each pellet was then teased apart using fine forceps and dissecting needles, and the contents were examined under a stereomicroscope (RSMr3, Radical Scientific) at 40×

magnification following established protocols [16]. Recognizable prey remains were separated and identified to the lowest possible taxonomic level, primarily to insect order, using the identification keys of [28]. Representative fragments were photographed using a digital imaging system attached to the stereomicroscope. Fragments lacking sufficient diagnostic characteristics were classified as unidentified and excluded from subsequent dietary analyses. The abundance of each prey order was estimated from the number of identifiable prey fragments recovered from all pellets. Relative abundance (%) of each prey order was calculated and graphically represented as the proportion of identifiable fragments belonging to that order relative to the total number of identified prey fragments.

Statistical analysis

Dietary diversity was quantified for each site × month sampling using identifiable prey remains. Four complementary diversity indices were calculated: prey-order richness (S), Shannon–Wiener diversity (H'), Simpson diversity (1-D), and Pielou's evenness (J'). Differences in dietary diversity among roosting sites and seasons were evaluated separately for each diversity index using linear mixed-effects models (LMMs), with roosting site and season specified as fixed effects and month included as a random intercept to account for repeated monthly sampling. The significance of fixed effects was assessed using Type III analysis of variance with Satterthwaite's approximation of degrees of freedom. Pairwise comparisons were performed using estimated marginal means (EMMs) with Tukey-adjusted *p* values when significant main effects or biologically relevant trends were detected. To examine patterns in prey composition, correspondence analysis (CA) was performed using a site × month matrix of identifiable prey remains, with sampling events as rows and the 12 identified insect orders as columns. Relationships among sampling events and prey orders were visualized using a biplot of the first two correspondence axes, and the relative

contributions of the axes were assessed from their eigenvalues and explained inertia. Variation in prey composition was further explored using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities calculated from the abundance of the 12 identified insect orders. A two-dimensional ordination was generated (stress = 0.144). Associations between prey orders and the NMDS ordination were evaluated using permutation-based vector fitting (*envfit*), and *p* values were adjusted using the Benjamini-Hochberg false discovery rate procedure. Differences in prey composition among roosting sites and seasons were tested using permutational multivariate analysis of variance (*Permanova*) based on Bray-Curtis dissimilarities. The effects of roosting site, season, and their interaction were evaluated, and pairwise *Permanova* comparisons were conducted where significant differences were detected using sequential Bonferroni correction. Homogeneity of multivariate dispersion (PERMDISP) was used to determine whether significant *Permanova* results reflected differences in group centroids rather than within-group dispersion. All statistical analyses were performed in R [29].

Results

Overall diet composition

A total of 432 prey remains were recovered from the analysed guano pellets of *Scotophilus heathii*. Of these, 369 (85.42%) were identified to 12 insect orders, whereas 63 remains (14.58%) could not be assigned to any insect order and were classified as unidentified (Fig. 1). Coleoptera constituted the largest proportion of the identified diet (27.78%), followed by Hemiptera (26.85%) and Orthoptera (12.73%). The remaining prey comprised Dermaptera (4.40%), Hymenoptera (3.47%), Diptera (2.55%), Zoraptera (2.08%), Dictyoptera (1.62%), Plecoptera (1.39%), Lepidoptera (1.39%), Odonata (0.93%), and Neuroptera (0.23%) (Fig. 1).

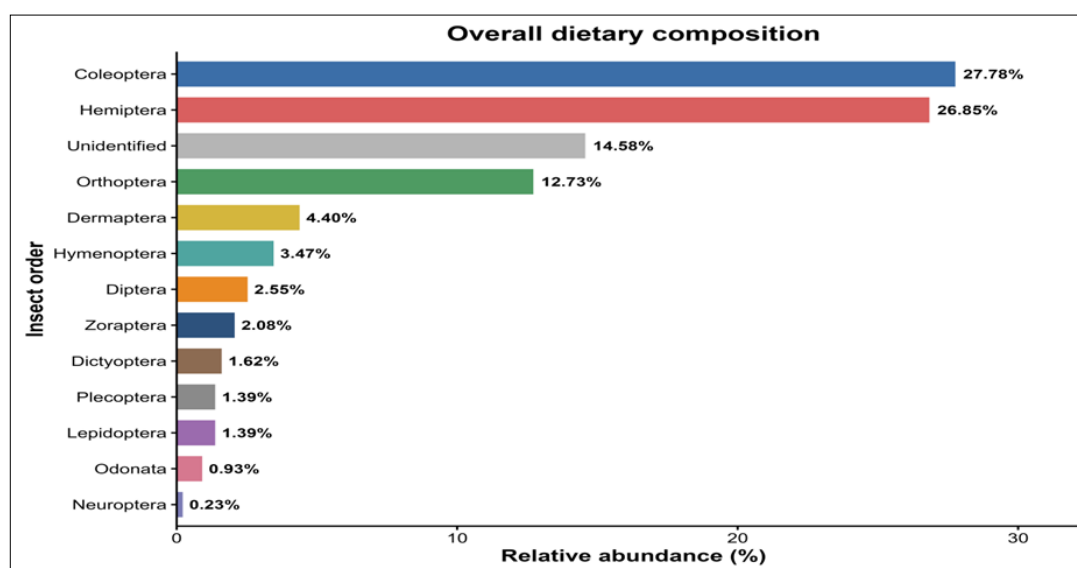


Fig 2: Overall dietary composition of *Scotophilus heathii* based on insect prey remains recovered from guano samples

Variations in dietary composition among roost sites

The variation in dietary composition among the three roosting sites is shown in Fig. 2. A total of 132 prey remains

were recovered from Amausi, 178 from Khairabad, and 122 from Qaiserbagh. Coleoptera was the dominant prey order at Amausi (49 remains; 37.12%), followed by Hemiptera (36;

27.27%) and Orthoptera (14; 10.61%). In contrast, Hemiptera was the most abundant prey order at both Khairabad (44; 24.72%) and Qaiserbagh (36; 29.51%), with Coleoptera representing

the second most abundant order at Khairabad (43; 24.16%) and Qaiserbagh (28; 22.95%). Orthoptera was the third most abundant prey order at Khairabad (28; 15.73%) and Qaiserbagh (13; 10.66%).

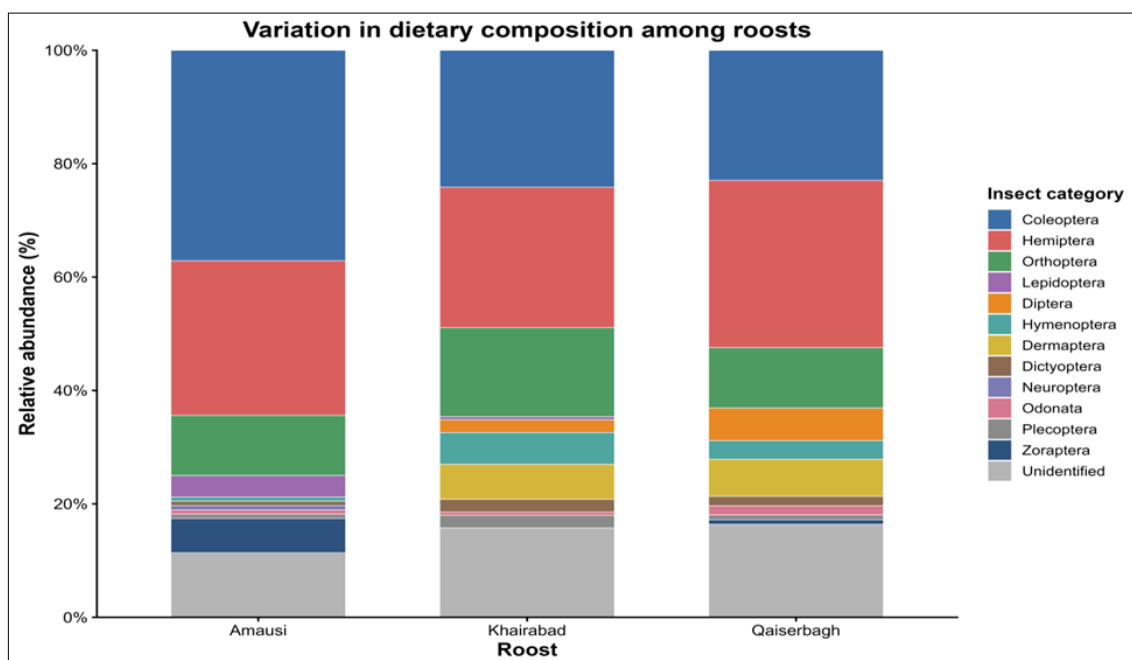


Fig 3: Relative abundance of insect prey orders in the diet of *Scotophilus heathii* among the three roosting sites.

Seasonal variation in dietary composition

Seasonal variation in dietary composition is presented in Fig. 3. A total of 111 prey remains were recovered during summer, 213 during the monsoon, and 108 during the post-monsoon period. Coleoptera was the dominant prey order during summer (38 remains; 34.23%) and the monsoon (73; 34.27%), whereas Hemiptera predominated during the post-monsoon period (40; 37.04%). During summer, Hemiptera (19; 17.12%) and

unidentified remains (19; 17.12%) were the next most abundant components of the diet. In the monsoon, Hemiptera (57; 26.76%) and unidentified remains (37; 17.37%) were also well represented. In contrast, the post-monsoon diet was characterized by a marked increase in Orthoptera (27; 25.00%) and Dermoptera (13; 12.04%), whereas Coleoptera declined to 9 remains (8.33%). Unidentified remains accounted for only 7 prey fragments (6.48%) during the post-monsoon period.

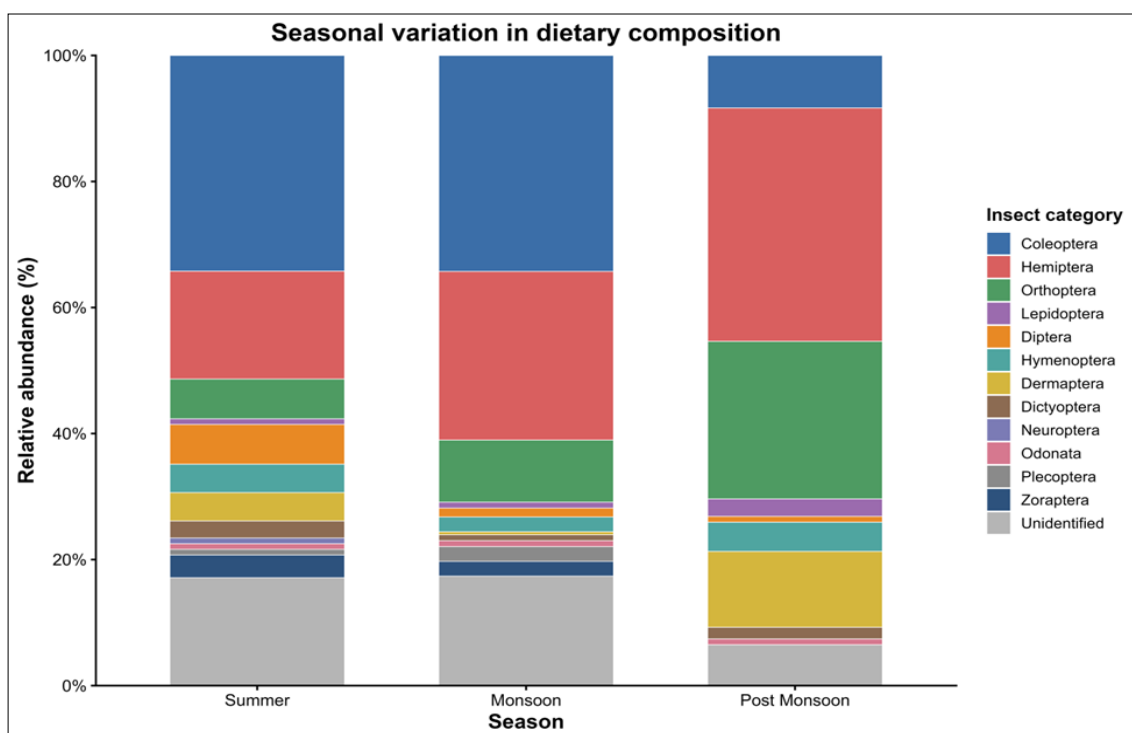


Fig 4: Seasonal variation in the relative abundance of insect prey orders in the diet of *Scotophilus heathii*.

Variation in dietary diversity among roosting sites and seasons

Dietary diversity varied among roosting sites, whereas seasonal variation was comparatively limited (Fig. 4; Tables 2 and 3). Khairabad exhibited the highest mean prey-order richness (4.78 ± 1.56) and Shannon diversity (1.27 ± 0.30), followed by Qaiserbagh (3.78 ± 1.20 and 1.09 ± 0.34 , respectively) and Amausi (3.22 ± 1.20 and 0.88 ± 0.39) (Table 2). The maximum prey-order richness (7 prey orders) and Shannon diversity ($H' = 1.68$) were recorded at Khairabad in September, whereas the minimum values occurred at Amausi in June, where only a single prey order was detected (Fig. 4A, C). Seasonally, mean prey-order richness and Shannon diversity were highest during the post-monsoon period (4.33 ± 1.03 and 1.24 ± 0.26 , respectively), followed by the monsoon (3.92 ± 1.68 and 1.04 ± 0.43) and summer (3.67 ± 1.41 and 1.03 ± 0.36). Simpson diversity followed a similar trend, with the highest mean value recorded at Khairabad (0.66 ± 0.10) and during

the post-monsoon season (0.66 ± 0.10). Pielou's evenness was highest at Qaiserbagh (0.86 ± 0.08) and during the post-monsoon season (0.85 ± 0.07), whereas Amausi exhibited the lowest Simpson diversity (0.50 ± 0.21) and Pielou's evenness (0.72 ± 0.29). Seasonal evenness was lowest during the monsoon (0.76 ± 0.26) (Table 2).

Linear mixed-effects models revealed that roosting site had a significant effect on Shannon diversity ($F_{2,16} = 3.67$, $P = 0.049$), whereas season had no significant effect ($F_{2,6} = 0.49$, $P = 0.633$) (Table 3). Tukey-adjusted pairwise comparisons showed that Shannon diversity was significantly higher at Khairabad than at Amausi ($P = 0.040$). Prey-order richness showed a marginal effect of roosting site ($F_{2,16} = 3.51$, $P = 0.054$), whereas season had no significant effect ($F_{2,6} = 0.31$, $P = 0.746$). Although the overall site effect was marginal, Tukey-adjusted pairwise comparisons indicated significantly greater prey-order richness at Khairabad than at Amausi ($P = 0.047$). No other pairwise comparisons were significant (Table 3).

Table 2: Mean ($\pm$ SD) dietary diversity indices of *Scotophilus heathii* across roosting sites and seasons

Group	Category	Prey-order richness	Shannon diversity	Simpson diversity	Pielou's evenness
Roosting site	Amausi	3.22 ± 1.20	0.88 ± 0.39	0.50 ± 0.21	0.72 ± 0.29
	Khairabad	4.78 ± 1.56	1.27 ± 0.30	0.66 ± 0.10	0.84 ± 0.10
	Qaiserbagh	3.78 ± 1.20	1.09 ± 0.34	0.60 ± 0.14	0.86 ± 0.08
Season	Summer	3.67 ± 1.41	1.03 ± 0.36	0.57 ± 0.14	0.83 ± 0.09
	Monsoon	3.92 ± 1.68	1.04 ± 0.43	0.57 ± 0.20	0.76 ± 0.26
	Post-monsoon	4.33 ± 1.03	1.24 ± 0.26	0.66 ± 0.10	0.85 ± 0.07

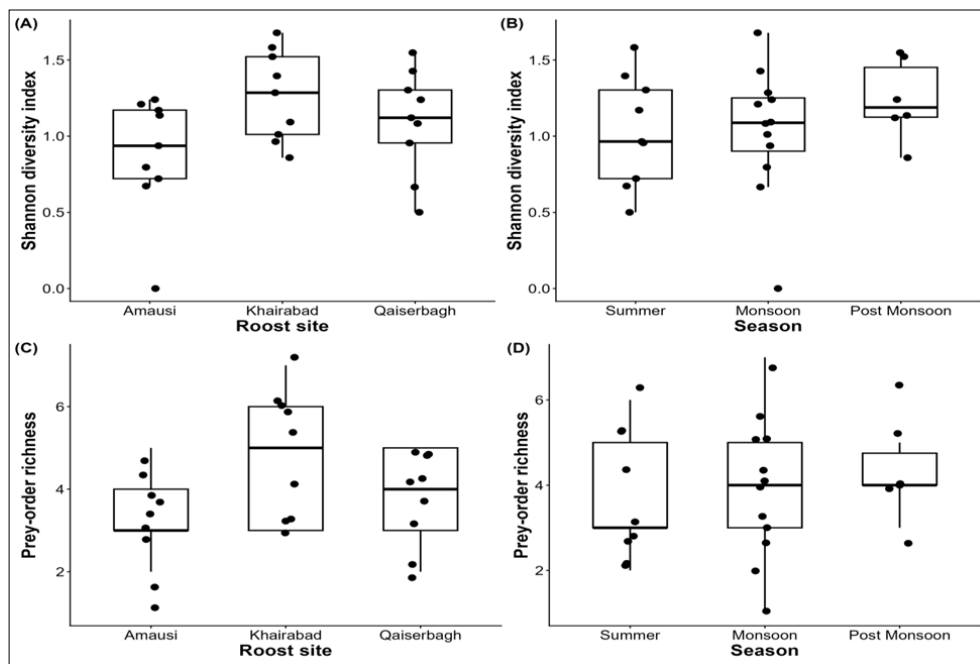


Fig 5: Boxplots show Shannon–Wiener diversity by roosting site (A) and season (B), and prey-order richness at roost site (C) and season (D), Points represent individual site $\times$ month sampling events.

Correspondence analysis of dietary composition

Correspondence analysis (CA) summarized variation in dietary composition among sampling events (Fig. 5). The first correspondence axis (CA1) explained 22.23% of the total inertia, while the second axis (CA2) explained 21.06%, together accounting for 43.29% of the variation in prey composition. The ordination indicated contrasting associations among insect orders. Coleoptera, Zoraptera, and Neuroptera were associated with the negative side of

CA1, whereas Hemiptera, Orthoptera, Dermaptera, and Dictyoptera were associated with the positive side. Along CA2, Plecoptera, Diptera, and Odonata were positioned toward the positive direction, while Lepidoptera and Neuroptera occurred toward the negative direction. Sampling events showed partial overlap among roosting sites, although several samples were separated along both correspondence axes, reflecting variation in the relative representation of prey orders among sampling events.

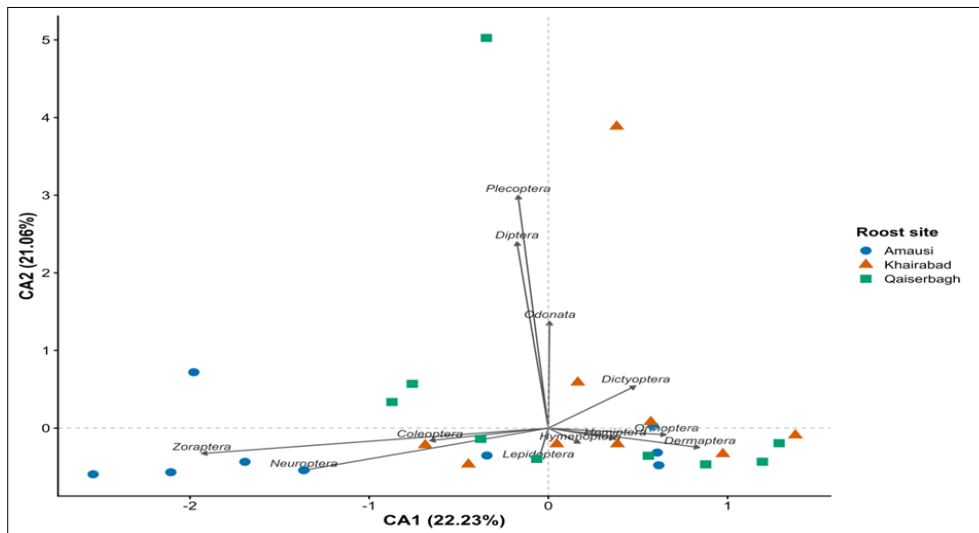


Fig 6: Correspondence analysis (CA) biplot showing relationships between sampling events and insect prey orders. Points represent site $\times$ monthly sampling events, and arrows indicate the direction of increasing association for individual prey orders. The percentages on the axes represent the proportion of total inertia explained by each correspondence axis

Non-metric multidimensional scaling of dietary composition

The two-dimensional NMDS ordination provided an acceptable representation of variation in dietary composition among the site $\times$ month sampling events (stress = 0.144; Figure 6). Sampling events showed considerable overlap among roosting sites and seasons, indicating that prey composition varied continuously rather than forming discrete groups. Nevertheless, group centroids suggested differences in dietary composition, with Amausi positioned toward the negative side of NMDS1, whereas Khairabad and Qaiserbagh were associated with positive NMDS1 values (Figure 6A). Seasonal centroids also indicated a shift in dietary composition from summer and monsoon toward the post-monsoon period along NMDS1 (Figure 6B).

Permutation-based vector fitting identified significant associations between the NMDS configuration and five insect orders following Benjamini-Hochberg correction (Table 3; Figure 6C). Hemiptera exhibited the strongest association with the ordination ($R^2 = 0.676$, adjusted $p = 0.0012$), followed by Coleoptera ($R^2 = 0.581$, adjusted $p = 0.0018$), Orthoptera ($R^2 = 0.427$, adjusted $p = 0.0088$), Plecoptera ($R^2 = 0.327$, adjusted $p = 0.0418$), and Zoraptera ($R^2 = 0.303$, adjusted $p = 0.0418$). Hemiptera and Orthoptera were associated with positive NMDS1 values, whereas Coleoptera and Zoraptera were associated with negative NMDS1 values. Plecoptera was primarily associated with the positive direction of NMDS2. The remaining insect orders were not significantly associated with the ordination after adjustment for multiple comparisons (Table 3).

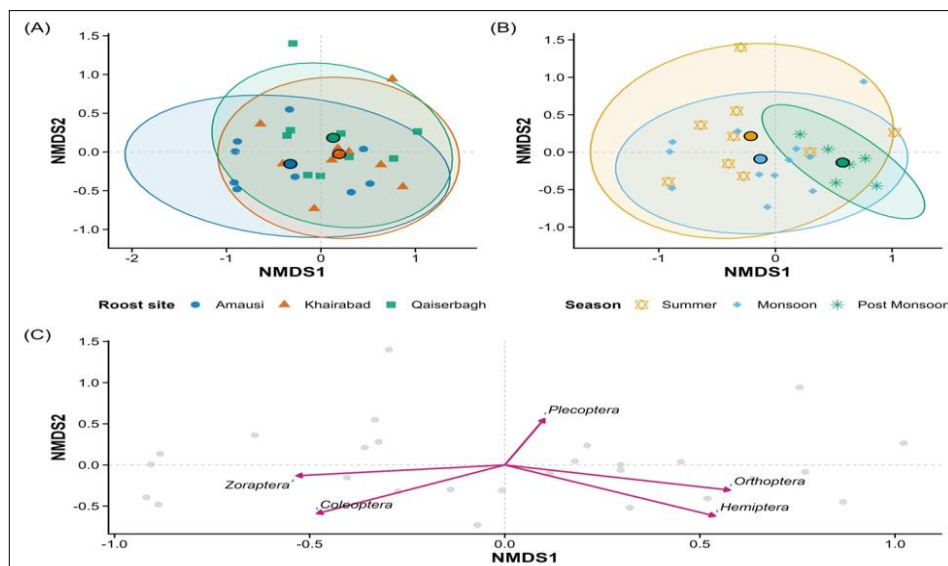


Fig 7: Non-metric multidimensional scaling (NMDS) ordination of dietary composition based on Bray–Curtis dissimilarities among site $\times$ month sampling events (stress = 0.144). (A) Ordination of sampling events grouped by roosting site. (B) Ordination grouped by season. Large black-outlined symbols indicate group centroids and shaded ellipses represent 95% confidence intervals. (C) Fitted vectors of insect prey orders obtained using permutation-based envfit analysis. Only prey orders significantly associated with the ordination after Benjamini–Hochberg correction ($p < 0.05$) are shown; arrow length indicates the strength of association and arrow direction indicates the direction of increasing abundance.

Table 3: Results of linear mixed-effects models (LMMs) testing the effects of roosting site and season on dietary diversity indices of *Scotophilus heathii*. Month was included as a random intercept in all models. Tukey-adjusted pairwise comparisons were shown wherever applicable.

Response	Effect	df	F- statistics	p value	Post hoc comparison
Richness	Site	2,16	3.51	0.054	Khairabad > Amausi ($P = 0.047$)
	Season	2,6	0.31	0.746	-
Shannon	Site	2,16	3.67	0.049	Khairabad > Amausi ($P = 0.040$)
	Season	2,6	0.49	0.633	-
Simpson	Site	2,16	3.25	0.065	-
	Season	2,6	0.53	0.616	-
Evenness	Site	2,22	1.38	0.272	-
	Season	2,22	0.60	0.558	-

Table 4: Results of permutation vector fitting (envfit) showing associations of insect prey orders with the NMDS ordination

Insect order	NMDS1	NMDS2	R ²	Adjusted p value
Hemiptera	0.539	-0.621	0.676	0.0012
Coleoptera	-0.482	-0.591	0.581	0.0018
Orthoptera	0.578	-0.306	0.427	0.0088
Plecoptera	0.102	0.562	0.327	0.0418
Zoraptera	-0.534	-0.131	0.303	0.0418
Diptera	-0.051	0.517	0.270	0.0778
Lepidoptera	0.075	-0.379	0.150	0.2261
Dermaptera	0.284	-0.138	0.100	0.4236
Odonata	0.019	0.240	0.058	0.6457
Neuroptera	-0.081	-0.148	0.029	0.6995
Dictyoptera	0.131	0.017	0.018	0.8851
Hymenoptera	0.015	0.002	<0.001	0.9975

Permanova of dietary composition

Permanova revealed that dietary composition differed significantly among seasons but not among roosting sites (Table 5). Season explained 18.1% of the variation in prey composition and had a significant effect (pseudo- $F = 2.751$, $R^2 = 0.181$, $p = 0.0094$), whereas the effects of roosting site (pseudo- $F = 1.897$, $R^2 = 0.125$, $p = 0.0567$) and the site $\times$ season interaction (pseudo- $F = 0.757$, $R^2 = 0.100$, $p = 0.7530$) were not significant (Table 5). Pairwise *Permanova* indicated significant differences between summer and post-monsoon

(pseudo- $F = 3.986$, $R^2 = 0.235$, adjusted $p = 0.0162$) and between monsoon and post-monsoon (pseudo- $F = 4.446$, $R^2 = 0.217$, adjusted $p = 0.0162$), whereas summer and monsoon did not differ significantly (adjusted $p = 0.7098$). Pairwise comparisons among roosting sites were not significant after adjustment for multiple comparisons (Table 6). PERMDISP showed no significant differences in multivariate dispersion among roosting sites ($F = 0.098$, $p = 0.9112$) or seasons ($F = 2.167$, $p = 0.1382$), indicating that the significant seasonal effect detected by *Permanova* was not attributable to differences in within-group dispersion.

Table 5: Permutational multivariate analysis of variance (*Permanova*) testing the effects of roosting site, season, and their interaction on dietary composition

Source	df	Sum of squares	R ²	Pseudo- F	p value
Site	2	0.637	0.125	1.897	0.0567
Season	2	0.923	0.181	2.751	0.0094
Site $\times$ Season	4	0.508	0.100	0.757	0.7530
Residual	18	3.020	0.594	—	—
Total	26	5.088	1.000	—	—

Note: *Permanova* was performed using Bray–Curtis dissimilarities with 9,999 permutations. R^2 represents the proportion of variation explained by each model term. Significant P-values ($P < 0.05$) are shown in bold.

Table 6: Pairwise *Permanova* comparisons of dietary composition among seasons and roosting sites

Factor	Comparison	R ²	Pseudo- F	Adjusted p value
Season	Summer vs Monsoon	0.033	0.653	0.7098
Season	Summer vs Post-monsoon	0.235	3.986	0.0162
Season	Monsoon vs Post-monsoon	0.217	4.446	0.0162
Site	Amausi vs Khairabad	0.146	2.728	0.1182
Site	Amausi vs Qaiserbagh	0.118	2.144	0.1520
Site	Khairabad vs Qaiserbagh	0.018	0.291	0.9625

Discussion

The present study provides the first comprehensive assessment of the diet of *S. heathii* from northern India, based on morphological analysis of guano. The results demonstrate that *S. heathii* has a wide diet breadth and

insectivorous bat consume at least twelve insect orders, with Coleoptera and Hemiptera together accounting for more than half of the identified prey remains, followed by Orthoptera. Although the species exploited a diverse assemblage of insect prey, the predominance of a few insect

orders indicates that *S. heathii* combines opportunistic foraging with preferential exploitation of abundant and energetically profitable prey. Such dietary flexibility is a characteristic feature of insectivorous bats, whose prey composition is largely determined by local prey availability rather than dietary specialization^[5, 27].

Coleoptera constituted the largest proportion of the diet and remained the dominant prey order during both the summer and monsoon seasons. Beetles are among the most abundant nocturnal insects in agricultural and urban ecosystems and provide a profitable food resource because of their relatively large body size and high energetic value^[30, 31]. Moreover, their heavily sclerotized exoskeleton increases their detectability in guano-based dietary analyses. The predominance of Coleoptera observed in the present study agrees with previous studies on *S. heathii*^[27], *Scotophilus kuhlii*^[17], and *Rhinopoma hardwickii*^[16]. Similar findings have also been reported for several cave-dwelling insectivorous bats in the Philippines, where coleopterans comprised a substantial proportion of prey consumed^[15]. Likewise,^[7] reported Coleoptera as the principal prey of *Pipistrellus mimus*, while^[32] emphasized the importance of coleopterans as a major food resource for insectivorous bats across different ecological regions. Collectively, these studies suggest that coleopterans represent a predictable and reliable prey resource for many insectivorous bats.

Although Coleoptera dominated the overall diet, Hemiptera constituted an equally important dietary component and became the predominant prey during the post-monsoon season. The increased contribution of hemipterans following the monsoon may reflect seasonal increases in their populations associated with enhanced vegetation growth and primary productivity after rainfall^[33]. Many hemipteran species are abundant in cultivated fields and urban green spaces, making them readily available to bats^[31]. The marked increase in Hemiptera observed in the present study therefore indicates that *S. heathii* responds to seasonal fluctuations in prey availability rather than maintaining fixed prey preferences. Similar seasonal increases in hemipteran consumption have been reported for *R. hardwickii*^[16]. Furthermore,^[31] identified Coleoptera and Hemiptera as the principal prey orders of several insectivorous bat species, whereas^[34], using DNA metabarcoding, found Lepidoptera to dominate the diets of four bat species. These contrasting observations highlight considerable interspecific and regional variations in prey use, suggesting that dietary composition reflects differences in prey availability, habitat characteristics, and species-specific foraging behaviour^[23].

Orthoptera represented the third major prey group and increased substantially during the post-monsoon period. Grasshoppers and crickets are relatively large insects that provide high energetic returns and are frequently exploited by aerial insectivorous bats^[7]. Previous investigations of *S. heathii*^[27], *S. kuhlii*^[17], and *R. hardwickii*^[16] similarly identified Orthoptera as an important dietary component, although its relative contribution varied among seasons and habitats. The increased abundance of orthopterans in the diet during the post-monsoon season may be associated with seasonal increase in insect abundance following monsoon, when favorable environmental conditions promote vegetation growth and overall insect productivity^[35]. The remaining prey orders, including Dermaptera, Hymenoptera, Diptera, Zoraptera, Dictyoptera, Plecoptera, Lepidoptera,

Odonata, and Neuroptera, each contributed relatively small proportions to the diet but collectively enlarged the trophic niche of *S. heathii*. Their consistent occurrence indicates opportunistic exploitation of locally available insects encountered during foraging flights rather than selective targeting of specific taxa. Similar broad dietary spectra have been documented in *S. kuhlii*^[17], *Ia io*^[23], and several cave-dwelling insectivorous bats from Southeast Asia^[15], demonstrating that dietary supplementation with less abundant prey taxa is a common characteristic of generalist insectivorous bats. Likewise,^[36] reported that insectivorous bats consumed a wide range of insect orders, including numerous agricultural pest species, reinforcing the ecological importance of dietary breadth in supporting ecosystem services such as natural pest suppression^[34].

The multivariate analyses further supported the observed patterns in dietary composition. *Permanova* demonstrated that season had a significant effect on prey composition, whereas differences among roosting sites were not statistically significant. These findings suggest that temporal variation in insect availability associated with seasonal environmental changes exerts a stronger influence on prey composition than local differences among roosting habitats. Pairwise *Permanova* further showed that prey composition during the post-monsoon season differed significantly from both summer and monsoon, whereas summer and monsoon communities were similar. The absence of significant differences in multivariate dispersion indicates that these seasonal differences reflect genuine shifts in prey composition rather than differences in within-group variability. Although the NMDS ordination showed considerable overlap among sampling events, it also suggested seasonal changes in the relative contribution of major prey groups while maintaining a broadly similar dietary spectrum. Such temporal flexibility in prey use is characteristic of opportunistic aerial insectivorous bats inhabiting heterogeneous landscapes^[9, 21, 23].

Limitations

Despite providing the first comprehensive assessment of the diet of *S. heathii* in northern India, this study has certain limitations. Dietary composition was determined using microscopic examination of guano, a well-established non-invasive method that allows identification of indigestible prey remains but generally provides taxonomic resolution only to higher taxonomic levels. Soft-bodied insects are often digested completely and may therefore be underrepresented, potentially leading to an incomplete assessment of dietary diversity^[7, 10]. Furthermore, the present study did not quantify seasonal insect availability within the surrounding habitats, making it difficult to distinguish between active prey selection and opportunistic feeding based solely on prey abundance.

Conclusion

In conclusion, this study provides the first comprehensive assessment of the spatial and seasonal diet of *Scotophilus heathii* across three roosting sites in northern India. Guano analysis showed that *S. heathii* is a dietary generalist feeding on a wide range of insects, with Coleoptera, Hemiptera, and Orthoptera forming the major components of its diet. Dietary diversity differed among roosting sites, whereas prey composition varied significantly among seasons, indicating that the species adjusts its diet in

response to changing prey availability while maintaining a broad dietary niche. The dominance of several insect orders that include important agricultural pests suggests that *S. heathii* may play a valuable role in the natural regulation of insect populations in urban and peri-urban landscapes. Protecting this species and its roosting habitats could therefore contribute not only to bat conservation but also to ecosystem services such as biological pest control. Future studies combining DNA metabarcoding with seasonal assessments of insect availability across a wider range of habitats will provide a more detailed understanding of the feeding ecology and ecological importance of this species.

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