



Dietary composition of two coexisting bat species, *Myotis ikonnikovi* and *Plecotus ognevi*, in the Mt. Jumbong forests, South Korea

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ARTICLE INFO

Received August 25, 2023

Revised September 26, 2023

Accepted October 2, 2023

Published on October 24, 2023

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Background: Many insectivorous bats have flexible diets, and the difference in prey item consumption among species is one of the key mechanisms that allows for the avoidance of interspecies competition and promotes coexistence within a microhabitat. In Korea, of the 24 bat species that are known to be distributed, eight insectivorous bats use forest areas as both roosting and foraging sites. Here, we aimed to understand the resource partitioning and coexistence strategies between two bat species, *Myotis ikonnikovi* and *Plecotus ognevi*, cohabiting the Mt. Jumbong forests, by comparing the differences in dietary consumption based on habitat utilization.

Results: Upon examining their dietary composition using the DNA meta-barcoding approach, we identified 403 prey items (amplicon sequence variants). A greater prey diversity including Lepidoptera, Diptera, Coleoptera, and Ephemeroptera, was detected from *M. ikonnikovi*, whereas most prey items identified from *P. ognevi* belonged to Lepidoptera. The diversity index of prey items was higher for *M. ikonnikovi* (H' : 5.67, D : 0.995) than that for *P. ognevi* (H' : 4.31, D : 0.985). Pianka's index value was 0.207, indicating little overlap in the dietary composition of these bat species. Our results suggest that *M. ikonnikovi* has a wider diet composition than *P. ognevi*.

Conclusions: Based on the dietary analysis results, our results suggests the possibility of differences in foraging site preferences or microhabitat utilization between two bat species cohabiting the Mt. Jumbong. In addition, these differences may represent one of the important mechanism in reducing interspecific competition and enabling coexistence between the two bat species. We expected that our results will be valuable for understanding resource partitioning and the coexistence of bats inhabiting the Korean forests.

Keywords: dietary comparison, *Myotis ikonnikovi*, *Plecotus ognevi*, resource partitioning

Introduction

Early ecological models based on intra- and inter-specific competition suggested that species responses to the environment must be sufficiently differentiated from multidimensional ecological resources to enable their stable coexistence (Andriollo et al. 2021; Bazzaz and Catovsky 2001; Finke and Snyder 2008). Resource use and partitioning are two of the main factors explaining ecological differences that lead to species coexistence (Finke and Snyder 2008; MacArthur 1984; Schoener 1974).

Bats serve as a fascinating example to explain resource partitioning in ecological communities, as they tend to form communities based on morphological and ecological

similarities (Arrizabalaga-Escudero et al. 2018) and have a flexible diet that varies among different species (Clare et al. 2014; Salinas-Ramos et al. 2015). Several studies have investigated food consumption and resource partitioning in insectivorous bat species (Andreas et al. 2012; Heim et al. 2021; Whitaker 2004). In Central Europe, a study comparing the dietary composition of three foliage-gleaning bat species (*Myotis nattereri*, *M. bechsteinii*, and *Plecotus auritus*) revealed that these three bat species exhibited effective resource partitioning despite important seasonal dietary changes (Andreas et al. 2012). The study also revealed that dietary composition varied more among the guild of forest foliage-gleaning bats than it did between these species and their morphological siblings or evolutionarily re-



lated species. Other studies have compared the prey of two morphologically similar and symbiotic bat species (*Murina ussuriensis* and *Myotis ikonnikovi*), demonstrating their ability to exploit different prey items within diverse microhabitats to avoid competition and promote coexistence.

In Korea, of the 24 bat species that are known to be distributed (Yoon et al. 2016) only 12 have been identified in the Korean forests through trapping and echolocation surveys (Han et al. 2012). Excluding some of the cave-dwelling bats (such as horseshoe bats, long-fingered bats, and greater tube-nosed bats), it is estimated that approximately eight bat species use forest areas as both roosting and foraging sites. These bats inhabiting the Korean forests are classified as insectivorous bats (Han et al. 2012). Two forest-dwelling bat species, *Plecotus ognevi* and *Myotis ikonnikovi*, living in Korea are listed as “Least Concern” on The International Union for Conservation of Nature (IUCN) Red List (GBIF 2022a; IUCN 2018; IUCN 2019). According to phylogenetic studies on the genus *Plecotus*, *P. auritus* is geographically separate from *P. ognevi* in northeastern Asia (IUCN 2018; Kruskop et al. 2012; Spitzenberger et al. 2006). Generally, the home range of forest bats is associated with their weight (body size), and it is known that smaller species have smaller home ranges compared to larger species (Fenton 1997). Previous studies on the habitat characteristics of *M. ikonnikovi* indicated typical characteristics for the *Myotis* genus, which is known to have small habitats (Kim et al. 2014). In addition, a study on the spatial behavior and habitat use of *P. auritus* also reported that it has a small range of space compared to other bats of the *Plecotus* genus (Starik et al. 2021). Based on echolocation type, the two bat species are classified as “narrow space gleaning foragers” or “edge space aerial/trawling foragers” (Fukui et al. 2015; Schnitzler et al. 2003), and similarly to studies in Central Europe, it is expected that they would require resource partitioning strategies for coexistence (Andreas et al. 2012). However, studies on bat ecology have mostly been conducted in Europe or the Americas, whereas such studies are rare in Asia (Heim et al. 2021). Despite the importance of the Korean Peninsula in the biogeography for Northeast Asian bats, ecological research related to bats is relatively limited compared to other mammals (Chung et al. 2015; Fukui et al. 2015). In addition, most of the research conducted in Korea mainly focuses on the distribution, home range, habitat use, and echolocation of bats (Chung et al. 2009; Chung et al. 2010; Kim et al. 2018; Yoon et al. 2016). Research on bat’s foraging is almost non-existent, except for studies on the dietary composition of the serotine bat, *Eptesicus serotinus* (Chung et al. 2015).

In this study, we compared the dietary composition of two forest-dwelling bat species, *M. ikonnikovi* and *P. ognevi*, cohabiting in the Mt. Jumbong forests, South Korea, using the DNA meta-barcoding approach. In addition, we aimed to understand the resource partitioning and coexis-

tence strategies among bat species by comparing the differences in dietary consumption based on habitat utilization.

Materials and Methods

Study area

This study was conducted on Mt. Jumbong (128°25′–128°30′ E, 38°0′–38°5′N) at the southern end of the Seoraksan National Park, South Korea. The area around Mt. Jumbong is one of the long-term ecological research sites in Korea, where research has been conducted since the first stage of the national long-term ecological monitoring project in 2005. Additionally, this area has been designated as a nature reserve and Forest Genetic Resource Reserve by the Korean government. This study was conducted at two different sites (Danmokryeong and Gombaeryeong) near the northern and eastern valleys of Jeombongsan Forest Ecological Management Center. These areas are located at an altitude of 740 m and consist mainly of deciduous broad-leaved forests dominated by oak trees. Previous research on insects revealed the identification of more than 60 species of moths, with belonging to the Noctuidae family (23 species) being the most frequently observed in Mt. Jumbong (Cho 2013). Moths are generally known to be one of the main food sources for forest bats. Access to hikers is strictly limited after 4 p.m., which makes it a suitable area for studying forest bats that are not affected by human activity.

Bat capturing and fecal sampling

Bat capturing was carried out in June and July 2017 at Danmokryeong and Gombaeryeong in Mt. Jumbong area based on the entry and research permission granted by the Korea Forest Service granted permission (Fig. 1). To capture bats, mist nets were installed within a radius of 50 m around the points estimated to be the main moving routes of bats. Two mist nets, 12 m in width and 3.2 m in height, were installed in the forest valleys for each site, covering a total area of 76.8 m². Additionally, three mist nets, 6 m in width and 3.2 m in height, were installed between the canopy and upper levels of low-cover herbaceous plants, covering a total area of 57.6 m². Extra mist nets were installed around the mist net installation site to block the space between trees and shrubs, which promoted bat capture.

The bat capture was conducted for approximately 4 hours after sunset, and the condition of the captured bats was checked every 5 minutes. Each captured bat in the mist net was removed and placed in a cotton bag until release. All the captured bats were identified based on the species and sex and tagged with a metal ring to mark the individual before release.

Fecal samples were collected either directly from the captured bats or from the feces that were collected during

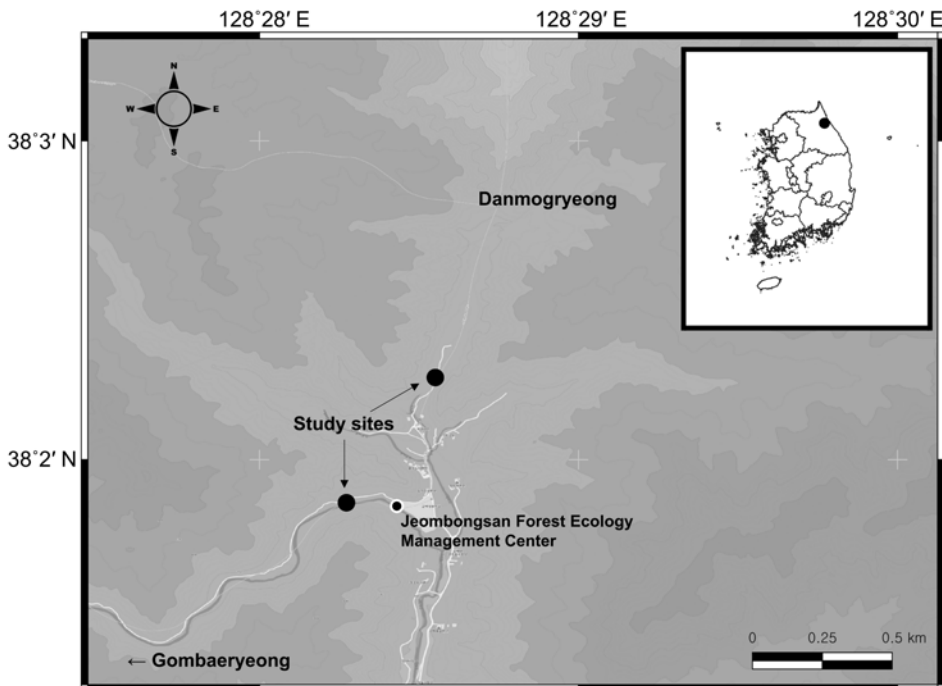


Fig. 1 Location of the study sites at Mt. Jumbong, South Korea.

their capture in the cotton bag. To minimize sample contamination and degradation, each individual feces were immediately sealed in a 2 mL Eppendorf tube containing 100% ethanol and stored at -20°C until transportation to the laboratory. After transportation, the samples were immediately stored in an ultra-low temperature freezer (-80°C) until DNA extraction.

Library construction of prey items and data analyses

DNA extraction was performed on less than 200 mg of feces using a QIAamp DNA Fast DNA Stool Kit (Qiagen, Hilden, Germany) following manufacturer's protocol, after removal of ethanol from the 2 mL Eppendorf tubes. We amplified the cytochrome c oxidase subunit 1 mitochondrial gene (*COI*) of targeted arthropod prey using the primer set ZBJ-ArtF1c: 5'-AGA TAT TGG AAC WTT ATA TTT TAT TTT TGG-3' and ZBJ-ArtR2c: 5'- WAC TAA TCA ATT WCC AAA TCC- 3' (Zeale et al. 2011).

The libraries for dietary analysis were prepared using the fusion primers modified at the 5' end by the addition of individual-specific 7-bp Multiplex IDentifiers (MIDs) and adaptors required for the emulsion polymerase chain reaction (emPCR) and the Ion PGM sequencing. All PCR amplifications were performed in 20 μL volumes using an Intron FastMix/Frenche™ Premix (iNtRON Biotechnology, Seoul, Korea). The reaction mixture contained 8 μL of master mix, 0.25 μM of each primer, and 10 μL template DNA. PCR conditions were as follows: an initial denaturation at 95°C for 5 minutes, 40 cycles of denaturation at 95°C for 30 seconds, annealing at 50°C for 30 seconds, and elongation at 72°C for 30 seconds, and a final extension step at 72°C for 5 minutes. PCR products were checked on 1.5% agarose gels. After the reactions, PCR products were

purified using a MEGAquick-spin™ Total Fragment DNA Purification Kit (iNtRON Biotechnology, Seongnam, Korea). After PCR pooling, libraries were quantified using a High Sensitivity DNA Chip kit on the Agilent 2100 Bioanalyzer (Agilent, Palo Alto, CA, USA). Emulsion PCRs were conducted using the Ion PGM Hi-Q OT2 kit (Life Technologies, Carlsbad, CA, USA) on the Ion OneTouch2 platform, following the manufacturer's instructions. The amplicon libraries were sequenced on an Ion PGM system using an Ion PGM Hi-Q Sequencing kit (Life Technologies) and Ion 316 Chip Kit v2 BC (Ion Torrent, Life Technologies).

Each dataset was pre-processed using Geneious Prime 2022.1. Raw sequences were trimmed based on primer sequences, and filtered when less than 50 bp. Pre-processed datasets were imported into the QIIME2 software platform (version 2022.2.0, <https://qiime2.org>) (Bolyen et al. 2019), and processed based on Catozzi's workflow, with some modifications (Catozzi et al. 2019). Briefly, DADA2 was used as the quality filtering method to denoise and dereplicate single-end sequences, and remove chimeras (Callahan et al. 2016); a truncation length of 157 bases was used. The naïve Bayesian classifier was used for taxonomic classification against the COins database (Magoga et al. 2022). After classifying the sequences, amplicon sequence variants (ASVs) that classified as low taxonomic levels (only Phylum level) were not analyzed further.

The proportion of prey items were calculated as both frequency of occurrence (FOO) and relative read abundance (RRA). Percent of occurrence (POO) is the %FOO rescaled so that the sum across all detected dietary items is 100%. All mathematical expressions are as follows (Deagle et al. 2019):

$$\%FOO_i = \frac{1}{S} \sum_{k=1}^S I_{i,k} \times 100\%$$

$$RRA_i = \frac{1}{S} \sum_{k=1}^S \frac{n_{i,k}}{\sum_{i=1}^T n_{i,k}} \times 100\%$$

where T is the number of prey items (taxa), S is the number of samples, I is an indicator function such that $I_{i,k} = 1$ if prey item i is present in sample k , and 0 if not, and $n_{i,k}$ is the number of sequences of prey item i in sample k .

Species diversity was defined as the number of ASVs identified in each sample. The Shannon–Wiener and Simpson’s diversity indices were respectively calculated as follows, based on the POO of prey items (Deagle et al. 2019):

$$H' = - \sum (p_i) \times \log_e p_i$$

$$D = 1 - \sum p_i^2$$

where p_i is the proportion of prey item i in the diet. Wilcoxon’s rank sum exact test was used to compare the group means statistically.

Pianka index of niche overlap index was calculated using “spaa” package (Zhang 2016) from the R software (version 4.1.2). This index represented the degree of dietary overlap between the two bat species, as follows:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where p_{ij} and p_{ik} is the proportion of prey item i in the diet of species j and k .

An ordination was performed using Bray–Curtis dissimilarity-based principal coordinate analysis (PCoA) using the “vegan” package from the R software (version 4.1.2) based on each fecal sample’s RRA of prey items at the genus level (Oksanen et al. 2022). All statistical analyses were performed using the R software (version 4.1.2).

Results

A total of 1,183,421 raw sequences were obtained from 27 bat fecal samples, and a final 406,304 reads passed trimming

and filtering. Of those, 328,785 reads (mean = 15,656 ± 17,433) were derived from 21 individuals of *M. ikonnikovi*, while 77,519 reads (mean = 12,920 ± 9,044) from six individuals of *P. ognevi*.

In total, 403 prey items (ASVs) were identified from the two bat species (Table 1, Tables S1, S2). Of these, 346 ASVs were detected in *M. ikonnikovi* and 79 in *P. ognevi* (Table 1). The dietary composition of the two bat species differed at the order level. Relative read abundance demonstrated that Lepidoptera was mostly detected from *P. ognevi*, whereas various prey items such as Lepidoptera, Diptera, Coleoptera, and Ephemeroptera were detected from *M. ikonnikovi* (Fig. 2A). In the case of *M. ikonnikovi*, there was a remarkable variation in the diet composition among individuals. However, for *P. ognevi*, Lepidoptera was the most detected prey item in all individuals, showing a similar pattern among individuals. The FOO for prey items also showed a remarkable difference between two bat species (Fig. 2B). *P. ognevi* showed a high frequency of feeding on the Noctuidae and Geometridae families of the Lepidoptera, whereas *M. ikonnikovi* exhibited a feeding frequency of over 50% on a variety of prey items belonging to families, such as Noctuidae in Lepidoptera, Tipulidae in Diptera, and Hemerobiidae in Neuroptera.

The prey item containing 6 orders (54.5%) and 27 families (25.9%) were overlapped between the two bat species (Fig. 3A). Two families, Cossidae and Drepanidae in Lepidoptera, and 16 genera were only detected from *P. ognevi*, while the diet of *M. ikonnikovi* had unique prey items ranging from 5 orders, 58 families, and 118 genera, making up 45.5%–73.7% of the total (Fig. 3A). The detected prey items in *M. ikonnikovi* showed higher diversity than those in *P. ognevi*. However, Pianka’s index value of 0.207 indicates a relatively low dietary overlap between the two bat species.

The comparison of prey diversity between the two bat species indicates that *M. ikonnikovi* utilized a wider range of prey items compared to *P. ognevi* (Fig. 3B). The species diversity index indicated that more diverse prey items were detected in *M. ikonnikovi* (H' : 5.67, D : 0.995) than in *P. ognevi* (H' : 4.31, D : 0.985). Although *M. ikonnikovi* exhibited higher median values for both diversity indices compared to *P. ognevi*, there was no statistically significant difference in diversity indices between the two bat species (Wilcoxon rank sum exact test, $p = 0.711$). Similarly, the

Table 1 Total number of prey items detected in the feces of the bats, *Myotis ikonnikovi* and *Plecotus ognevi*, at different taxonomic levels

Species	No. of individuals	Taxonomic level			
		Order	Family	Genus	ASVs
<i>Myotis ikonnikovi</i>	21	11	79	145	346
<i>Plecotus ognevi</i>	6	6	23	43	79
Total	27	11	81	161	403

ASV: amplicon sequence variants.

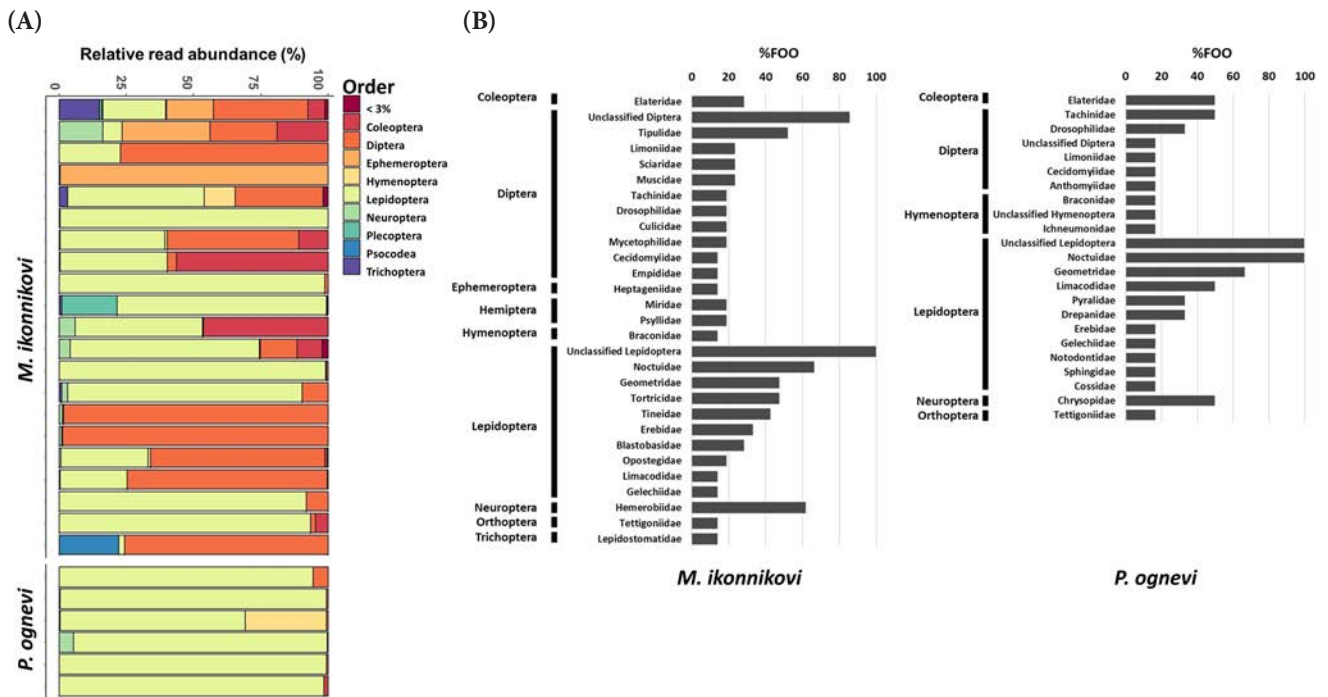


Fig. 2 Prey items detected in the feces of the bat species, *Myotis ikonnikovi* and *Plecotus ognevi*, using the DNA meta-barcoding approach. (A) Relative read abundance of prey items consumed by these two bat species from each fecal sample at the order level. Prey items with an abundance of less than 3% were merged and represented as “<3%”. (B) Frequency of occurrence for prey items consumed by two bats at the family level. Only prey items detected at a frequency of more than 10% are indicated in the graph. %FOO: frequency of occurrence.

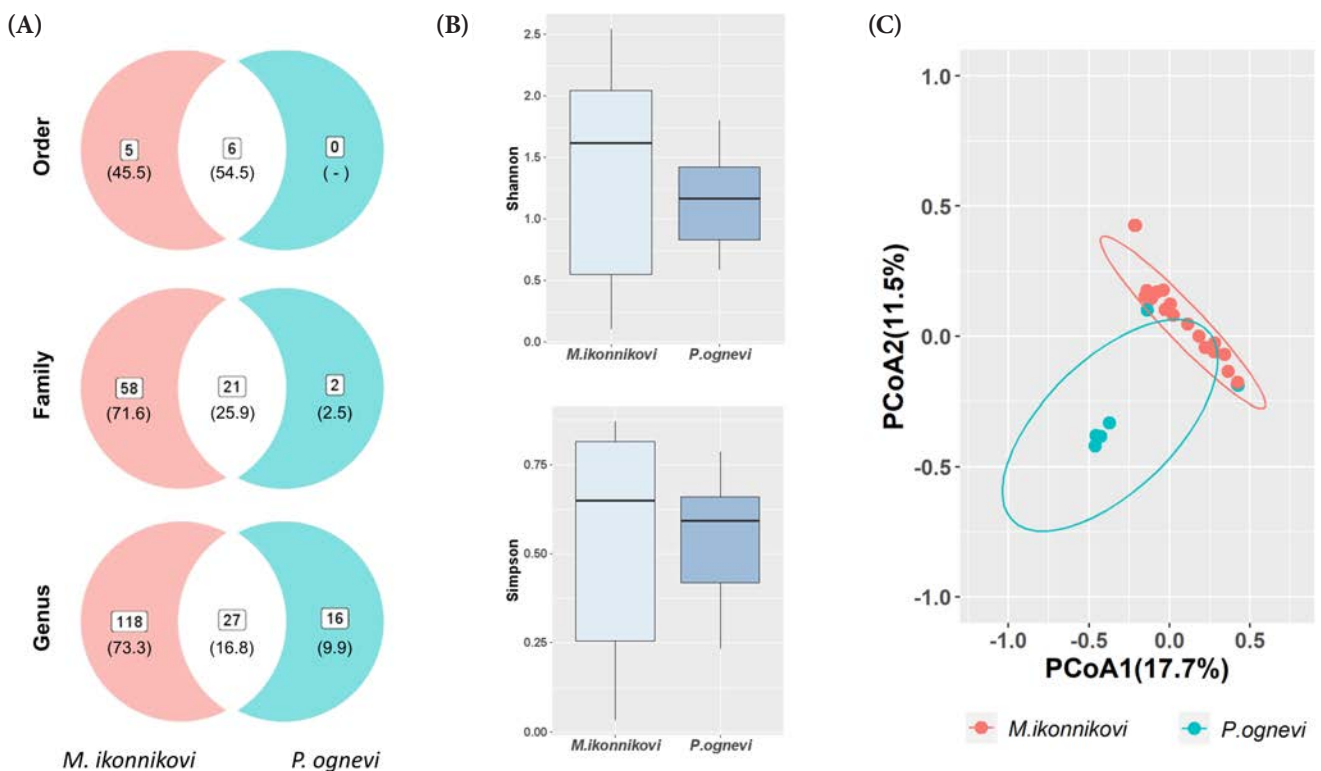


Fig. 3 Comparison of the differences in prey items of the two bat species. (A) Venn diagram showing the dietary overlap at different taxonomic levels. Numbers in box indicate the number of prey items detected from bat species and numbers in parentheses indicate the relative proportion of detected prey items. (B) Boxplots showing the differences in varieties of the prey items between *Myotis ikonnikovi* and *Plecotus ognevi*. (C) Principal coordinate analysis plots by Bray–Curtis dissimilarity metrics for prey items. First two axes explained 17.7% and 11.5% of total variance, respectively. PCoA: principal coordinate analysis.

PCoA based on the Bray–Curtis dissimilarity matrix also revealed a tendency for the samples to cluster according to their respective bat species (Fig. 3C). However, the first two axes of the PCoA only explained 17.7% and 11.5% of the total variance, respectively.

Discussion

The dietary information of two bat species can provide insights into understanding the mechanisms of stable coexistence through resource partitioning. Resource partitioning is described as one of the mechanisms that prevents competition between species in an ecosystem upon resource limitation (Gómez-Llano et al. 2021; Matthews et al. 2010). Therefore, each species also can adopt a strategy to reduce inter-specific competition by partitioning habitats through spatial or temporal segregation (Matthews et al. 2010). From this perspective, inter-specific spatial partitioning can result in different feeding patterns based on the preferences for selected feeding sites. Our results showed that there were differences in the dietary composition depending on the species, through the comparison of two bat species cohabiting the Korean forests. *M. ikonnikovi* ate a wide range of prey items, whereas *P. ognevi* primarily consumed Lepidoptera and exhibited minimal individual variation in its diet. The Pianka index value of 0.207 indicates that the diet compositions of the two bat species did not strongly overlap and suggests differences in prey resource use spatially.

The diet consumption of insectivorous bats is primarily determined by their morphological and flight characteristics, echolocation, and foraging strategies (Fenton 1982; Norberg and Rayner 1987). Previously, 14 bats species inhabiting Korea were categorized into three types based on their echolocation call structure (Fukui et al. 2015). Based on that categorization, the two species (*M. ikonnikovi* and *P. ognevi*) are placed into the same foraging group or guilds. Although clear differences in the pulse structure of echolocation were detected between all *Myotis* species and *P. ognevi*, two bats (*M. ikonnikovi* and *P. ognevi*) in this study were classified as frequency-modulated (FM) type species and were classified as either “narrow space gleaning foragers” or “edge space aerial/trawling foragers” (Fukui et al. 2015; Schnitzler et al. 2003). In addition, these two bat species may exhibit similar flight characteristics based on their morphological features. *Plecotus* and most *Myotis* species in Vespertilionidae exhibit an average wingspan and a low aspect ratio (Norberg and Rayner 1987). Due to their long and narrow wing shape, *P. ognevi* may exhibit similar slow-flight characteristics like *M. ikonnikovi* and employ foraging strategies such as aerial hawking or gleaning (Bininda-Emonds and Russell 1994; GBIF 2022a, 2022b; Norberg and Rayner 1987). Therefore, we considered that

the differences in morphological characteristics or echolocation may not be the major factors explaining the dietary differences between the two bat species.

The difference in prey diversity may be interpreted as differences in foraging site preference or differences in space utilization within microhabitats among species. The previous study explains that sympatric living species within the same guild should exhibit differences in at least one niche dimension to avoid competition due to limited food resources, and spatial separation of foraging areas is described as one of the mechanisms to achieve the niche differentiation (Denzinger and Schnitzler 2013). Our results showed that *M. ikonnikovi* consumed a wider range of food sources compared to *P. ognevi*. The bat species, *M. ikonnikovi*, consumed a higher proportion of prey items belonging to Lepidoptera, Diptera, and Ephemeroptera, whereas *P. ognevi* diet was dominated by Lepidoptera. *M. ikonnikovi* exhibited a diverse range of consumed prey items per individual, albeit with a relatively small sample size, *P. ognevi* showed a similarity in the composition of prey items consumed by individuals. In addition, at the genus level, 9.9% of the detected overall prey items were exclusively found in *P. ognevi*. A previous study on the dietary analysis of *M. ikonnikovi* conducted in Japan revealed that *M. ikonnikovi* exhibited higher prey diversity than other bat species (Heim et al. 2021). Although the reproductive status of prey items was not observed in this study, considering the similar temperature conditions (21.1°C–29°C in July at study area) in Japan and Korea, the majority of prey items consumed by both bat species (Diptera, Ephemeroptera Noctuidae, Geometridae, and Limacodidae) are likely to be predominantly adults. In addition, some moths with known habitat characteristics belonging to the Noctuidae family (*Stenoloba* sp.) are known to mainly inhabit deciduous forests, which is consistent with the main forest type in the study area (NIBR 2023). Our results are consistent with the explanation of previous studies, which indicate that long-eared bat species have narrow dietary preferences, primarily focusing on moths and mosquitoes (Anderson and Racey 1991; Entwistle et al. 1996). Taken together, these findings suggest that both bat species probably fed on adult prey via aerial-hawking mode and that *M. ikonnikovi* uses more diverse foraging sites, including around valleys, within the same micro-environment condition compared to *P. ognevi*. Therefore, the differences in spatial selection of foraging areas between the two bat species may be interpreted as one of the important factors in explaining the variation in their dietary consumption and avoiding resource competition.

Conclusions

There are various bat species inhabiting Korea; however,

their dietary preferences based on the habitat characteristics are not well understood. This study suggests the possibility of differences in foraging site preferences or microhabitat utilization between two bat species inhabiting the Mt. Jumbong, based on their dietary analysis. Although our study was limited to a specific time period and dietary competition among bat species may vary regionally and seasonally considering insectivorous bats' relatively flexible diet, our findings contributed to understanding the mechanisms associated with resource partitioning and coexistence among insectivorous bats in Korea. In addition, our results may provide further information on the dietary consumption and resource partitioning of the two bat species inhabiting the forests of Northeast Asia.

Supplementary Information

Supplementary information accompanies this paper at <https://doi.org/10.5141/jee.23.049>.

Table S1 Percentage of occurrence data for two bats. **Table S2** Relative of abundance data for each samples.

Abbreviations

ASV: Amplicon sequence variant

FOO: Frequency of occurrence

RRA: Relative read abundance

POO: Percent of occurrence

PCoA: Principal coordinate analysis

Acknowledgements

Not applicable.

Authors' contributions

SJ and SSK developed the concept of this study. SJ and IA analyzed and interpreted data regarding dietary composition of two bats. All authors participated in the investigation. SJ was a major contributor in writing, review and editing the manuscript. All authors read and approved the final manuscript.

Funding

This research was funded by research projects of the National Institute of Ecology, Republic of Korea, grant numbers NIE-2017-02 and NIE-2023-38.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

The study was conducted according to the Wildlife Protection and Management Act of the Republic of Korea and the Institutional Research Guidelines of the National Institute of Ecology (RPMT-245, 17 Feb. 2017). All academic survey permission was approved by the

Inje National Forest Management Office (No. 2678, 19 April, 2017).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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