

Wing Morphology of Japanese Bats: Predicting Ecological Features for Data-insufficient Species

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Received 19 August 2023 / Accepted 26 June 2024 / Published 19 December 2024
Communicated by Chi-Chien Kuo

Wing morphology, one of the most important morphological traits in bats, is closely related to their foraging habitat and strategies and has been explored as a pivotal trait for ecological and conservation studies. However, studies on wing morphology, as well as the ecology of Japanese bats, are largely lacking. In this study, we aimed to enrich the wing morphology data of Japanese bats. The wing variables, including forearm length, aspect ratio, relative wing loading, and wing tip shape index, were assessed using museum and private specimens of 34 Japanese bat species. Hierarchical clustering of the wing variables classified the bats into nine clusters to predict their foraging ecology, including the species for which ecological knowledge was lacking. Based on the ecological knowledge of Japanese bats, the aspect ratio of bats belonging to the open-space foraging guild was significantly higher than that of those belonging to other guilds. In contrast, the wing tip shape index of bats belonging to the narrow-space foraging guild was significantly higher than those belonging to the other guilds. In conclusion, our study sheds light on the complex interplay between wing morphology and foraging ecology in Japanese bats, offering insights for future research and conservation efforts.

Key words: Wing morphology, Chiroptera, Morphological trait, Specimens, Japan

BACKGROUND

In ecology, a trait is defined as “a well-defined, measurable property of organisms, usually measured at the individual level and used for comparison across species” (McGill et al. 2006; Violle et al. 2007). Morphological traits are strongly linked to life history in animals and provide crucial insights into understanding fundamental ecological processes such as macroevolution (Zamudio et al. 2016) and community assembly (Ricklefs 2012). They also play a key role in evaluating extinction risk (Pacifi et al. 2015) and provide valuable information for animal conservation, as adaptation to various environments or natural selection drives the patterns observed in these traits (Castillo-

Figuerola and Pérez-Torres 2021; Farneda et al. 2018; García-Llamas et al. 2019).

Chiroptera, the order of bats, is the second-most diverse order of mammals (Mammal Diversity Database 2023; Burgin et al. 2018). Bats are unique among mammals for their powered flights. The morphological traits of bat wings are closely related to their foraging habitats and strategies (Aldridge and Rautenbach 1987; Norberg and Rayner 1987). For example, bats that forage in open spaces tend to have long and narrow wings with high wing loading (WL; ratio of body mass to wing area), whereas those that forage in dense vegetation tend to have short and broad wings with low WL (Aldridge and Rautenbach 1987; Rhodes 2002; Stockwell 2001). Norberg and Rayner (1987), in a seminal study on

wing morphology and ecology of bats, elucidated the relationship between lifestyle and wing variables, especially WL, aspect ratio (AR), and wing tip shape index. The authors highlighted the relationship between each variable and flight performance; for instance, high WL contributes to a high flight speed, and a high wing tip shape index contributes to good maneuverability. In addition, these variables are not only related to flight space (e.g., cluttered space vs. open space) selection on a fine scale, but are also related to other ecological features, such as flight altitude (Roemer et al. 2019), distribution range (Luo et al. 2019), and climatic niche (Conenna et al. 2021).

These variables have also been used to infer the ecological relationships between traits and the focal environment, aiding in the conservation of bats. Jung and Threlfall (2018) reviewed the urban tolerance of bats and revealed a correlation between tolerance and increased AR. They suggested that urbanization caused global non-random selection of bats. Conenna et al. (2021), studying the relationship between wing morphology and aridity, showed that bats with enhanced AR, WL, and forearm length inhabit arid zones. The study suggested that high mobility helps bats track patchy and temporary resources in arid conditions, indicating the involvement of an environmental filter. Collectively, these studies show that data on wing morphology are crucial for the evaluation of the effects of climatic change and human activity on bats and to make sound conservation decisions in the Anthropocene.

Data on wing morphological variables have been accumulated worldwide (Webb et al. 1998; Rhodes 2002; Marinello and Bernard 2014; Castillo-Figueroa 2020). For example, Marinello and Bernard (2014) measured the ARs and relative wing loadings of 51 Amazonian bat species. Castillo-Figueroa (2020) analyzed wing structures, which included metacarpals and phalanges, in 97 neotropical bat species. Crane et al. (2022) reviewed global wing morphology data, assessed the geographic biases of the wing morphology databases, and indicated a relatively low coverage of wing morphology data in Palearctic Asia, Australasia, and tropical Africa.

In Palearctic Asia, the Japanese archipelago is a biodiversity hotspot (Marchese 2015), with 37 bat species recorded, excluding two extinct species (Ohdachi et al. 2015; Funakoshi et al. 2022; Kobayashi et al. 2022). Preble et al. (2021), in a systematic review of research on Japanese bats, showed that endemic and threatened species were relatively less studied compared to non-endemic and non-threatened species, with 19 species being investigated in no or only one ecological study by 2020. Moreover, data on wing morphology are largely lacking in Japan, with only a

few studies reporting the wing variables such as AR and WL (e.g., Yokoyama et al. 1975), and their use in inferring the relationship between the morphology and ecology of bats, such as forest utilization (Fukui et al. 2011) and diet (Fukui et al. 2009). However, these studies reported only the mean values of the variables. Furthermore, approximately two-thirds of all Japanese bat species lack reported data. Therefore, enriching the wing morphology data of Japanese bats is essential to better understand their ecology and develop appropriate knowledge-based strategies for their conservation.

This study aimed to elucidate the wing morphology of Japanese bat species. Firstly, the ecology of species for which information is lacking was predicted to fill the knowledge gap between well-studied and less-studied bat species based on hierarchical clustering. Secondly, to reveal the relationship between wing morphology and the ecology of Japanese bats, we compared each wing variable among guilds in the species with ecological knowledge.

MATERIALS AND METHODS

Target bat species

Thirty-seven species have been identified in the Japanese archipelago (Ohdachi et al. 2015; Funakoshi et al. 2022; Kobayashi et al. 2022). Most bats were insectivorous, except for two *Pteropus* species. In the present study, the wing morphology of 34 species was assessed, excluding *Murina tenebrosa* and *Taphozous melanopogon*, with only one individual each reported in the Japanese archipelago, and *Hypsugo pulveratus*, a recently reported species (Funakoshi et al. 2022), for which we could not obtain the specimens. Furthermore, a specimen from the Korean Peninsula for *Myotis rufoniger* was evaluated due to the lack of appropriate specimens from Japan. The studied species and their foraging guilds based on previous ecological studies in Japan are listed in tables 1 and S1. A portion of the data obtained in this study were used in Maki et al. (2024). Foraging guilds were defined following Schnitzler et al. (2003) as “open,” “edge,” and “narrow” foraging spaces, and the guilds of species lacking quantitative research on the foraging environment were categorized as “unknown”. Scientific names were based on Ohdachi et al. (2015) and Simmons and Cirranello (2023), except for *Rhinolophus nippon*, *Barbastella pacifica*, *Myotis longicaudatus*, and *Myotis sibiricus*, which have been taxonomically revised in recent years (Kruskop et al. 2012 2019; Ruedi et al. 2015; Ikeda et al. 2020).

Photographing specimens

All wing morphological data were obtained from the dried skin specimens stored at the National Museum of Nature and Science, Tokyo and private collections from Dr. Kishio Maeda, Mr. Mitsuru Mukohyama and Dr. Dai Fukui. Most of the specimens were prepared by Dr. Kishio Maeda, Mr. Mitsuru Mukohyama, Dr. Dai Fukui, or Dr. Mizuko Yoshiyuki. To avoid misidentification of the species during specimen preparation, the authors re-identified each specimen using the identification keys reported by Yoshiyuki (1989) and Maeda (2008). The specimens meeting the following criteria were included in this study: 1) adult individuals based on the described age on the label and the degree of ossification of metacarpal-phalangeal joints (the described age on the label and the degree of ossification were consistent in all specimens), 2) clear documentation of body mass (M) of specimens at the time of collection and 3) neatly and completely extended specimen with tail membrane and either left or right wing. Additionally, wings that were fully extended but stretched in an unnatural manner (*e.g.*, the forearm and upper arm were overstretched to the point of being straight) were not photographed. Before measuring wing morphology, the skin specimens of all selected bat specimens were photographed on white paper next to a scale using a digital camera (Optio 330, Asahi Optical

Co., Ltd., Tokyo, and E-520, OLYMPUS IMAGING Corp., Tokyo) in the vertical upward direction.

Measurement of wing morphology

The following variables were measured from the photographs of the specimens: forearm length, half of the wingspan, half of the tail membrane area, half of the body area without the head, length and area of the arm-wing (l_{aw} and S_{aw}), and length and area of the hand-wing (l_{hw} and S_{hw}) (Fig. 1). All measurements were performed using the image processing and analysis software ImageJ ver. 1.44 (<https://imagej.nih.gov/ij/>). The halves of the tail membrane area, body area, arm-wing area, and hand-wing area were summed to obtain half of the wing area. Halves of the wingspan and wing area were doubled to obtain the total wingspan (B) and wing area (S). The tip length ratio ($T_1 = l_{hw} / l_{aw}$) and tip area ratio ($T_s = S_{hw} / S_{aw}$) were calculated following the method described by Norberg and Rayner (1987). The AR ($= B^2/S$), WL ($= 9.81M/S$) and wing tip shape index ($I = T_s/(T_1 - T_s)$) were calculated following Aldridge and Rautenbach (1987). Additionally, the relative wing loading (RWL), to measure the WL corrected for body mass, was calculated using the following formula: $RWL = WL/M^{1/3}$.

All whole measured specimens were dried skin specimens, which might have shrunk during

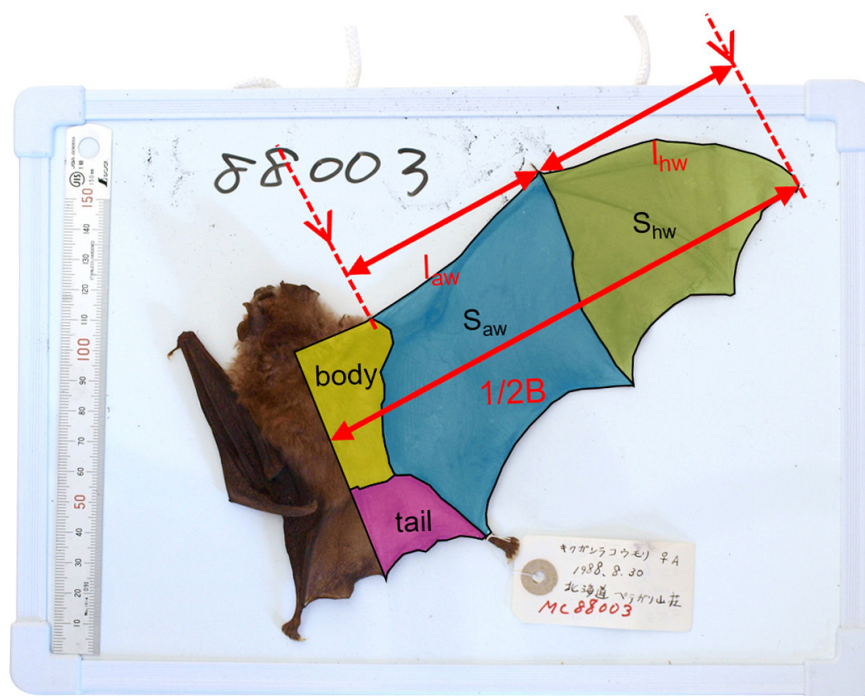


Fig. 1. Measured wing variables from bat specimens. Half of the wingspan ($1/2 B$), half of the tail membrane area (tail), half of the body area (body) without the head, length and area of the arm-wing (l_{aw} and S_{aw}), and length and area of the hand-wing (l_{hw} and S_{hw}) are shown.

preservation. This process may be responsible for the differences in variables between living individuals and specimens. However, the relative shrinkage of morphological characters was reported to be consistent across species (Brokaw and Smotherman 2020). Therefore, we speculated that the selected specimens could be used to compare the wing variables among species.

Statistical analysis

In this study, the wing morphology variables of insectivorous bats were analyzed, excluding those of two flying foxes. The analyses were conducted using the mean values of forearm length, AR, RWL, and wing tip shape index for each species. Hierarchical clustering (UPGMA) was conducted based on the Euclidean distance of the scaled wing morphology variables to predict the foraging ecology of each species and group guild. The cutoff of each branch representing the guild is difficult to determine using only objective methods (Cardoso et al. 2011). Therefore, we established rules to guide the clustering of guilds. Firstly, the clusters were based on guilds, and the cutoff points were set at the split points between the groups of guilds. Species without ecological knowledge were assigned to the closest cluster. If clusters included only species without ecological knowledge from multiple guilds at equal distances, the cluster was labeled as “Unknown.” If clusters included two or more guilds, the guilds of clusters were assigned to the guild to which more species belonged.

To test the differences in each variable among guilds based on species with ecological knowledge, we conducted a one-way analysis of variance (ANOVA) with Tukey post-hoc tests. Before the test, the frequency distribution of each wing variable in each guild was examined for normal distribution using the Shapiro-Wilk test. A significant difference from normal distribution was observed on the wing tip shape index of edge guild ($W = 0.746$, p -value = 0.027); therefore, the wing tip shape index was natural-log-transformed for ANOVA. Equality of variances was tested for each variable among guilds using Levene’s test, and no significant differences were observed in this study. Furthermore, principal component analysis (PCA) was conducted to examine the relative contribution of each wing variable to differences among guilds based on scaled wing variables and principal components. All statistical analyses were performed using R version 4.0.0 (R Core Team 2020) with the “car” package (Fox and Weisberg 2019).

RESULTS

The wing morphology of 34 species was recorded, with sample sizes ranging from 1 to 79 (Table 1, Table S2), totaling 813 samples. AR, RWL, and wing tip shape index ranged from 5.79 (*Myotis rufoniger*) to 11.66 (*Tadarida latouchei*), 30.53 (*Hipposideros turpis*) to 63.76 (*T. latouchei*), and 1.05 (*Miniopterus fuliginosus*) to 3.78 (*Myotis yanbarensis*) in insectivorous bats, respectively (Table 1).

Hierarchical clustering categorized the insectivorous bats into nine clusters. Each cluster was assigned a unique ID (Fig. 2). Cluster 1 was separated from the others at the first node and comprised *Tadarida* species lacking ecological knowledge about their foraging habitats in previous studies. Thus, it was categorized as “Unknown” (Fig. 2). Cluster 2 also separated from the others, including *Hypsugo alaschanicus*, *Vespertilio sinensis*, and *Nyctalus* species belonging to the open-space foraging guild. Cluster 3 comprised *Hipposideros turpis* and *R. nippon* in the narrow-space foraging guild. Cluster 4 included *Miniopterus* bats and *V. murinus* with open-space foraging guild. Cluster 5 included only *Myotis rufoniger* because the closest clusters were split into two guilds: edge and narrow, and the species was clustered by itself and categorized as “Unknown.” Cluster 6 consisted of *Plecotus sacrimontis* and three *Rhinolophus* species with narrow-space foraging guild. Cluster 7 comprised *B. pacifica*, *Eptesicus japonensis*, *Myotis longicaudatus* with edge-space foraging guild. Cluster 8 consisted of four *Myotis* species, *E. nilssonii*, and *Pipistrellus* species with edge-space foraging guild. Cluster 9 comprised three *Myotis* species and *Murina* species. *Myotis* species were positioned in various branches of the functional dendrogram with edge and narrow-space foraging guild.

ANOVA revealed that AR and wing tip shape index were significantly different among the guilds based on ecological knowledge about foraging habitats (AR: $F_{2,13} = 7.553$, p -value = 0.007; Wing tip shape index: $F_{2,13} = 9.378$, p -value = 0.003). Open-space foraging guild species had a significantly higher AR than the other species (Open-Edge: p -value = 0.039; Open-Narrow: p -value = 0.006; Table 2; Fig. 3). On the other hand, the bats belonging to the narrow-space foraging guild had a significantly higher wing tip shape index than the other guilds (Narrow-Edge: p -value = 0.015; Narrow-Open: p -value = 0.004; Table 2; Fig. 3).

In the PCA, PC1 and PC2 explained 52.9% and 22.56% of the variance in wing morphology, respectively (Fig. 4). PC1 was associated with forearm length, RWL, and AR, whereas PC2 was related to the wing tip shape index. Species belonging to the open-space foraging guild were distributed in relatively

larger PC1 values than other guilds within the morphofunctional space, whereas species belonging to the narrow-space foraging guild were distributed in relatively smaller PC2 values than the others (Fig. 4).

DISCUSSION

Our study provides comprehensive information on the wing morphology of most Japanese bat species. Our prediction of the foraging guild using hierarchical clustering was supported by statistical tests of wing variables among the guilds aligning with previous studies (Aldridge and Rautenbach 1987; Norberg and

Rayner 1987). Our results show that species in the open-space guild had wings with an elevated AR (Table 2, Fig. 3), which enables them to conserve energy during flight (Norberg and Rayner 1987). However, they did not exhibit specific trends in other variables compared to other guilds, even though previous studies have reported that open-space guild species tend to have high WL (Aldridge and Rautenbach 1987; Marinello and Bernard 2014). This discrepancy could be due to a lack of preliminary information about foraging habitats of some open-space foraging bats, such as *Tadarida* species, which are known to have high WL (Altringham 2011). Japanese bat species belonging to the narrow environmental guild have a relatively higher wing tip

Table 1. Wing morphology variables of the examined bat species including shortened name, sampling effort (n), aspect ratio, forearm length, relative wing loading, wing tip shape index, diet, and guild based on previous studies. The represented variables are mean values $\pm$ standard deviation

Family	Name	Shortened name	n	Forearm length (mm)	Aspect ratio	Relative wing loading	Wing tip shape index	Diet	Guild
Pteropodidae	<i>Pteropus dasymallus</i>	Pt_das	3	128.1 $\pm$ 4.55	6.26 $\pm$ 1.52	37.2 $\pm$ 7.29	0.61 $\pm$ 0.09	Frugivore	-
Pteropodidae	<i>Pteropus pselaphon</i>	Pt_pse	1	138	6.92	36.33	0.73	Frugivore	-
Rhinolophidae	<i>Rhinolophus nippon</i>	Rh_nip	48	60.34 $\pm$ 1.61	6.34 $\pm$ 0.77	37.22 $\pm$ 4.95	2.26 $\pm$ 0.89	Insectivore	Narrow
Rhinolophidae	<i>Rhinolophus cornutus</i>	Rh_cor	65	41.56 $\pm$ 1.48	6.47 $\pm$ 0.58	36.22 $\pm$ 2.74	1.61 $\pm$ 0.62	Insectivore	Unknown
Rhinolophidae	<i>Rhinolophus pumilus</i>	Rh_pum	9	41.11 $\pm$ 1.02	6.41 $\pm$ 0.59	36.94 $\pm$ 3.79	1.62 $\pm$ 0.16	Insectivore	Narrow
Rhinolophidae	<i>Rhinolophus perditus</i>	Rh_per	9	41.69 $\pm$ 0.7	6.35 $\pm$ 0.39	36.94 $\pm$ 4.55	1.77 $\pm$ 0.37	Insectivore	Unknown
Hipposideridae	<i>Hipposideros turpis</i>	Hi_tur	2	61.35 $\pm$ 2.33	6.8 $\pm$ 0.44	30.53 $\pm$ 0.27	1.97 $\pm$ 0.31	Insectivore	Narrow
Vespertilionidae	<i>Eptesicus japonensis</i>	Ep_jap	2	40.25 $\pm$ 0.35	6.65 $\pm$ 0.32	40.71 $\pm$ 0.95	1.37 $\pm$ 0.33	Insectivore	Unknown
Vespertilionidae	<i>Eptesicus nilssonii</i>	Ep_nil	31	39.46 $\pm$ 1.41	6.91 $\pm$ 0.79	45.85 $\pm$ 5.53	1.15 $\pm$ 0.31	Insectivore	Edge
Vespertilionidae	<i>Nyctalus aviator</i>	Ny_avi	27	60.63 $\pm$ 2.37	7.29 $\pm$ 0.85	56.9 $\pm$ 8.19	1.22 $\pm$ 0.29	Insectivore	Open
Vespertilionidae	<i>Nyctalus furvus</i>	Ny_fur	8	50.63 $\pm$ 1.34	7.83 $\pm$ 0.59	59.01 $\pm$ 9.07	1.26 $\pm$ 0.24	Insectivore	Unknown
Vespertilionidae	<i>Pipistrellus abramus</i>	Pi_abr	32	33.16 $\pm$ 1.38	6.49 $\pm$ 0.61	41.86 $\pm$ 7.08	1.54 $\pm$ 0.42	Insectivore	Open
Vespertilionidae	<i>Pipistrellus endoi</i>	Pi_end	13	32.22 $\pm$ 1.44	6.94 $\pm$ 0.91	48.84 $\pm$ 6.23	1.22 $\pm$ 0.33	Insectivore	Unknown
Vespertilionidae	<i>Barbastella pacifica</i>	Ba_pac	13	40.81 $\pm$ 1.28	6 $\pm$ 0.48	36.95 $\pm$ 4.22	1.25 $\pm$ 0.43	Insectivore	Edge
Vespertilionidae	<i>Plecotus sacrimontis</i>	Pl_sac	38	41.84 $\pm$ 1.39	6.32 $\pm$ 0.63	33.66 $\pm$ 4.71	1.81 $\pm$ 0.92	Insectivore	Narrow
Vespertilionidae	<i>Hypsugo alaschanicus</i>	Hy_ala	1	36.4	8.19	53.28	2.34	Insectivore	Unknown
Vespertilionidae	<i>Vespertilio murinus</i>	Ve_mur	1	44.77	6.9	39.71	1.24	Insectivore	Open
Vespertilionidae	<i>Vespertilio sinensis</i>	Ve_sin	79	48.58 $\pm$ 2.22	7.53 $\pm$ 0.74	47.01 $\pm$ 7.21	1.55 $\pm$ 0.46	Insectivore	Unknown
Vespertilionidae	<i>Myotis rufoniger</i>	My_ruf	1	47.6	5.79	36.68	1.72	Insectivore	Unknown
Vespertilionidae	<i>Myotis longicaudatus</i>	My_lon	37	38.15 $\pm$ 1.05	6.58 $\pm$ 0.62	38.03 $\pm$ 5.55	1.32 $\pm$ 0.52	Insectivore	Unknown
Vespertilionidae	<i>Myotis sibiricus</i>	My_sib	22	34.97 $\pm$ 0.81	6.26 $\pm$ 0.62	41.82 $\pm$ 8.81	1.38 $\pm$ 0.33	Insectivore	Unknown
Vespertilionidae	<i>Myotis ikonnikovi</i>	My_iko	78	34.05 $\pm$ 0.99	6.53 $\pm$ 0.75	41.29 $\pm$ 5.14	1.33 $\pm$ 0.36	Insectivore	Edge
Vespertilionidae	<i>Myotis macrodactylus</i>	My_mac	67	38.11 $\pm$ 1.08	6.71 $\pm$ 0.79	39.81 $\pm$ 6.55	2.24 $\pm$ 0.76	Insectivore	Edge
Vespertilionidae	<i>Myotis bombinus</i>	My_bom	11	39.97 $\pm$ 1.14	6.59 $\pm$ 0.56	32.01 $\pm$ 4.05	2.73 $\pm$ 1.06	Insectivore	Unknown
Vespertilionidae	<i>Myotis petax</i>	My_pet	34	36.77 $\pm$ 1.05	6.5 $\pm$ 0.58	42.15 $\pm$ 4.91	1.07 $\pm$ 0.27	Insectivore	Edge
Vespertilionidae	<i>Myotis pruinosus</i>	My_pru	19	31.64 $\pm$ 0.64	6.49 $\pm$ 0.6	36.77 $\pm$ 5.36	1.84 $\pm$ 0.57	Insectivore	Unknown
Vespertilionidae	<i>Myotis yanbarensis</i>	My_yan	1	37.5	6.13	40.25	3.78	Insectivore	Unknown
Vespertilionidae	<i>Murina hilgendorfi</i>	Mu_hil	24	42.61 $\pm$ 1.27	6.03 $\pm$ 0.63	38.22 $\pm$ 6.15	3.28 $\pm$ 2.29	Insectivore	Narrow
Vespertilionidae	<i>Murina ryukyuana</i>	Mu_ryu	12	35.68 $\pm$ 1.56	6.3 $\pm$ 0.71	39.56 $\pm$ 5.76	2.63 $\pm$ 1.73	Insectivore	Unknown
Vespertilionidae	<i>Murina ussuriensis</i>	Mu_uss	38	30.71 $\pm$ 1.42	6.19 $\pm$ 0.66	39.96 $\pm$ 5.51	2.96 $\pm$ 1.59	Insectivore	Narrow
Miniopteridae	<i>Miniopterus fuliginosus</i>	Mi_ful	74	47.49 $\pm$ 0.99	7.55 $\pm$ 0.61	39.45 $\pm$ 4.22	1.05 $\pm$ 0.32	Insectivore	Open
Miniopteridae	<i>Miniopterus fuscus</i>	Mi_fus	7	43.92 $\pm$ 0.53	7.46 $\pm$ 0.38	34.56 $\pm$ 3.63	1.09 $\pm$ 0.24	Insectivore	Open
Molossidae	<i>Tadarida insignis</i>	Ta_ins	5	60.58 $\pm$ 2.8	10.4 $\pm$ 0.73	51.5 $\pm$ 5.75	1.57 $\pm$ 0.4	Insectivore	Unknown
Molossidae	<i>Tadarida latouchi</i>	Ta_lat	1	55.7	11.66	63.76	1.68	Insectivore	Unknown
Mean				48.13	6.93	41.50	1.71		

shape index (Table 2, Fig. 3) than the other bat species. A high wing tip shape index indicates more rounded wings that enable maneuverable flight (Norberg and Rayner 1987), and this is required to pursue prey in highly cluttered forest interiors. Species belonging to the edge-space guild did not exhibit significant

differences in wing morphology variables compared to other guilds, suggesting that they possess traits that are intermediate between the other guilds.

In the hierarchical clustering, insectivorous bats were grouped into nine clusters (Fig. 2). Species in Clusters 2 and 4, which included *Nyctalus*, *Vespertilio*,

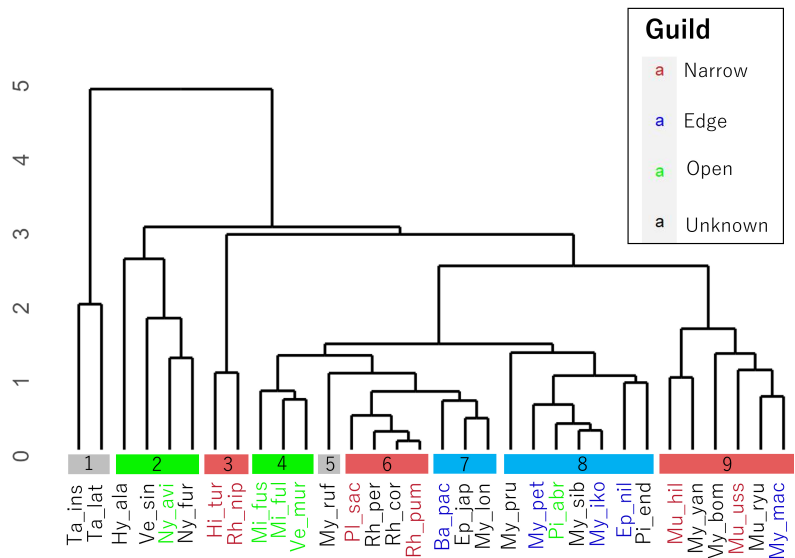


Fig. 2. Result of cluster analysis (UPGMA) based on forearm length, aspect ratio, relative wing loading, and wing tip shape index of Japanese insectivorous bats. Euclidean distance was calculated as functional distance and used in this dendrogram. The shortened species names refer to table 1. The colors of names correspond to each of the guilds based on previous studies, and the colors of boxes correspond to each of the guilds based on the clusters of the current analysis.

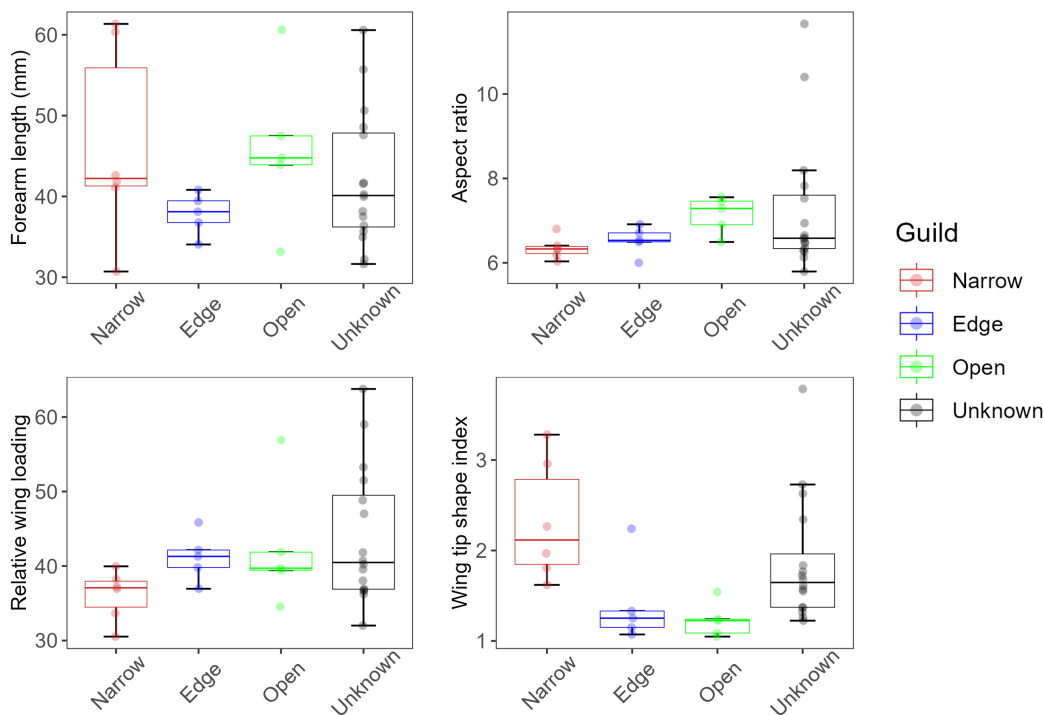


Fig. 3. Difference in wing morphology variables among foraging guilds. The dots indicate the mean variables of each species.

Miniopterus, and *Hypsugo* species, were predicted to belong to the open-space foraging guild group (Fig. 2). Species such as *V. sinensis*, *Hypsugo alaschanicus*, and *Nyctalus* bats, grouped to Cluster 2, were predicted to be in the open-space foraging guild. A GPS-based study has demonstrated that *N. aviator* utilizes open spaces, such as rivers, as foraging habitats (Niga et al. 2023), and *N. furvus* was also predicted to be an open-space forager. Phylogenetically related species of *V. sinensis* are known to use open spaces for foraging (*V. murinus*; Safi et al. 2007), supporting the prediction that *V. sinensis* belongs to the open-space foraging guild. *H. alaschanicus* was predicted to be an open-space forager per the clustering analysis; however, a related species was reported to use an edge habitat (Langridge et al. 2019). The high AR may have contributed to this prediction, and further investigation is necessary to determine whether this species forages in open or edge spaces. In Cluster 4, *V. murinus* and *Miniopterus* species were predicted to be open-space foragers based

on previous studies (Table S2), with their high AR supporting this inference (Table 1).

Open-space foraging species tend to fly at high altitudes and may be at risk of collision with wind turbines (Roemer et al. 2017). For example, *N. furvas*, a high-conservation priority species with no ecological knowledge, has been reported to collide with wind turbines, highlighting the risks faced by other species (Hokkaido Shinbun 2019). Furthermore, some Japanese open-space foraging species are known to travel long distances (*N. aviator*: 65 km; *Miniopterus fuliginosus*: 170 km; *V. sinensis*: 599 km) (Sawada 1993; Sato et al. 2013 2017). Therefore, understanding their habitat selection and seasonal movement is crucial for the conservation of these species.

In contrast, bat species in Clusters 3, 6, and 9, which include three *Myotis* species, as well as species from *Rhinolophus*, *Hipposideros*, *Plecotus*, and *Murina*, were predicted to belong to the narrow-space foraging guild (Fig. 2). *R. nippon* and *Hipposideros turpis* in

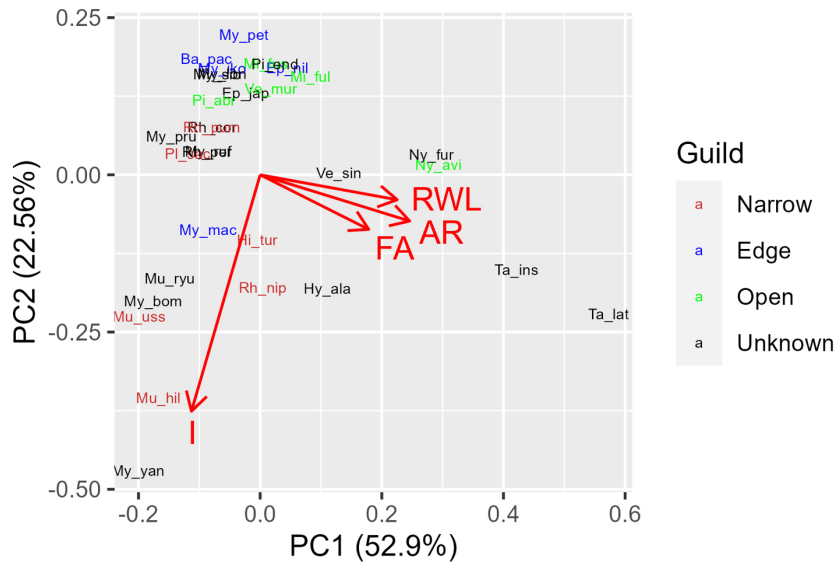


Fig. 4. Result of principal components analysis based on forearm length (FA), aspect ratio (AR), relative wing loading (RWL), and wing tip shape index (I) of Japanese insectivorous bats. The colors of the name correspond to each of the guilds predicted by the hierarchical analysis. Each species name indicates their ordered position based on the analysis. PC1 and PC2 explained 75.46% of the variance of wing morphological variables.

Table 2. The results of Tukey post-hoc tests in each wing variable among guilds

	Forearm length		Aspect ratio		Relative wing loading		Wing tip shape index	
	Difference in the mean value	p-value	Difference in the mean value	p-value	Difference in the mean value	p-value	Difference in the mean value	p-value
Edge-Narrow	-8.487	0.325	0.182	0.67	5.121	0.303	-0.501	0.015*
Open-Narrow	-0.334	0.998	0.792	0.006**	6.407	0.168	-0.61	0.004*
Open-Edge	8.153	0.381	0.61	0.039*	1.286	0.927	-0.109	0.777

The significance value is indicated as follows: ** $p \leq 0.01$; * $p \leq 0.05$.

Cluster 3 were categorized as narrow-space foragers based on previous studies of their foraging ecology (Tables 1, S2). Cluster 9, comprising three *Murina* and three *Myotis* species, was predicted to belong to a narrow environmental guild based on the ecological knowledge of *Murina hilgendorfi* and *Murina ussuriensis*, which belong to the narrow-space foraging guild. *Myotis bombinus* is known to preferentially forage on spiders (Funakoshi and Takeda 1998; Sato and Katsuta 2018), suggesting they are likely to forage near vegetation in narrow spaces. *Myotis nattereri*, a closely related species in Europe, belongs to a narrow environmental guild (Siemers and Schnitzler 2000; Siemers and Swift 2006), supporting our prediction. The high wing tip shape index of these species also supports their guild prediction. Regarding the two native species inhabiting only the southern smaller islands, *Murina ryukyuana* is consistent with the ecology of related species, such as *Murina ussuriensis* (Kawai et al. 2002); however, *Myotis yanbarensis* was reported to forage only near rivers in the forest interior (Preble et al. 2020). Although the wing tip shape index of this species was remarkably high, only one specimen was examined due to the lack of available specimens. More information on their ecology and wing morphology is needed to determine whether the wing variables are biased by the poor condition of the specimens. *Myotis macrodactylus*, an edge-space foraging bat, was located in this cluster. Their foraging strategy, known as trawling, involves foraging for prey over the water surface (Mizuguchi et al. 2022). Bats with this foraging strategy are generally classified as edge guild species, and need further study to understand the function of their wing morphology. For example, how often does it forage by gleaning in the forest interior? The guild of Cluster 6, comprising three *Rhinolophus* species and *Plecotus sacrimontis*, was predicted to be a narrow-space forager based on ecological knowledge of *R. pumilus* and *Plecotus sacrimontis* (Table S1). Although the bat species in this cluster did not have a very high wing tip shape index, they had a low RWL, ranging from 33.66 to 36.94 compared to the mean value of 41.50. Low WL is related to maneuverable slow flight, especially during hovering, which is favored for foraging in dense forest interiors (Norberg and Rayner 1987). This feature might enable the three *Rhinolophus* species and *Plecotus sacrimontis* to forage in narrow spaces.

Clusters 7 and 8 include five species of *Myotis* as well as *Pipistrellus*, *Eptesicus*, and *Barbastella*, which were predicted to belong to the edge-space foraging guild (Fig. 2). Cluster 8, which consisted of four *Myotis* species, two *Pipistrellus* species, and *E. nilssonii*, was predicted to belong to the edge-space foraging guild owing to prior knowledge of their ecology (Table S2).

Despite previous studies suggesting that *Pipistrellus abramus* primarily forages in open spaces (Tosuji and Shibata 2003; Hiryu et al. 2008), a dietary study indicates that they also feed on Lepidoptera larvae, which can forage on interior vegetation or surrounding areas (Sato and Katsuta 2018). Based on this dietary and wing morphology information, this species might be categorized as an edge guild that can forage in both open spaces and close to vegetation. This information supports the prediction that *Pipistrellus endoi*, phylogenetically related to *Pipistrellus abramus*, belongs to the edge-space foraging guild. Based on the edge-space foraging ecology of species with similar wing morphology, the bats with insufficient ecological knowledge, *Pipistrellus endoi* and *Myotis sibiricus*, were predicted to belong to the edge-foraging guild. *Myotis sibiricus* is phylogenetically related to *Myotis brandtii*, which belongs to the edge-foraging guild (Wermundsen and Siivonen 2008; Ruedi et al. 2013), further supporting this prediction. In Cluster 7, *E. japonensis*, *B. pacifica*, and *Myotis longicaudatus* were predicted to be edge-space foragers. *E. nilssonii*, considered a phylogenetically related species to *E. japonensis* (Ohdachi et al. 2015), is known as an edge-foraging bat (Wermundsen and Siivonen 2008), aligning with our prediction for *E. japonensis*. Regarding *Myotis longicaudatus*, foraging flights have been reported in edge spaces such as near buildings or long, narrow-open spaces near vegetation (Endo 1967). These observations are consistent with our predictions for this species. The lower-intermediate AR and wing tip shape index ranges of 6.00 to 6.91 and 1.25 to 1.37, respectively, compared to the mean values of 6.93 and 1.71, further support our prediction.

Clusters 1 and 5 were not assigned a guild due to a lack of ecological information. Cluster 1 includes two *Tadarida* species, which exhibit a remarkably high AR of wings. Their phylogenetically related species are known to utilize open spaces (Lee and McCracken 2002), suggesting that they belong to the open-space foraging guild. In contrast, Cluster 5 comprises only one species, *Myotis rufoniger*. This species has the lowest AR among Japanese bats, and its wing tip shape index is similar to the mean value among Japanese bats in this study (Table 1). The low AR and intermediate wing tip shape index suggest that the species belongs to the edge-space foraging guild. This prediction is supported by the knowledge that closely related species to *Myotis rufoniger* use edge-space habitats (Moyo and Jacobs 2020).

The genus *Myotis*, which comprises more than 126 species worldwide (Burgin et al. 2018), is one of the most diversified genera in the order Chiroptera. Nine species are distributed in Japan. Our study indicated that

Japanese *Myotis* species exhibit a wide range of wing tip shape indices ranging from 1.07 (*Myotis petax*) to 3.78 (*Myotis yanbarensis*), covering almost the entire range of Japanese bats wing tip shape (1.05–3.78). In contrast, other variables were more conserved among the *Myotis* species. PCA analysis indicated that the variance of wing tip shape index is distinct from other variables and uniquely contributes to the difference in ecology among Japanese bats (Fig. 4). Therefore, it can be hypothesized that the evolution of wing roundness was more strongly influenced by their foraging strategy than by other wing morphologies, such as forearm length. Variation in roundness, related to flight maneuverability and agility (Norberg and Rayner 1987), could be a key trait in the diversification of *Myotis* species. Castillo-Figueroa (2020) reported that the bat terminal phalanges, which partly shape the wing tip, are strongly related to their foraging habitat, supporting our hypothesis. However, further studies are essential to examine this hypothesis based on the wing morphology of *Myotis* bats worldwide.

All variables except forearm length had many outliers, especially the wing tip shape index. The condition of specimens is known to affect the measurement of wing morphology (Bininda-Emonds and Russell 1994). In addition, potential biases may exist among collectors during the specimen preparation process. Although our study selected specimens based on specific criteria, differences in storage conditions might have affected the results. Furthermore, our dataset did not account for intraspecific variation caused by environmental conditions or sexual dimorphism (Violle et al. 2012). However, the observed trends in wing morphology correlated with foraging habitats, as supported by previous studies. Therefore, our results for the wing morphology variables can be considered robust and reasonable. In terms of sampling effort, only one specimen each was examined for six species due to their rarity. Future studies with more comprehensive data would provide more accurate information on the foraging ecology of these species.

CONCLUSIONS

Rare species generally face a high risk of extinction due to their small population sizes or limited habitats. Their ecological information is particularly important compared to other species, but it is challenging to obtain such information because of their scarcity. We reaffirm that museum and private collections have the potential to address these issues (Castillo-Figueroa 2018; Meineke et al. 2018). This study contributes to a better understanding of the

relationship between the wing morphology of bats and their feeding ecology in the Japanese archipelago. The data obtained in this study can be useful for studies on the evolution, behavior, and community assembly of bats in Japan and Palearctic Asia, where wing data are relatively lacking.

List of the abbreviations

AR, aspect ratio.
RWL, relative wing loading.
ANOVA, analysis of variance.
PCA, principal component analysis.
WL, wing loading.

Acknowledgments: We are sincerely grateful to Shin-Ichiro Kawada, Mitsuru Mukohyama, and Kishio Maeda for allowing us to access the specimens in their collections. We are also grateful to Masashi Murakami and Toshihide Hirao for their assistance in photographing the specimens. This work was supported by JSPS KAKENHI, Grant Number JP 21H04923, JST SPRING, Grant Number JPMJSP2108, and “Innovative model fusing conservation of biological and cultural diversity with regional revitalization in the Amami archipelago,” Mission Progressive Strategy at Kagoshima University.

Authors' contributions: T.M.: Conceptualization, data curation, formal analysis, validation, writing-original draft. D.F.: Conceptualization, funding acquisition, data collection, project administration, supervision, validation, writing-review and editing.

Competing interests: The authors have no competing interests.

Availability of data and materials: Measured variables in wing morphology are available in the supplementary data.

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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Supplementary materials

Table S1. List of references pertaining to the guilds of bat species in the Japanese archipelago. (download)

Table S2. Measured wing variables in each specimen. (download)