

Original Article

The relationship between wing morphology and foraging guilds: exploring the evolution of wing ecomorphs in bats

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ABSTRACT

Different aspects of foraging strategies in bats have been studied to understand the evolution of flight in mammals. General descriptors of wing morphology associated with flight performance, such as aspect ratio and wing loading, allowed us to describe ecomorphs determined by the dietary preferences of bat species. However, the role of wing shape divergence in the evolution of bat foraging strategies remains little explored. We adopted a two-dimensional geometric morphometric approach to quantify the wing shape and size variation explained by phylogenetic relatedness (families) and to evaluate the covariance between foraging guilds and flight descriptors based on phylogenetic comparative methods in 69 Neotropical bat species. We tested whether wing morphology represents a reliable marker of the foraging guild, and we explored the rate of shape evolution among foraging guilds to describe divergent trends that could explain the morphological and ecological diversification. Our results suggest that the earliest bat ancestor was an aerial forager occupying the edge space, which is congruent with the observed evolution of wing shape from an edge space wing morphology. The relationship between wing shape and foraging space defines wing ecomorphs, which probably evolved early in bat ancestors; a process other than convergence could explain this association.

Keywords: Chiroptera; bat evolution; ecomorphology; Mexico; Phyllostomidae; wing shape; geometric morphometrics; foraging space

INTRODUCTION

Variation in wing shape has been studied widely in the context of flight evolution, dispersion capacity, and foraging performance in flying animals (Norberg and Rayner 1987, Dudley 2002, Altshuler 2006, Dillon *et al.* 2006). In these animals, flight represents an advantage in terms of dispersing and colonizing new environments (Wang and Clarke 2015, Luo *et al.* 2019), and it is key to the understanding of foraging patterns and habitat preferences (Roff 1986, Johansson *et al.* 2009, Marinello and Bernard

2014, Magalhães de Oliveira *et al.* 2020). In this context, wing morphology is related to biomechanics and flight performance in birds (Altshuler 2006, Segre *et al.* 2016), insects (Dillon *et al.* 2006, Pitchers *et al.* 2013, Montejo-Kovacevich *et al.* 2021), and bats (Norberg and Rayner 1987, Altshuler *et al.* 2004, Luo *et al.* 2019). In general, variation in wing shape and size has been used to compare the biomechanical properties of flying patterns within and among taxa (Norberg and Rayner 1987, Wootton 1992, Dillon *et al.* 2006, DeVries *et al.* 2010).

From an aerodynamic perspective, flight performance is described by biomechanical variables related to body mass and wing shape (Dudley and Ellington 1990, Stiles *et al.* 2005). Among these variables, the wing aspect ratio (WAR) has been widely used to compare the sustainability and manoeuvrability of flight (Warham 1977, Bininda-Emonds *et al.* 1994, Dudley 2002, Hodgkison *et al.* 2004, Luo *et al.* 2019), where low values indicate increased manoeuvrability but slower flight, whereas high values indicate efficient gliding flight (Dingle 1996). In contrast, wing loading (WL) quantifies the amount of mass carried by the wing per unit area, where higher values indicate slow wing beat frequency and short flight duration, and low values indicate increased manoeuvrability and prolonged sustained flight, with higher speed (Norberg and Rayner 1987, Dudley 2002). In general, narrow wings tend to have small wing areas and high wing loadings, unless they are very long (Norberg and Rayner 1987).

Variation in wing shape in bats was first studied with an ecomorphological approach by Norberg and Rayner (1987), who classified bat species into several foraging guilds based on their body mass, WAR, WL, and wing tip index. These ecomorphs were defined in relationship to the taxonomic family and flight descriptors (species with high, average, and low WAR), and were associated with their dietary preferences. In an evolutionary context, the capacity for flight and the variety of dietary preferences observed in bats have influenced the present diversity of cranial and wing morphologies, which have been explained by adaptive radiations in the case of phyllostomid bats (Monteiro and Nogueira 2011, Dumont *et al.* 2012) or by ecological convergences in the case of some insectivorous families (Ruedi and Mayer 2001, Gregorin and Cirranello 2016, Morales *et al.* 2019). Given its association with flight parameters, the evolution of wing morphology constrains the ecological roles of each bat species (Norberg and Rayner 1987), but the adaptive nature of wing morphology through its evolution, and its influence on dietary preferences and the search and capture of dietary items, remain poorly explored.

The key morphological innovations that confer ecological opportunity to animal species could be reflected in morphological diversification rates within clades and assessed through morphological disparity (Alfaro *et al.* 2009, Claramunt *et al.* 2012, Zelditch *et al.* 2017). Adaptive radiation is characterized by a link between diversification and niche divergence, and therefore adaptively radiating clades are diverse and morphologically disparate (Harmon *et al.* 2003, Kozak and Weins 2010, Rowe *et al.* 2011, Smith *et al.* 2011, Zelditch *et al.* 2017). Some hypotheses have proposed that certain clades will have an intrinsically greater capacity to evolve novel morphologies and new designs of pre-existing structures (Lovette *et al.* 2002), as suggested by the wing morphology of bats (Arita and Fenton 1997). This could act to favour the exploitation of a wider variety of niches (Rabosky *et al.* 2013). The other possible scenario, as suggested by wing ecomorphs (defined from wing biomechanics; Norberg and Rayner 1987), is a morphological convergence in wing shape of species exhibiting similar foraging strategies, which is complemented by characteristic parameters of their acoustic signal (Jones and Holderied 2007, Denzinger and Schnitzler 2013).

The inclusion of size and shape in evolutionary models could provide stronger support for adaptive hypotheses. Size is a widely used trait in studies of adaptive radiation or ecological specialization in mammals (Slater *et al.* 2010, Ghazali and Dzeverin 2013, Zelditch *et al.* 2015). Zelditch *et al.* (2017) suggested that niche-dependent allometries and morphologies are evidence of ecological adaptation. Among bats, adaptive radiation has been proposed to explain the close association between diet and cranial morphology in the New World family Phyllostomidae (Baker *et al.* 2012). Convergence has been also suggested from recent definitions of foraging guilds based on the foraging space (narrow, edge, and open) and food capture strategy (aerial, water surface trawling, gleaning, and flutter detection foraging; Denzinger and Schnitzler 2013), even within diverse families such as Phyllostomidae (Stockwell 2001, García-Herrera *et al.*, 2023). However, wing shape, as a functional character involved in the mode of food search and capture, has not been explored in the analysis of bat evolution.

We applied a two-dimensional geometric morphometric approach to quantify the variation in wing shape and size related to phylogenetic relatedness (families), and we implemented phylogenetic comparative methods to evaluate their covariance with previously defined foraging guilds (Denzinger and Schnitzler 2013) and flight descriptors in 69 Neotropical bat species. Specifically, we tested whether wing morphology represents a reliable marker of the foraging guild. Following the aerodynamic predictions of flight performance, we tested the hypothesis that species foraging in open areas and using an aerial foraging mode present morphological features (thin, long, and pointed wings) that are related to high sustainability and flight velocity (i.e. high aspect ratio and large wings), in contrast to species foraging in narrow spaces (thick, short, and rounded wings) and using a gleaning strategy; species foraging in edge space have intermediate wing elongation and wing area but vary in flight performance (aspect ratio and wing loading), depending on the foraging mode (aerial hawking and trawling). Considering the suggested convergence in wing shape and foraging guilds (Norberg 1994, Stockwell 2001, García-Herrera *et al.*, 2023), we also described the mode of wing shape and size evolution, and we tested whether there is a consistency with early adaptive radiation or ecological convergence in regions of morphospace defined by foraging strategies.

MATERIALS AND METHODS

Morphometric data

Our sample comprised 836 images of 69 bat species belonging to seven families, representing three main foraging guilds (Denzinger and Schnitzler 2013) based on foraging space (open space, edge space, and narrow space) and four guilds based on foraging mode (aerial foragers, trawling foragers, flutter detecting, and gleaning foragers). Most samples were collected during the creation of a library of Mexican bat echolocation calls (SONOZOTZ project; Zamora-Gutierrez *et al.* 2020). Sample sizes and foraging guilds for all species are listed in Table 1. Details about sample localities for each species are presented in the Supporting Information (Table S1). We obtained digital photographs of the dorsal view of the right wings of living individuals using a Nikon D3100 reflex camera (Nikon, Inc.),

Table 1. List of families and species included in this study, with assigned foraging guild, mean centroid size (CS), wing aspect ratio (WAR), and relative wing loading (RWL) for each species. Foraging modes: aerial foragers (AF), trawling foragers (TF), flutter detecting (FD), and gleaning foragers (GF).

Family	Species (Ramírez-Pulido et al., 2014)	Foraging guild	Sample size	Wing CS (cm)	WAR	RWL
Emballonuridae	<i>Balantiopteryx io</i>	Open space AF	8	13.058	5.934	36.114
Emballonuridae	<i>Balantiopteryx plicata</i>	Open space AF	7	13.161	6.362	44.915
Emballonuridae	<i>Peropteryx kappleri</i>	Open space AF	13	17.083	6.947	35.417
Emballonuridae	<i>Peropteryx macrotis</i>	Open space AF	13	15.512	6.585	33.128
Emballonuridae	<i>Rhynchonycteris naso</i>	Edge space TF	38	14.193	5.376	32.55
Emballonuridae	<i>Saccopteryx bilineata</i>	Edge space AF	17	16.421	5.698	31.189
Noctilionidae	<i>Noctilio leporinus</i>	Edge space TF	10	32.689	6.589	36.677
Mormoopidae	<i>Mormoops megalophylla</i>	Edge space AF	41	18.97	5.616	33
Mormoopidae	<i>Pteronotus fulvus</i>	Edge space AF	49	15.267	6.144	35.532
Mormoopidae	<i>Pteronotus gymnonotus</i>	Edge space AF	7	18.388	5.836	32.279
Mormoopidae	<i>Pteronotus mesoamericanus</i>	Narrow space FD	46	19.754	5.598	34.693
Mormoopidae	<i>Pteronotus psilotis</i>	Edge space TF	20	14.387	6.034	37.775
Phyllostomidae	<i>Anoura geoffroyi</i>	Narrow space GF	1	17.758	5.714	47.637
Phyllostomidae	<i>Artibeus jamaicensis</i>	Narrow space GF	11	24.142	5.074	43.078
Phyllostomidae	<i>Artibeus lituratus</i>	Narrow space GF	4	29.144	6.155	44.127
Phyllostomidae	<i>Carollia perspicillata</i>	Narrow space GF	6	18.857	5.218	45.646
Phyllostomidae	<i>Carollia sowelli</i>	Narrow space GF	67	18.335	5.203	45.751
Phyllostomidae	<i>Centurio senex</i>	Narrow space GF	3	17.083	4.291	37.269
Phyllostomidae	<i>Chiroderma villosum</i>	Narrow space GF	3	19.522	5.151	46.445
Phyllostomidae	<i>Chrotopterus auritus</i>	Narrow space GF	2	32.156	3.76	32.167
Phyllostomidae	<i>Dermanura azteca</i>	Narrow space GF	3	18.744	5.525	51.827
Phyllostomidae	<i>Dermanura phaeotis</i>	Narrow space GF	19	16.465	4.743	40.745
Phyllostomidae	<i>Dermanura tolteca</i>	Narrow space GF	11	17.297	4.951	45.129
Phyllostomidae	<i>Dermanura watsoni</i>	Narrow space GF	1	16.071	4.503	40.417
Phyllostomidae	<i>Desmodus rotundus</i>	Narrow space GF	3	20.665	6.005	50.594
Phyllostomidae	<i>Diphylla ecaudata</i>	Narrow space GF	5	20.686	5.533	41.814
Phyllostomidae	<i>Glossophaga mutica</i>	Narrow space GF	8	15.115	5.309	48.375
Phyllostomidae	<i>Lampronnycteris brachyotis</i>	Open space AF	1	14.302	4.281	46.18
Phyllostomidae	<i>Leptonycteris yerbabuena</i>	Narrow space GF	9	20.315	5.192	40.366
Phyllostomidae	<i>Lonchorhina aurita</i>	Narrow space GF	1	22.96	5.891	44.726
Phyllostomidae	<i>Macrotus waterhousii</i>	Narrow space GF	2	19.049	5.156	33.126
Phyllostomidae	<i>Micronycteris microtis</i>	Narrow space GF	6	13.542	4.183	39.255
Phyllostomidae	<i>Mimon cozumelae</i>	Narrow space GF	11	22.202	4.339	30.852
Phyllostomidae	<i>Platyrrhinus helleri</i>	Narrow space GF	4	16.335	5.112	42.415
Phyllostomidae	<i>Sturnira hondurensis</i>	Narrow space GF	67	18.89	5.359	50.961
Phyllostomidae	<i>Sturnira parvidens</i>	Narrow space GF	71	17.009	5.477	53.209
Phyllostomidae	<i>Trachops cirrhosus</i>	Narrow space GF	2	23.38	4.621	32.846
Phyllostomidae	<i>Uroderma convexum</i>	Narrow space GF	2	18.634	4.874	40.119
Natalidae	<i>Natalus mexicanus</i>	Edge space TF	8	15.311	5.019	23.803
Molossidae	<i>Molossus alvarezii</i>	Open space AF	4	18.494	8.388	66.327
Molossidae	<i>Molossus nigricans</i>	Open space AF	66	20.123	8.103	76.815
Molossidae	<i>Nyctinomops laticaudatus</i>	Open space AF	4	16.192	8.832	63.12
Molossidae	<i>Tadarida brasiliensis</i>	Open space AF	26	15.883	6.998	54.284
Vespertilionidae	<i>Antrozous pallidus</i>	Narrow space GF	24	18.566	5.55	38.676
Vespertilionidae	<i>Corynorhinus mexicanus</i>	Narrow space GF	6	15.976	5.4	30.768
Vespertilionidae	<i>Corynorhinus townsendii</i>	Narrow space GF	1	15.506	4.458	32.127
Vespertilionidae	<i>Eptesicus brasiliensis</i>	Edge space AF	7	15.442	5.502	39.123
Vespertilionidae	<i>Eptesicus furalis</i>	Edge space AF	19	15.075	5.457	39.484
Vespertilionidae	<i>Eptesicus fuscus</i>	Edge space AF	7	19.453	5.422	39.496
Vespertilionidae	<i>Lasiurus borealis</i>	Open space AF	2	17.141	6.448	42.067

Table 1. Continued

Family	Species (Ramírez-Pulido et al., 2014)	Foraging guild	Sample size	Wing CS (cm)	WAR	RWL
Vespertilionidae	<i>Lasiurus cinereus</i>	Open space AF	8	21.284	7.424	46.649
Vespertilionidae	<i>Lasiurus ega</i>	Open space AF	2	17.264	7.117	40.053
Vespertilionidae	<i>Lasiurus frantzii</i>	Edge space AF	1	16.7	7.267	43.839
Vespertilionidae	<i>Lasiurus xanthinus</i>	Open space AF	1	18.684	6.776	46.811
Vespertilionidae	<i>Myotis albescens</i>	Edge space TF	1	11.966	5.865	40.629
Vespertilionidae	<i>Myotis californicus</i>	Edge space AF	6	12.539	5.459	31.857
Vespertilionidae	<i>Myotis elegans</i>	Edge space AF	1	12.451	5.944	41.029
Vespertilionidae	<i>Myotis fortidens</i>	Edge space AF	6	14.801	5.994	41.294
Vespertilionidae	<i>Myotis nigricans</i>	Edge space AF	11	13.147	5.974	36.93
Vespertilionidae	<i>Myotis peninsularis</i>	Edge space TF	8	13.837	5.081	34.407
Vespertilionidae	<i>Myotis pilosatibialis</i>	Edge space AF	13	12.973	5.368	32.89
Vespertilionidae	<i>Myotis thysanodes</i>	Narrow space GF	1	17.11	7.167	38.22
Vespertilionidae	<i>Myotis velifer</i>	Edge space TF	18	16.064	5.275	38.819
Vespertilionidae	<i>Myotis vivesi</i>	Edge space TF	15	23.621	6.646	35.035
Vespertilionidae	<i>Myotis yumanensis</i>	Edge space AF	1	12.651	4.988	31.942
Vespertilionidae	<i>Parastrellus hesperus</i>	Edge space AF	1	11.097	4.572	37.51
Vespertilionidae	<i>Rhogeessa aenea</i>	Edge space AF	3	10.813	5.021	37.212
Vespertilionidae	<i>Rhogeessa parvula</i>	Edge space AF	1	11.834	5.84	38.219
Vespertilionidae	<i>Rhogeessa tumida</i>	Edge space AF	5	12.402	5.472	49.793

maintaining, as far as possible, the same position of the wing relative to the body by placing the forearm at 90° to the body axis and the pollex at the level of the ear. We used these photographs to describe wing shape and size variation and to calculate flight descriptors. The software TpsDIG v.2.31 (Rohlf 2017) was used to describe wing shape from images based on the configuration of 15 two-dimensional landmarks located in the joints of phalanges and bones, and at the wing tip (Fig. 1A). Owing to high variance in the wing position of specimens in the photographs, we discarded outlier configurations within the morphospaces of families (distances from the consensus shape outside the normal distribution). The anatomical definition of landmarks is presented in the Supporting Information (Table S2).

We analysed the variation in wing shape using a geometric morphometrics protocol implemented in the R package GEOMORPH v.4.0 (Adams et al. 2021) and RRPP (Collyer and Adams 2018, 2019). After the digitization process, a size estimator called ‘centroid size’ was obtained for each specimen. This estimator is calculated as the square root of the sum of the squared distances between each landmark and the centroid of the configuration (Zelditch et al. 2012). Landmark configurations were then superimposed by generalized Procrustes analysis (GPA) to remove individual differences attributable to scale, orientation, and position (Bookstein 1997, Zelditch et al. 2012). Mean aligned configurations of species and shape vectors obtained from the ordination and projection of these configurations into a Euclidean ‘tangent space’ were used in comparative analyses as dependent variables. To ensure that the variance in the digitization process was not >5%, we digitized two replicates of a subsample of 100 photographs randomly assigned and tested differences between replicates using a Procrustes ANOVA model; we did not obtain significant differences between replicates ($F_{1,199} = 0.046, P > .1$).

Flight descriptors

The flight capacity of individual species was described based on the WAR and relative wing loading (RWL), two biomechanical descriptors that are widely used in bats to describe foraging strategies and dispersal patterns (Norberg and Rayner 1987, Thollesson and Norberg 1991, Luo et al. 2019). To obtain the average of these variables for each species, we measured the wingspan (Ws) and wing area (Wa) from individual scaled photographs (Fig. 1B) using the software IMAGEJ v.1 (<https://imagej.net/ij/>; Schneider et al. 2012). Although different measurement protocols to capture wing distances and wing areas have been reported, and some recommendations have been provided (Crane et al. 2022), we defined the wingspan as being from the insertion of the wing into the shoulder to the wing tip, and we measured the full area of the patagium to calculate flight descriptors. Owing to a lack of sufficient standardized views, it was not possible to measure reliably the area of uropatagium and the area of both wings from photographs, as suggested by Norberg and Rayner (1987). Finally, body mass (Bw), obtained from live captured specimens using a Pesola spring balance (100 ± 0.5 g), was used in the calculation of RWL, a ratio proposed to make wing loading (WL) independent of size for morphometrically similar species (Marinello and Bernard 2014). Calculations were performed following Norberg and Rayner (1987):

$$WAR = \frac{Ws \text{ (in metres squared)}}{Wa \text{ (in metres squared)}}$$

$$WL = \frac{Bw \text{ (in newtons)}}{Wa \text{ (in metres squared)}}$$

$$RWL = WL/Bw$$

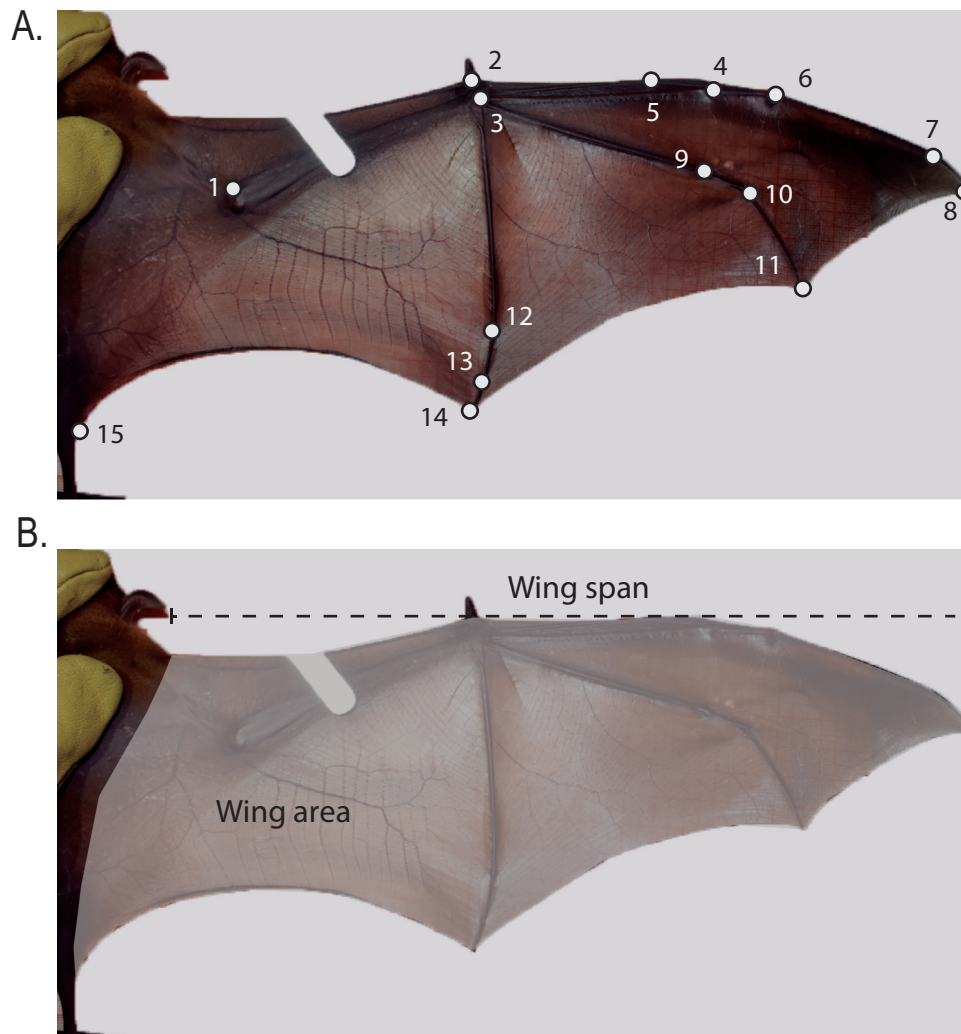


Figure 1. A, landmark configuration used to describe wing shape and size variation in 69 bat species analysed. Landmarks are located on the intersection of phalanges and wing bones, the wing membrane insertion, and the wing tip. B, measurements were drawn from wing photographs to calculate biomechanical descriptors.

Differences in shape and size between families and foraging guilds

We explored the amount and direction of variation in wing shape in a morphospace constructed from wing geometric configurations using a principal component analysis (PCA), identifying families and foraging guilds as groups for comparison. We performed a PCA of average species configurations and plotted the phylogenetic hypothesis of relationships for this set of species using a phylomorphospace to describe shape variance in the data that could be explained by ecological or phylogenetic signals. We then compared the PCA morphospace with the distribution of configurations in a phylogenetically aligned PCA (PaCA), which maximizes the variance explained by phylogeny to visualize trends of morphological variation aligned to the phylogenetic signal (Collyer and Adams 2021). We expected that characters with a strong phylogenetic signal would produce similar data distribution in the original morphospace and the PaCA and high values in the RV coefficient, which is the statistical parameter that measures the strength of association between phylogeny and data through the PaPCs (more details are provided by Collyer

and Adams 2021). Maximum shape variance among the average wing shapes for the species was described using deformation grids derived from the first two principal components (PCs). The phylogeny of reference was obtained by pruning species from the 100 most credible Bayesian trees (Upham *et al.*, 2019), downloaded from <http://vertlife.org/phylosubsets>, and calculating the maximum credibility tree in the package PHANGORN (Schliep 2011). All the comparative and statistical analyses were performed in the program R v.4.3.0 (R Core Team 2021).

We described the amount of phylogenetic signal in wing shape data and the congruence between morphological similarities and phylogenetic relationships. We verified the phylogenetic signal in the wing shape data, using the multivariate version of the K statistic, which reflects the degree of congruence between the trait and the phylogeny (Blomberg *et al.* 2003), estimating its significance through a permutation test with 1000 replicates (Adams and Collyer 2016). Finally, to describe the morphological similarities explained by relatedness or foraging guilds, we compared the maximum credibility tree and a cluster dendrogram derived from Procrustes distances among average wing

shapes for species, using the unweighted pair group method with arithmetic mean (UPGMA) in the R package PHYTOOLS (Revell 2011). Two species were not included in the phylogeny (*Corynorhinus mexicanus* and *Pteronotus mesoamericanus*) and were therefore excluded from subsequent comparative analyses.

We used phylogenetic comparative methods to evaluate whether the mode of wing shape and centroid size evolution are congruent with Brownian motion (BM) mode, or to detect deviation towards an adaptive radiation or a single stationary peak Ornstein–Uhlenbeck mode of evolution. The latter has been used to test whether lineages have evolved convergently towards adaptive peaks (Grossnickle, 2020). Given that the dynamics through evolutionary time of disparity of wing shape or wing size have not been documented previously in bats, we presented an initial picture of the evolution of wing shape and size by testing the adjustment of the observed divergence in shape and centroid size data through phylogeny using the morphological disparity index (MDI) (Harmon *et al.* 2003), which measures the deviation of subclade disparities from the expected relative within-clade disparity in the BM mode. In accordance, the MDI was calculated as the area between the line describing the observed relative disparities (inside subclades) and the median relative disparity simulated through 1000 permutations. The *P*-values obtained from this analysis indicate the proportion of replicates in which an MDI is obtained that is more extreme than that observed (Zelditch *et al.* 2012). The statistical significance of the MDI was assigned using the function dttFULLCIs (Slater *et al.* 2010), implemented in R package GEIGER v.2.0.11 (Harmon *et al.* 2008).

We explored the fit of the data to alternative basic evolutionary models previously applied to geometric morphometric configurations of anatomical structures in mammals (Zelditch *et al.* 2017, Arbour *et al.* 2019, Giacomini *et al.* 2022) to evaluate deviations from a BM mode of wing shape and size evolution (i.e. early burst and a single stationary peak Ornstein–Uhlenbeck). In the former model, a taxon that exhibits rapid diversification early in its evolution can accelerate and then decelerate the rate of change (σ^2) with a rate of decay parameter (a) and is expected to present more variation among subclades (Harmon *et al.* 2010) and negative MDI values (Slater *et al.* 2010). In the latter case, the model assumes that phenotypes evolve towards a stationary optimum under a Brownian rate parameter (σ^2) and a constant strength of attraction to the stationary peak (α) (Hansen and Martins 1996, Hansen *et al.* 2008, Zelditch *et al.* 2015). Under this model, the subclades contain a substantial proportion of the total variation, and they overlap in morphospace, showing positive MDI values close to one (Harmon *et al.* 2003, Zelditch *et al.* 2015). In the Ornstein–Uhlenbeck model, the within-subclade variance, described by morphological disparity, is greater than that among subclades (Buttler and King 2004). Additionally, we used a selective regime BM model with variable means but constant evolutionary rate and with variable evolutionary rates (σ^2) according to Grossnickle *et al.* (2020). We used likelihood ratio tests and the corrected Akaike information criterion (AICc) to compare models; these analyses were performed in the R package mvMORPH (Clavel *et al.* 2015). For shape data, we reduced the dimensionality of the matrix using the first five PCs of the PCA of species average shapes and used the diagonals of the rate matrix to obtain the Brownian rate parameter (σ^2) and to adjust models following Zelditch *et al.* (2015).

To test possible morphological convergences among species in the same foraging space, we also used the metrics of convergence proposed by Stayton (2015), implemented in the R package CONVEVOL v.2.0.0 (Brightly and Stayton 2023). This method proposes four distances to measure convergence in the phenotypic space (C1, C2, C3, and C4), all of them from a pattern-based definition of convergence, which occurs when lineages evolve similar phenotypes independently (Stayton 2015). The distance C1 represents the proportion of the maximum distance between two lineages that has been brought together by subsequent evolution; it has values from zero to one as convergence increases. The distance C2 represents the absolute amount of evolution that has occurred during convergence. The distance C3 is the proportion between C2 and the total amount of evolutionary change along the lineages leading from the common ancestor of the convergent taxa to those taxa. C4 is the proportion between C2 and the total amount of evolution in the entire clade defined by the common ancestor of the convergent taxa. Statistical tests of convergence measurements were evaluated using 500 evolutionary simulations via a BM model. Although most of the family members share the same foraging guild, we included all species in view of the dispersion observed in the second PC of wing morphospace.

To test the hypothesis of gradual morphological changes in relationship to foraging guilds, considering the phylogenetic structure in the residuals, we evaluated the contribution of centroid size, foraging guilds, and their interaction, to the average variance in species shape, using a phylogenetic generalized least squares (PGLS) analysis. This method was adapted to multivariate morphometric data to conduct ANOVA and regression models in a phylogenetic context, calculating a phylogenetic transformation matrix under different evolutionary models applied to dependent and independent variables (Adams 2014a). We used the phylogenetic distances matrix to obtain phenotypic covariance for species and perform PGLS models, rather than a covariance matrix based on a BM model of evolution (Adams and Collyer 2018), in view of the lower shape variance than would be expected under the BM model of evolution ($K_{multiv} = 0.20$). Considering the limited sample size and the problem of clade aggregation (Adams and Collyer 2018), we used a type II sum of squares. The significance of the *F* statistics of each factor or variable was estimated from a permutation test with 1000 replicates across the terminals of phylogeny, in the package RRPP (Collyer and Adams 2018, 2019). The observed statistic was then compared with resampled statistics to assign its probability. We also performed pairwise comparisons between allometric vectors (wing shape regressed on the centroid size logarithm) of foraging guilds from this model to identify changes in the number of morphological changes between different foraging modes. For this, we obtained the difference between the slope vector angles (Collyer *et al.* 2015) and performed a permutation resample procedure with 1000 replicates to assign a probability (Adams and Otárola-Castillo 2013). We used the morphological disparity test, accounting for the wing centroid size effect on shape variance, to compare morphological variances (as Procrustes distance from the group mean) between foraging guilds, and permutation procedures to test for significant differences between groups.

To evaluate the wing centroid size variance that could be related to foraging guilds, we performed a PGLS model. In this model, we considered the phylogenetic structure of residuals through the phylogenetic distances matrix to calculate the phylogenetic covariance matrix, estimated in the package *APE* (Paradis *et al.* 2004). The significance of the *F* statistics, assigned to the foraging guilds effect, was tested using the permutation procedures previously described. To describe the direction of changes in wing shape among foraging guilds in the species, we optimized foraging guilds in the phylogeny using the stochastic mapping function in the package *GEIGER* (Pennell *et al.* 2014) and fitted three likelihood models for discrete character evolution: an equal-rate (ER) model, with a single parameter determining all transition rates, a symmetric (SYM) model, in which forward and reverse transitions have the same rate parameter, and an all-rates-different (ARD) model, where each rate is determined considering the terminal states. Possible states and transition probabilities were estimated using continuous-time Markov models (Yang 2006) with 1000 simulations. Considering the limited number of species, we used a constant rate of change across the tree.

The relationship between wing shape and size and flight descriptors

To evaluate the covariance between the average wing shape and flight descriptors per species, we performed a phylogenetic partial least squares (PLS). The PLS method evaluates the covariance between the two matrices, using a singular value decomposition of the covariance matrix between two sets of variables to extract a pair of PLS axes for each set and to evaluate their integration (Klingenberg and Marugán-Lobón 2013). The phylogenetic approach to the PLS quantified the degree of phylogenetic morphological integration between the two matrices, based on the previously calculated phylogenetic covariance matrix. Correlation between vectors was assessed statistically using permutation procedures inside data matrices (Adams and Felice 2014) with 1000 replicates.

RESULTS

Variation in wing shape and size related to foraging guilds

The reconstructed phylomorphospace for the average wing shape for species showed the greatest shape variance in the direction of families and foraging guilds (Fig. 2). A total of 59% of wing shape variance was described by the first two PCs (39% and 20%, respectively). On PC1, we observed the greatest variance in the middle and distal parts of the wing (landmarks 4:14; Fig. 2), indicating broad wings in the negative direction of the axis, where the family Phyllostomidae and the narrow space gleaners were located. In contrast, the longest, thinnest, and most pointed wings were observed in the positive direction of the axis, where the insectivorous family Molossidae was located. The other families were observed in the middle of the space, with the greatest variance on PC2. On this axis, we observed the greatest variance in the fifth digit (landmarks 12:14; Fig. 2) and in the wing tip (landmarks 7 and 8), with shorter digits and downward-oriented wing tips indicated in the negative direction of the axis, where edge space foragers and most of the Vespertilionidae species were located. Some narrow and edge space foragers were found

in the opposite positive direction of the axis, showing longer digits and broader wings. The wing shape phylomorphospace recovers morphological similarities between closely related species, indicated by the proximity of species from the same family within the PCA space (Fig. 2A). This pattern of grouping is more evident in the family Phyllostomidae and is in contrast to the family Vespertilionidae, in which greater variance is observed in both of the principal axes plotted.

The PaPC analysis showed a low phylogenetic signal in wing shape evolution, considering the dissimilarities in data distribution in both spaces (Fig. 2). The covariance between the data and phylogeny associated with the first two components (PaPCs) was < 1 ($RV = 0.037$), and the PaPC space indicated similarities in shape among most families and the highest divergence in some vespertilionid species (Fig. 2B). A low phylogenetic signal was also recovered from the statistical analysis. Although we found a significant phylogenetic signal in wing shape ($K_{\text{multiv}} = 0.20$, $P = .002$), this value indicated lower shape variance than would be expected under the BM model of evolution, meaning that shape variance does not depend on the elapsed evolutionary time.

Morphological divergence does not depend on the time of evolution, but a comparison of the phylogeny and morphological cluster dendrogram indicates similarities between shape and phylogenetic relationships in the families Molossidae and Phyllostomidae (Fig. 3). Moreover, some differences in the position of species between trees were observed within Phyllostomidae. Only the haematophagous phyllostomid species *Desmodus rotundus* was closer to the edge space foraging vespertilionids. Likewise, vespertilionid species were grouped in the morphological dendrogram, with a high mixture of non-closely related species in the morphological cluster, except for *Corynorhinus townsendii*, which is closer in shape to the phyllostomid species.

The evolutionary mode for both wing shape and centroid size variables indicates differences in the diversification of both characters. The MDI statistic shows higher deviations from the BM model of evolution for the wing shape ($MDI = 0.058$) than wing centroid size ($MDI = 0.0047$). We obtained *P*-values $> .157$ for the MDI, suggesting that the observed MDI values are unlikely to be the result of a BM mode (Slater *et al.* 2010). The Disparity Through Time (DTT) for the 67 species included in the phylogeny showed a single disparity peak at the end of the relative time scale (0.8–0.99). Considering the age of the root (58 Mya), this time is equivalent to the period between 11.6 and 0.5 Mya (Fig. 4). Accordingly, the lowest AICc and highest log-likelihood were obtained in a selective regime BM model with constant rate ($AICc = -1277.53$, $\log\text{-likelihood} = 677.971$; Table 2); it was based on symmetric rates of transition across foraging guilds supported by previously described foraging guilds optimization models. Likewise, for wing centroid size, the lowest AICc was obtained in the BM model, and similar log-likelihoods were observed among basic models (Table 2).

Statistical tests of convergence were applied to the foraging space, considering morphospace ordination. These results do not support convergence in the open or narrow space ($C1-C4 < .07$, $P > .25$), but significant convergence measurements were found to species occupying the edge foraging space

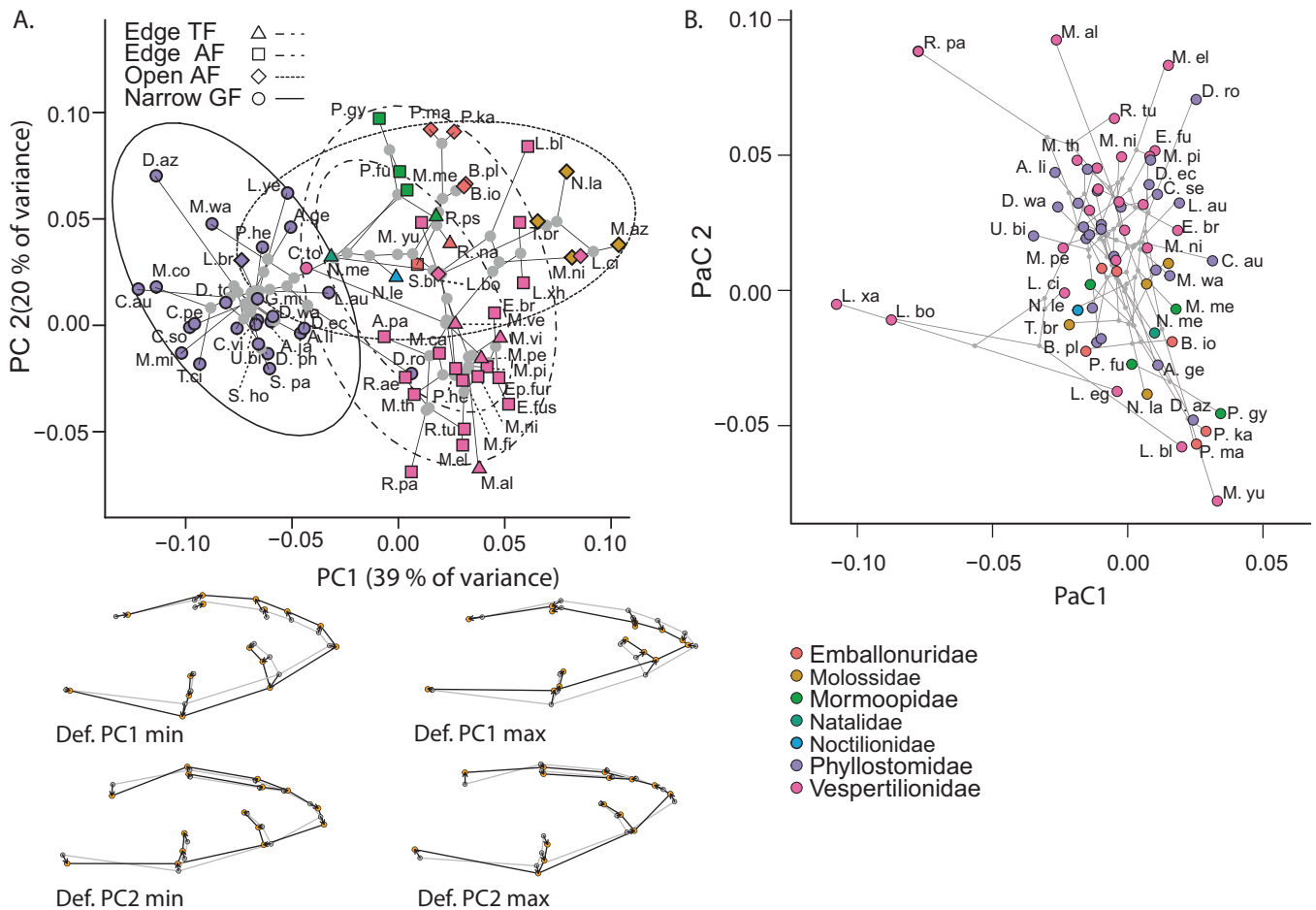


Figure 2. A, phylomorphospace of the first two components (PCs) of wing shape for 67 bat species, illustrating families (colours), foraging guilds (symbols), and the relationship among species. B, phylogenetically aligned principal component analysis (PaCA) morphospace of the first two phylogenetically aligned components (PACs) of wing shape variation, illustrating families (colours). Deformation grids below panel A are indicating landmark displacements from consensus shape (grey configurations) on the first two principal components (PCs). Ellipses including foraging guilds were drawn on the principal component analysis space.

($P < .03$). Inside edge space species, the levels of convergence were low but significant ($C1 = .161$, $C2 = .013$, $C3 = .073$, and $C4 = .001$). According to the $C1$ estimator, ~17% of the phenotypic divergence inside this group is explained by convergence; the other estimators presented lower values than $C1$, with convergence explaining 7% of the total evolution of lineages and 1% of evolution in the clade containing convergent lineages.

The statistical models did not indicate a significant effect of relatedness in wing shape variance of foraging guilds, but a significant effect of centroid size and its interaction with foraging guilds was found (Table 3). In accordance, the pairwise comparison between allometric vectors (shape regressed on centroid size) of foraging guilds showed a significant angle between edge space trawling foragers and open space aerial foragers (angle = 2.52, $P = .007$), whereas the other comparisons between vectors were not significant ($P > .17$). The species average regression score of the first PC of shape variance on the species average centroid size, within the foraging guilds, indicated a greater range of centroid size in edge space trawling foragers than in edge space aerial foragers, but similarities (overlapping) were found in the shape axis (Fig. 5). A high shape variance around the ordinary least-squares adjustment within groups was observed (Fig. 5).

The highest disparity was found in the open space aerial foragers (0.014), followed by edge space aerial foragers (0.0074), narrow space gleaners (0.007), and finally, edge space trawling foragers (0.006). We observed significant differences in morphological disparities in the comparison of the open space aerial foragers with other foraging guilds ($P < .01$). This group is divergent in shape but overlapped with narrow space gleaners in terms of the range of wing centroid size (Fig. 5).

We did not find a significant effect of foraging guilds on centroid size variance. The generalized linear squares model, considering the phylogenetic structure of residuals, indicated a non-significant proportion of centroid size variance ($R^2 = 0.11$, $F_{3,66} = 2.477$, $P = .08$) assigned to foraging guilds. We observed greater wing size in species from narrow spaces, most of which were phyllostomids (node 109), compared with families grouping as open space (nodes 72 and 99) or edge space (node 75; Fig. 6) foragers. A trend of wing centroid size increase was observed on the phylogenetic tree of the 67 species analysed, with the more recent ancestors presenting larger sizes than the earlier ones. We used the symmetric rate (SYM) model to optimize foraging guilds, given its lower AICc value (120.281) compared with those of ARD (126.278) and ER

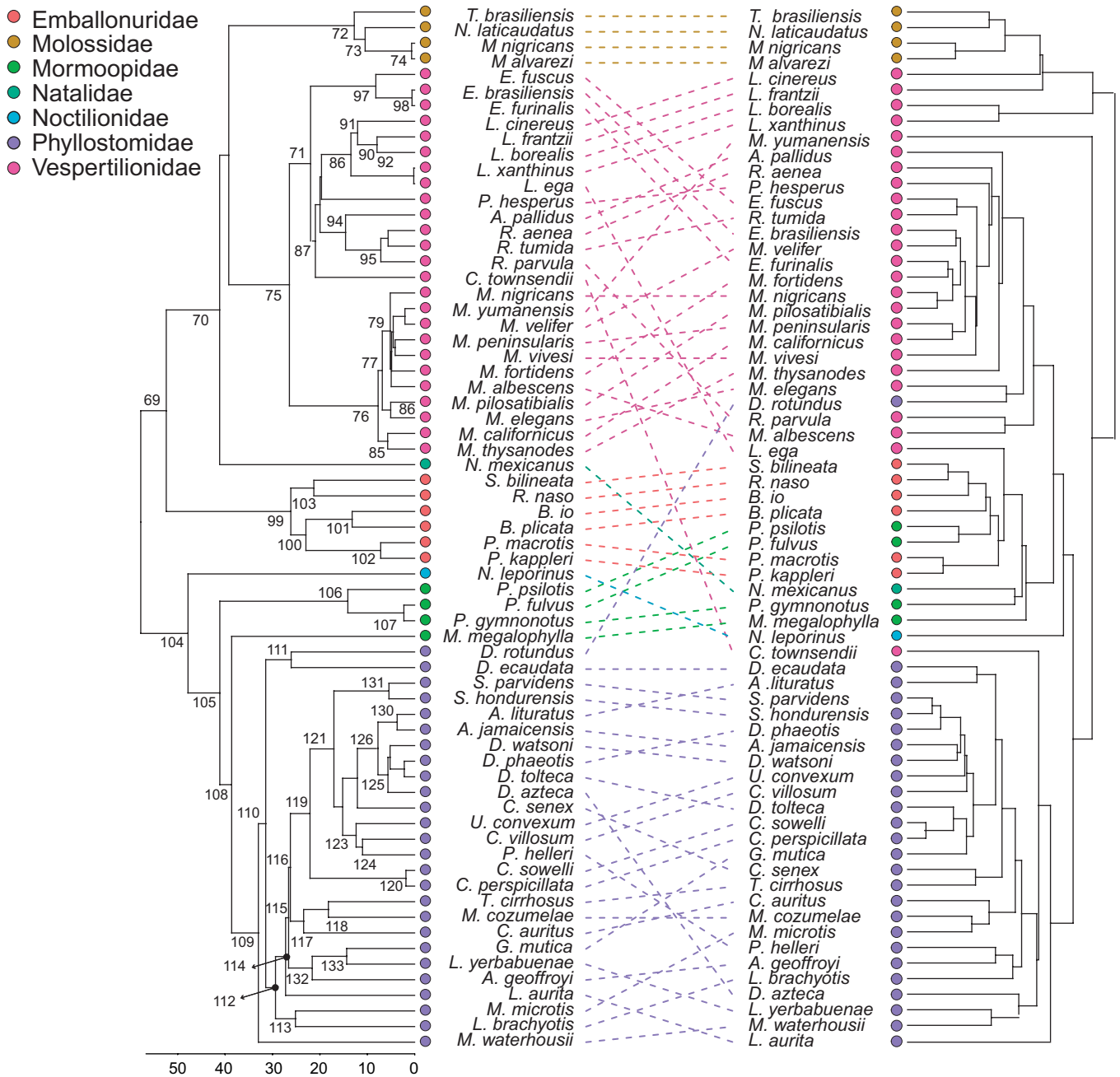


Figure 3. Pruned tree from Upham *et al.* (2019), illustrating the position of species and nodes (left) used as a reference of bat species relationships connected to a dendrogram based on wing shape similarities (right) among 67 species, illustrating changes in species position. Family membership is indicated with colours.

(122.604). The optimization of foraging guilds (Fig. 6B) suggested that edge space aerial foragers was the most likely ancestral state in the family Vespertilionidae (node 75), in contrast to the primary insectivorous families Molossidae (node 72) and Emballonuridae (node 99), in which the most likely ancestral state was open space aerial foragers. The narrow space gleaners seems to be the ancestral state of the family Phyllostomidae (node 109), first appearing in the node shared with the family Mormoopidae. At the most basal node, the edge space aerial foragers was the most likely ancestral state for all the bat families considered here.

Covariation between wing morphology (shape and centroid size) and flying descriptors

The phylogenetic PLS identified a significant and positive association between wing shape and biomechanical descriptors of flight, considering the phylogenetic structure of the residuals. We found a high and significant correlation ($R = 0.692$, $P = .001$) between the first PLS vector of each matrix, the wing shape, and biomechanical descriptor matrices. Similar results were found in the two-block PLS analysis ($R = 0.765$, $P = .001$), without considering the phylogenetic relatedness among species. Differences in wing shape thus have consequences for

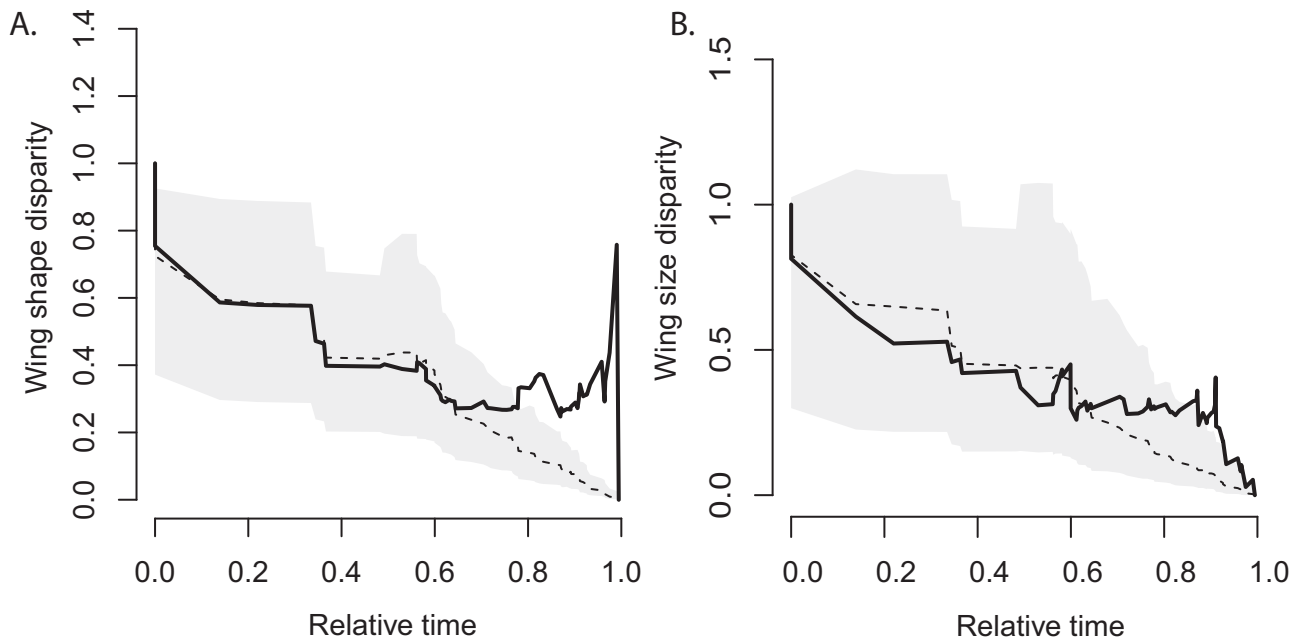


Figure 4. Wing shape (A) and wing size (B) disparities through evolutionary time (relative time) of a phylogenetic tree for the 67 bat species analysed. Shaded areas indicate the morphological disparity index (MDI) statistic through 1000 replicates; dotted lines indicate the expected MDI under the Brownian motion model; and continuous lines indicate the observed average extant disparity at that relative time, representing the average disparity of subclades with ancestral lineages that were present at that time, relative to the disparity of the entire taxon (Harmon et al. 2003).

Table 2. Results of the evolutionary models compared with wing shape and centroid size. We present the corrected Akaike information criterion (AICc) and the likelihood-ratio tests (log-likelihood) for each model. Abbreviations: BM1, Brownian motion including selective regime and constant rate; BMM, Brownian motion including selective regime and variable rates among states.

Model	Wing shape		Wing centroid size	
	AICc	Log-likelihood	AICc	Log-likelihood
Brownian motion	-1117.231	568.9	383.655 ^a	-189.733
Ornstein-Uhlenbeck	-1080.39	567.2987	384.326	-188.972
Early burst	-1060.964	552.958	384.326	-188.972
Selective regime BM1	-1277.53	677.98 ^a	403.816	-199.814
Selective regime BMM	-1025.061	618.042	409.7283	-195.623

^aModel with better performance.

biomechanical flight descriptors independently of the degree of relatedness between species. Regression of the flight descriptor with wing shape presented extreme values on both axes for both the narrow space gleaners and open space aerial foragers (Supporting Information, Fig. S1).

Overall, species with the highest WAR also presented the highest RWL (Supporting Information, Fig. S2), as was the case for molossid species, including those of the genus *Molossus*, *Nyctinomops laticaudatus*, and *Tadarida brasiliensis*, all of which also had a small wing centroid size (ranging from 14.38 to 19.75; Fig. 5). In contrast, low values of WAR and RWL were accompanied by high values of centroid size (Supporting Information, Fig. S2). In the case of large carnivorous phyllostomids, such as *Trachops cirrhosus* and *Chrotopterus auritus*, the lowest values of WAR were observed. Deviations from this pattern were observed in *Natalus mexicanus*, an insectivorous species of intermediate WAR value but with the lowest RWL value.

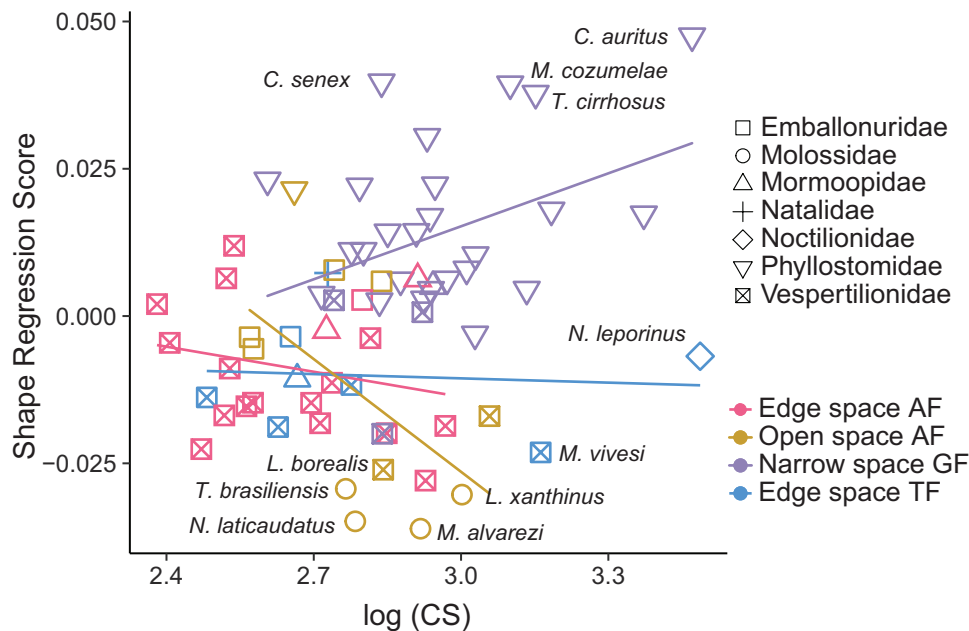
DISCUSSION

Our results partly support the hypothesis that wing shape evolution in bats has mainly been influenced by food search and capture mode (foraging strategy), characterized in foraging guilds. The evolution of wing shape does not significantly fit an ordinary BM model and seems to adjust to different evolutionary processes depending on the family and foraging space, instead of the capture modes. This means that its evolution is not dependent on the evolutionary time elapsed (Harmon et al. 2003, Zelditch et al. 2015, Collyer and Adams 2021). In contrast, the evolution of wing size (centroid size) seems to fit better to a BM model of evolution and shows lower correspondence to foraging guilds than to shape, meaning that the variables used as flight performance descriptors are correlated with the wing shape. Consequently, species foraging in open areas and using an aerial foraging strategy (thin, long, and small wings) have the opposite

Table 3. Results from the phylogenetic generalized least squares model testing the effect of mean centroid size (CS), foraging guild, and their interaction (model structure: Shape ~ log(CS) + Foraging guild + log(CS) × Foraging guild).

Response: wing shape	d.f.	Sum of Squares (SS)	Mean Squares (MS)	R ²	F	Z	Pr(>F)
Log(CS)	1	0.004	0.004	0.047	3.751	1.787	0.027*
Foraging guilds	3	0.002	0.001	0.033	0.888	0.339	0.358
Log(CS): foraging guilds	3	0.012	0.004	0.173	4.632	2.003	0.034 ^a
Residuals	59	0.052	0.001	0.735			
Total	66	0.070					

^aSignificant proportions of variance explained by a factor or covariable.

**Figure 5.** Regression score of the average wing shape of species with the logarithm of wing centroid size (CS) and with ordinary linear squared adjustments within each foraging guild. Families (symbols) and foraging guilds (colours) are indicated. Foraging modes: aerial foragers (AF), trawling foragers (TF), flutter detecting (FD), and gleaning foragers (GF).

morphology to that of species foraging in narrow spaces and using a gleaning strategy (thick, short, and large wings), while species foraging in the edge space present an average morphology. These morphological extremes also represent opposite values in terms of flight biomechanical descriptors and different families, an association that is maintained when we consider the phylogenetic context. Our results indicate that wing evolution could be influenced by foraging space in bats, but different scenarios from convergence in wing shape and size evolution are discussed below.

Evolution of wing shape in relationship to foraging guilds: morphological and ecological convergence?

The low phylogenetic signal recovered for wing shape evolution ($K_{\text{multiv}} = 0.20$) indicates lower shape variance than was expected, depending on the time of divergence, based on the BM model of evolution (Adams 2014b, Collyer and Adams 2021). A low phylogenetic structure in patterns of shape variance is often associated with ecological opportunities covered by different species (Blomberg *et al.* 2003), and it is the scenario under which morphological and ecological convergence could

be detected (Zelditch *et al.* 2017). The presence of convergence is the evidence that the observed phenotypes are predictable from ecological niches (Losos *et al.* 2006, Losos 2011), and it is most likely to occur when ecological constraints limit the array of niches and when functional constraints limit the expression of a single morphological optimum for each of them (Zelditch *et al.* 2017). Considering the dissimilar morphospace ordinations (phylomorphospace and PaPC), we expect that mechanisms other than phylogenetic relatedness, such as a combination of ecological and phylogenetic signals in particular groups, could explain wing shape evolution in bats. The phylogenetic signal levels might simply indicate something concerning the fit of a BM model or the correlation between shape divergence and the evolutionary time, but different evolutionary processes can produce particular patterns of phylogenetic signal (Blomberg *et al.* 2003, Revell *et al.* 2008, Adams 2014b). Our findings suggest that ecological constraints could promote the wing shape evolution of edge space foragers close in morphospace, which exhibit significant but low values of convergence that could be explained by incomplete convergence. In this case, species are located closer together in morphospace than their ancestral relatives

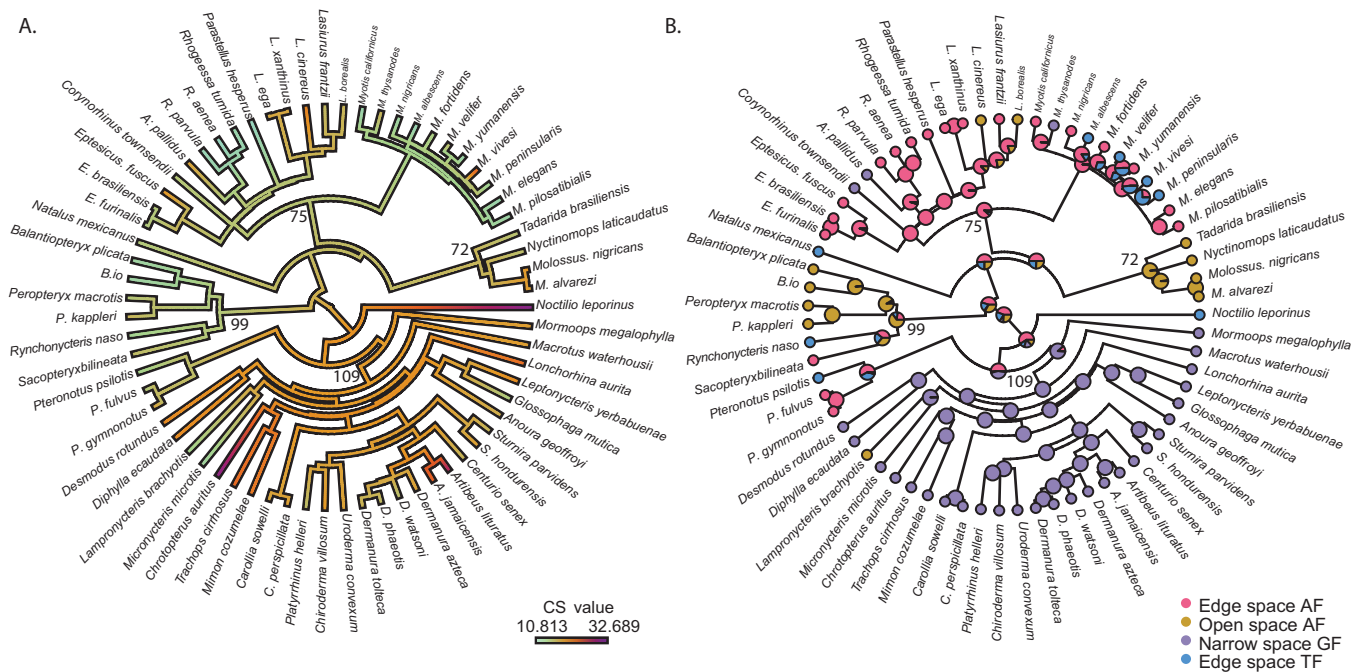


Figure 6. Optimization of wing centroid size (CS) and diet on the phylogeny of bats. A, optimization of CS changes using squared parsimony. B, optimization of foraging guilds using symmetrical rates of change. Foraging guilds and their probabilities of transition at nodes are illustrated with colours. Foraging modes: aerial foragers (AF), trawling foragers (TF), and gleaners (GF).

but remain separated (Stayton, 2006, Grossnickle *et al.* 2020). Species with an edge space strategy do not overlap completely in the first two PCs of morphospace as is noted in incomplete convergence (Grossnickle *et al.* 2020), but remain separated on the first PC.

In our study, ecological signal can be observed in some distantly related species that appear close in shape ordination (particularly in the first PC), occupying the same foraging space (e.g. *Corynorhinus townsendii*, *Antrozous pallidus*, and most of phyllostomid species). In addition, low RV1 values from the PaCA analyses (e.g. 0.067), even greater than those observed in our data (0.037), have been related to ecological signals regardless of phylogenetic variation (Collyer and Adams 2021). Although when considering the phylogenetic structure of the PGLS model, the significance of the foraging guild disappears, some ecological signal could be detected in wing shape ordination. Extreme morphologies and foraging spaces were concentrated in clades that correspond to the families Phyllostomidae (narrow space) and Molossidae (open space), with only a few species of Vespertilionidae and Emballonuridae exhibiting these strategies and locating close in morphospace to clades sharing the same strategy. This ordination has been defined as non-reciprocal convergence because only one terminal converges onto a clade, but it is not the nearest neighbour of any of those taxa (Stayton, 2008). The observed family dependence in the occurrence of extreme morphologies and the non-reciprocal convergence could explain the lack of significance of foraging guilds in the PGLS model.

Another possible explanation for the concentration of extreme values in morphology and foraging space within the Phyllostomidae and Molossidae families could be that wing shape was fixed early in their evolutionary history, with

subsequent low rates of morphological change within these clades. In agreement, the most probable model of wing shape evolution was the selective regime model with a constant Brownian rate, which is consistent with incomplete convergence and the lack of strength of attraction towards trait optima (Grossnickle *et al.* 2020). This model suggests different trait optima among regimes but a constant rate of change inside them and could potentially be explained by a broad adaptive zone (Polly 2004, Grossnickle *et al.* 2020). These families are moving towards opposite foraging guilds owing to their differences in dietary and habitat preferences (Norberg and Rayner 1987, Denzinger and Schnitzler 2013, Schmieder *et al.* 2015); however, they resemble in morphology and foraging space the lineages from other families in the phylomorphospace, as is the case with vespertilionid bats foraging in narrow spaces (e.g. *Corynorhinus townsendii* and *Antrozous pallidus*) or the open space foragers from the families Vespertilionidae and Emballonuridae.

Ecomorphological associations in bats demonstrate the high fitness of a particular wing morphology in a particular environment. However, it is not possible to determine whether wing morphology evolved as an adaptation to a particular environment, because we do not know the historical origin of the selective pressure (Losos 2011). Our results suggest the association of wing morphology and foraging patterns during bat evolution and divergent morphological trends between lineages currently recognized as families, probably from an edge space forager ancestor. Long-term differences between incompletely convergent clades have been related to unique ancestral conditions (Losos 2011) and support the idea of edge space as the foraging ancestral space. Our findings also suggest low evolutionary rates in morphological evolution, and this is supported by the low disparity observed in narrow space gleaners,

a foraging guild observed mainly in Phyllostomidae. In contrast, the most disparate morphologies from a consensus shape observed in open space aerial foragers could be an effect of the poor sampling of species, which are more difficult to capture with direct methods. However, the open space aerial foraging could be a character state that probably first evolved in the ancestors of Molossidae, considering their divergence time of ≥ 28 Mya in America (Ammerman *et al.* 2012).

Despite a limited sampling of the total bat diversity worldwide (4.6% of the species and 16.2% of genera, respectively), the pattern of morphological diversification among foraging guilds reveals a possible scenario of incomplete convergence in species occupying the edge space and lower divergence in species from narrow space than from open space, but sampling more species is required to make inferences about evolutionary rates. Our results indicate an increased MDI in the recent evolutionary history of bats, which presented a broader peak for wing shape than for wing centroid size, and a positive deviation from the median expected disparity, under a BM model. The observed disparity increment could explain the fit of a selective regime model of evolution to wing shape, in addition to deviations from the expected disparity under a BM model. This has been related to a high diversification of subclades with an overlap in morphospace occupation (Harmon *et al.* 2003, Slater *et al.* 2010). Considering that positive MDI values and those closer to one imply that the subclades account for a substantial proportion of the total variation and are likely to overlap in similar regions of morphological space (Harmon *et al.* 2003, Zelditch *et al.* 2015), the single disparity peak at the end of the time scale of bat species evolution could be related to the evolution of broad adaptive zones of wing morphologies.

Overlapping in the morphospace occupation of morphologies from the same foraging space generates high values of subclade disparities owing to greater intraclade than interclade morphological variance (Blomberg *et al.* 2003, Harmon *et al.* 2003, Buttler and King 2004). This pattern of high subclade disparity is observed in the recent history of bats by the contribution of vespertilionid subclades (nodes 94 and 76), representing the tribes Antrozoini and Myotinae (Roehrs *et al.* 2010). These tribes also exhibit greater variance in body size than other vespertilionid tribes, as is the case with *Antrozous* and *Rhogeessa* species, and convergences in morphology, foraging strategies, and diet, as in the case of *Myotis* species (Findley 1972, Fenton and Bogdanowicz 2002, Ospina-Garcés *et al.* 2016). However, this high level of disparity seems to be related to ecological differences in habitat use, such as the transition from open to edge foraging space in *Lasiurus cinereus* in particular, or wing shape differences between closely related groups, such as *Parastrellus* and *Lasiurus*, with the former being more similar to the wing morphology of *Myotis* or to the foraging patterns of this genus, such as hunting above ground or water (Wilson and Mittermeier 2019).

Wing ecomorphs associated with foraging space are supported by the comparison of phylogeny and the morphological cluster dendrogram, where the greatest correspondence between shape similarity and phylogenetic relationships was observed in the families Molossidae and Phyllostomidae (Fig. 3). In the latter group, only the haematophagous species *Desmodus rotundus* was close to vespertilionid species foraging in edge space. Previous studies have shown that *Desmodus rotundus* prefers to fly near

linear landscape features and to avoid open areas, as most captures occur at live fences and forest edges (Ávila-Flores *et al.* 2019). In contrast, the only phyllostomid suggested as an aerial forager in the canopy is *Lamproncycteris brachyotis*, which captures insects in the upper canopy or open spaces (Weinbeer and Kalko 2004). However, our results show that this species does not exhibit an open space foraging morphology. Considering the conservative wing shape presented in Phyllostomidae to occupy a high diversity of ecological niches, it is possible that minor changes in wing morphology could allow this species to alternate foraging patterns. In the other case, a more generalist morphology was observed in edge space foragers. For example, vespertilionid species were grouped in the same family cluster, but with a high mixture of non-closely related vespertilionid species of trawling and aerial foragers, apart from *Corynorhinus townsendii*, which is closer in shape to phyllostomid species considering its hovering–gleaning foraging behaviour and habitat preferences (Norberg and Rayner 1987, Fellers and Pierson 2002). Given that the family Vespertilionidae exhibits the highest diversity in foraging strategies, with a dominance of species foraging in the edge space, these results support the idea of edge space aerial foraging as the most probable ancestral state of the foraging guild in bats.

The evolution of morphological and ecological similarities, defined as ecomorphs or similar phenotypes in similar environments (Losos *et al.* 1998), comes from the partition of habitat resources among species (Losos 2011). The divergence of wing shapes between families and species restricted to a particular foraging space (open, edge, and narrow), considering the overlap between aerial foragers and trawling foragers from the edge space, supports the idea that foraging ecomorphs in bats have probably evolved by processes other than convergence. These ecomorphs were described previously by Norberg and Rayner (1987) in terms of body mass, general descriptors of wing morphology, and flight parameters, and are related to dietary groups, families, and resource partitioning. Likewise, Zuo *et al.* (2022) evaluated the correlated evolution of wing morphology and echolocation call parameters among foraging guilds and concluded that wing morphology, call duration, and call peak frequency could predict foraging guilds, supporting our finding about the existence of wing morphologies defined by the foraging space and by a particular combination of echolocation parameters. All these results support the idea that the evolution of wing morphology is accompanied by high variability within foraging ecomorphs, determined by dietary preferences, which are driven by body size, acoustic signals, and other niche dimensions (Denzinger and Schnitzler 2013, Zou *et al.* 2022), as mechanisms by which to avoid competition (Losos *et al.* 2006, Denzinger and Schnitzler 2013). This can be observed in the family Phyllostomidae, which is characterized by its great ecological diversity, including all the dietary items possible in bats, and our results show that it presents more stable wing morphology. In this sense, some divergent trends in wing morphology have been recognized in this family and are explained by differences in the habitat use by species (García-Herrera *et al.*, 2023). The inclusion of new species and other dimensions of the foraging niche, such as the acoustic signals, to compare evolutionary rates, could provide new evidence regarding the evolution of wing ecomorphs within bat families.

Variations in wing centroid size and flight descriptors among ecomorphs

With respect to variation in wing size, centroid size optimization in the phylogenetic hypothesis indicates a trend of increased wing size in the evolutionary history of bats. This trend is also dependent on the foraging guild, but not on changes in wing shape. We detected a weak association between wing shape and wing centroid size, indicating that different shapes could have similar wing size. Nevertheless, some interesting trends of centroid size variation were observed within the foraging guilds. Our results revealed a significant effect of the interaction between wing centroid size and foraging strategies on shape variance when we considered the relatedness of species. This means that different allometric patterns are observed among these groups and are not explained by phylogenetic structure. However, centroid size seems to be more dependent on divergence time, considering the MDI values and the adjustment to a BM model, and this is probably an effect of the increase in centroid size evolution, optimized in Phyllostomidae, which has been noted previously in the evolution of bat size (Giannini *et al.* 2012). However, it is necessary to consider that our species sample does not include biggest species of families of global distribution, such as Vespertilionidae (*Scotophilus nigrita*, 88–91 g), Molossidae (*Cheiromeles torquatus*, 150–196 g), or Emballonuridae (*Saccolaimus flaviventris*, 60 g; Wilson and Mittermeier 2019).

In the ecomorphological context, we found a greater range of centroid size variation in edge space trawling foragers than in edge space aerial foragers, but there were similarities (overlapping) in the shape axis (Fig. 5), promoting differences in allometric trajectories with respect to the other morphological extremes. A similar range of centroid size variation between edge space and open space foragers is attributable to the contribution of some species foraging over water; however, trawling species showed less change in shape in relationship to centroid size than the other groups. Within the trawling foragers, the greater body size of piscivores (*Noctilio leporinus* and *Myotis vivesi*) compared with aerial foragers has been explained by their prey preferences and the positive relationship between prey size and the dimensions of the bat skulls (Santana and Cheung 2016, Ospina-Garcés *et al.* 2017). Conversely, species of the family Phyllostomidae generally presented larger and more variable wing sizes than those of the other families. In this context, we observed that low values of RWL were accompanied by high values of wing size (Supporting Information, Fig. S2) in carnivorous species. This relationship has been related to the ability to carry prey and to the presence of a large membrane tail, owing to low wing loading values that generate the increased lift necessary to take large animal prey directly from the ground (Norberg and Rayner 1987). Although we did not include the tail membranes in the wing area calculations, our observations support the idea that carnivorous species have a relatively large wing area to carry their weight in flight, in addition to that of heavy prey.

In general, the variability in wing size of species in the family Phyllostomidae agrees with the evolution of a diversity of trophic niches and body sizes that has occurred within Phyllostomidae (Giannini and Kalko 2005, Giannini *et al.* 2020). The diversity of diets presented by members of this family is congruent with divergent trends in the body size of its species, with the magnitude

of change biased towards increased body size, but with decreased size in some particular dietary groups (Giannini *et al.* 2020), as in the case of plant specialist frugivores or small insectivores. This ecological diversity was colonized with a wing morphology of greater stability (lowest shape disparity) and could be the result of different evolutionary dynamics, compared with other ecomorphs.

In the opposite direction of wing shape variance, the open space aerial foragers showed an increase of wing centroid size in Molossidae and some Vespertilionidae species, particularly from the genus *Lasiurus* (Fig. 5). Although vespertilionids did not present the largest wing size (centroid size), they did exhibit the highest RWL, meaning that they can carry more weight per unit wing area than the largest phyllostomids, considering that RWL is an index of wing loading corrected for the effect of body size. Species with low wing loading are expected to fly slowly and make tight turns, compared with those having high wing loading and more rapid flight (Thollessen and Norberg 1991). For example, insectivorous species that fly primarily in open areas exhibit longer hand wings and more pointed wing tips, in addition to the highest wing loadings (Norberg and Rayner 1987, Thollessen and Norberg 1991). This is particularly true for species from the Molossidae family and for open space aerial forager vespertilionids (some *Lasiurus* and *Myotis* species), which present greater WAR and RWL than other species at the family level. Moreover, species with higher aspect ratios experience lower drag and enhanced aerodynamic efficiency and could therefore have the greatest capacity for dispersion (Luo *et al.* 2019).

In terms of flight descriptors, our results indicate that species foraging in edge space present a general wing shape (intermediate range of shapes on the PC1) and support the intermediate biomechanical values observed in vespertilionids (Luo *et al.* 2019), with movement towards more extreme flight descriptors and wing shapes in species of open vs. narrow foraging space. Moreover, the high and significant association between wing shape and flight descriptors (WAR and RWL) is maintained even when the phylogenetic structure in the PLS regression model is considered, as has been reported previously for the relationship between wing morphology and the geographical range of species (Luo *et al.* 2019), which supports the idea of some grade of morphological and ecological similarities.

Given that aerodynamic characteristics are the result of variations in wing elements (i.e. metacarpals and phalanges), the relative importance of these elements in wing shape variation changes among ecomorphs. Morphometric variation in wing distance among foraging guilds has been reported. The thin, long, and pointed wings of species foraging in the open space differ significantly from other guilds in the proportion between forearm and the third digit length, being highest in this group. In contrast, guilds that forage in highly cluttered spaces using a gleaning strategy show higher values for the proportion between the forearm and fifth digit and lower ones for the proportion between the third and fifth digits (Castillo-Figueroa 2020). In agreement, our results indicate that wing elements contribute to place in opposite regions of morphospace the open and narrow space foragers, with the former showing an enlargement of the third digit, corresponding to landmarks 4 and 6–8 in our morphospace (Fig. 2A), that has been related

to longer hand-wing length in fast and economic flights typical of aerial insectivores (Dietz *et al.* 2006, Castillo-Figueroa 2020). In addition, the wing shape deformation in narrow space foragers recovered landmark displacements on the fifth digit (landmarks 12–14), indicating its lengthening. In agreement, it has been documented that phyllostomid species foraging in narrow spaces show a pattern of modular wing variance, with particular allometric trends in the first phalanges (Stevens and Guests, 2022). These morphological traits have been considered as indicative of wider wings, with high manoeuvrability and hovering ability, in narrow space foragers (Dietz *et al.* 2006, Castillo-Figueroa 2020).

The ecomorphological differentiation, revealed by wing shape and biomechanical variation, agrees with the expected patterns of variation in flight descriptors among foraging guilds, with the associations of high wing loading and pointed wing tips with high-speed flight and of low wing loading and rounded wing tips with low-speed flight. Both associations of descriptors can be observed in opposite foraging styles and diets, such as aerial foragers vs. gleaners foragers (Findley 1972) or insectivores vs. frugivores (Norberg and Rayner 1987). In addition, some interesting deviations from the expected flight descriptor values were observed; in the case of *Natalus mexicanus*, we recovered a lower RWL than expected for the wing size and foraging space of this species. This is consistent with previous observations that classify *Natalus mexicanus* as a species with an extremely slow and maneuverable flight, hovering or fluttering while picking insects from surfaces (Torres-Flores and López-Wilchis 2018, Santos-Moreno and Soriano-Cruz 2019). Particularly in the case of *Natalus mexicanus*, the observed lowest RWL could indicate the consumption of large, heavy prey relative to its size (Norberg and Rayner 1987). Other deviations were observed in the emballonurids *Balantiopteryx* and *Peropteryx*, considered as foragers in open space (Jung *et al.* 2007), but more similar in WAR and RWL to species that forage in the edge space.

Methodological considerations

We recognize the limitations of our study in terms of the number of species representing the entire diversity of bats worldwide (Simmons & Cirranello, 2023). This limited sample size reflects a bias towards foraging guilds, in the case of narrow space gleaners foragers, which are generally easier to capture than other guilds. However, it does not seem to affect the pattern of similarities among species in the same foraging space, because convergence was not detected inside the most abundant groups, whereas it was observed in the middle of morphospace corresponding to the edge space foragers. Additionally, we did have representation of seven families from the nine families distributed in America and covered most of the foraging guilds, which exhibited a divergent pattern in wing shape and flight descriptors that agrees with previous findings. Considering the correspondence between wing morphology, foraging space, and flight descriptors, deviations from the assigned foraging guilds in the bat species analysed suggest the need for a revision of foraging strategies and dietary habits. Although incomplete convergence was identified only between species occupying the edge space, it is probable that a larger dataset might reveal some grade of convergence in other groups.

CONCLUSIONS

The evolutionary mode suggested for wing shape is independent of the time of divergence for bat families but seems to be influenced by ecological pressures associated with foraging space, promoting ecomorphological relationships between wing shape and foraging strategies. Although morphological convergence could not be detected, the findings that a selective regime model presented the best fit to the observed variation in wing shape in 67 different species, and the significant deviations from MDI disparity expected under the BM model, suggest different optima and, probably, a broad adaptive zone visited during the evolution of wing shape (Zelditch *et al.* 2015). Different disparity trends were observed among families, with Phyllostomidae being more stable than those families occupying the edge or open foraging species, in contrast to open space aerial foragers, with the open space aerial foragers having the most divergent wing shapes relative to a consensus shape. However, these hypotheses require further testing with a greater representation of true bat diversity.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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AUTHOR CONTRIBUTIONS

SMOG: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing - Original Draft. VZG: Methodology, Resources, Writing- Reviewing and Editing; JMLG: Methodology, Resources, Writing-Reviewing and Editing; MMM: Methodology, Resources, Writing-Reviewing and Editing; RAF: Methodology, Resources, Writing- Reviewing and Editing; AK: Conceptualization, Funding acquisition, Methodology, Resources, Writing-Reviewing and Editing. JO: Methodology, Resources, Writing- Reviewing and Editing. CISS: Methodology, Resources, Writing- Reviewing and Editing; MCMG: Conceptualization, Funding acquisition, Methodology, Project administration, Writing- Reviewing and Editing.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

All data used as input for our analyses are available upon request. The nexus files containing the trees used to comparative analyses are available at: <https://vertlife.org/phylosubsets/>

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