

Article

Wing Shape and Size Variation in Migratory Sylviid Warblers: Links to Ecology and Migration

Alexis Agtzidis ^{1,*} , Christos Barboutis ²  and Sinos Giokas ¹ ¹ Department of Biology, University of Patras, 26500 Patras, Greece; sinosg@upatras.gr² Antikythera Bird Observatory, Hellenic Ornithological Society, BirdLife Greece, 52 Ag. Konstantinou Str., 10437 Athens, Greece; cbarboutis@ornithologiki.gr

* Correspondence: alagtzidis@gmail.com

Simple Summary

The wings of birds are finely tuned by evolution to meet specific ecological demands. We investigated this assumption by comparing the wing morphology of three migratory warblers that have a common ancestry—the Garden Warbler, Eurasian Blackcap, and Common Whitethroat—during their autumn stopover on the Greek island of Antikythera. Our analysis combined traditional biometrics with geometric morphometrics to reveal distinct wing shapes aligned with each species' behavior. The Garden Warbler's long, pointed wings are adapted for energy-efficient, long-distance flight. In contrast, the Eurasian Blackcap's shorter, rounder wings provide superior maneuverability for navigating dense foliage. The Common Whitethroat exhibited an intermediate form, balancing both efficiency and agility. These findings underscore how morphology reflects a species' lifestyle and improve our understanding of how physical adaptations relate to different environments and migration challenges. These insights are particularly relevant in the context of habitat fragmentation and climate change, as wing morphology is often used to indicate dispersal ability and species resilience.

Abstract

Avian morphology is a product of complex interactions among ecology, behavioral traits, and phylogeny. The wing, as a primary aerodynamic structure, is particularly indicative of these selective pressures, which are especially pronounced in migratory species. This study investigates interspecific variation in wing morphology among three migratory warblers of the family Sylviidae: the Garden Warbler (*Sylvia borin*), Eurasian Blackcap (*Sylvia atricapilla*), and Common Whitethroat (*Curruca communis*). We combined traditional morphometric measurements (body mass, wing length, primary feather lengths, and wing area) with functional aerodynamic indices (wing loading, aspect ratio, Kipp's index) and geometric morphometric analysis of wing shape. Data were collected during autumn migration on the Greek island of Antikythera, a key stopover site in the Mediterranean. Our analysis revealed distinct morphological adaptations: Garden Warblers possessed elongated, pointed wings with a high aspect ratio, indicative of selection for long-distance, energy-efficient flight. Conversely, Eurasian Blackcaps exhibited shorter, rounder wings, a morphology associated with high maneuverability and quicker takeoffs in dense habitats. Common Whitethroat displayed an intermediate wing morphology, balancing aerodynamic efficiency with maneuverability. These findings possibly demonstrate how wing morphology reflects a compromise shaped by selective pressures, including migratory distance, habitat structure, foraging behavior and predation risk.



Academic Editor: Reuven Yosef

Received: 30 December 2025

Revised: 6 February 2026

Accepted: 28 February 2026

Published: 5 March 2026

Copyright: © 2026 by the authors.

Licensee MDPI, Basel, Switzerland.

This article is an open access article distributed under the terms and

conditions of the [Creative Commons](https://creativecommons.org/licenses/by/4.0/)[Attribution \(CC BY\)](https://creativecommons.org/licenses/by/4.0/) license.

Keywords: wing morphology; geometric morphometrics; shape variation; garden warbler *Sylvia borin*; Eurasian blackcap *Sylvia atricapilla*; common whitethroat *Curruca communis*

1. Introduction

The morphology of an organism is the outcome of a dynamic interaction between intrinsic structure and extrinsic pressures. It reflects a reciprocal process where environmental demands shape functional design, which in turn defines the ecological opportunities and constraints an organism faces [1,2]. Wing morphology is a key component of the functional anatomy of birds, forming the principal aerodynamic structure that enables flight across nearly all avian taxa.

Because flight is a highly energy-demanding mode of locomotion, strong selective pressures are exerted for optimal structure and form of the flight apparatus to enhance flight performance and minimize energy expenditure [3–7]. Consequently, wing morphology is subject to a complex suite of interacting and often opposing selective pressures [8], resulting in functional trade-offs among the demands of many ecological and behavioral variables [4,5,9]. These selective pressures are associated with migration and aerodynamic efficiency [8,10–14], foraging strategies [15], habitat type [11,16], predation risk [17] and spring phenology of vegetation at breeding grounds [18]. Wing morphology has been shown to vary across different species, populations, age classes and sexes [14,19–22].

A fundamental trade-off exists between adaptations for efficient, sustained flight and those for high maneuverability and rapid take-off. For birds undertaking long-distance migrations, a substantial body of literature suggests that selection favors longer, more pointed and higher aspect ratio wings (i.e., $\text{wingspan}^2 / \text{total wing area}$; [8,23–25]). Based on avian flight aerodynamics [4,5], these types of wings minimize induced drag, as they generate little lift due to weaker tip vortices [26], reducing the energetic cost of transport and providing greater flight efficiency [5]. Wing sweep has also been shown to influence aerodynamic performance, with more swept wings allowing for less drag during flapping flight [27]. Conversely, shorter and rounder wings are known to generate greater lift at the tip, shed larger vortices and hence create greater induced drag [26], providing greater maneuverability and takeoff ability [11,23]. These wing traits are advantageous for birds living and foraging in cluttered habitats with dense vegetation [4,28,29] or birds susceptible to high ground predation rates [26]. Accordingly, wing morphology reflects a compromise between selective pressures associated with migratory flight and habitat-specific flight performance.

Investigating this adaptive compromise among species with differing degrees of relatedness can be informative, particularly when comparisons include both closely related taxa and more distantly related species within the same family. The present study focuses on three migratory passerines of the family Sylviidae: the Garden Warbler *Sylvia borin* (Boddaert, 1783), Eurasian Blackcap *Sylvia atricapilla* (Linnaeus, 1758) and Common Whitethroat *Curruca communis* (Latham, 1787). These species are all widely distributed, medium-sized Afro-Palearctic passerines (Figure 1), with most of their populations undertaking annual migrations along the European–African flyway. Garden Warblers and Eurasian Blackcaps are considered sister species, and Common Whitethroats represent a more distantly related lineage within the family [30,31]. In addition, there is strong evidence of sympatry across many parts of their breeding and migratory ranges [32–34].

The Garden Warbler and Common Whitethroat (hereafter ‘Whitethroat’) are long-distance trans-Saharan migrants that breed across much of Europe and western Asia, and winter in a wide range of areas in Africa [35–38]. The Eurasian Blackcap (hereafter ‘Black-

cap') exhibits striking variation in migratory patterns [39], ranging from long-distance trans-Saharan populations to short-distance or resident populations in southern Europe and North Africa [40]. Breeding populations of northern, central and eastern Europe are obligatory migrants, whereas southern European and north-western African populations are partial migrants, and Mediterranean and Atlantic Island populations are primarily residents [41,42].

In this study, we investigated interspecific variation in wing size and shape among the three Sylviid warblers, collecting data during their autumn passage from the small island of Antikythera, Greece, located in the eastern Mediterranean Sea. Our objectives were to a) achieve a holistic description of their wing morphology by using a combination of traditional morphometric measurements, aerodynamic indices and landmark-based geometric morphometric analyses and b) quantify differences in wing morphology among the three species. We predicted that the trans-Saharan long-distance migrants (Garden Warbler, Whitethroat) would exhibit more pointed and elongated wings compared to the more variable Blackcap, based on principles of avian flight aerodynamics. Furthermore, we discuss our results in the context of possible selective pressures related to daily survival and habitat use once migration is complete.

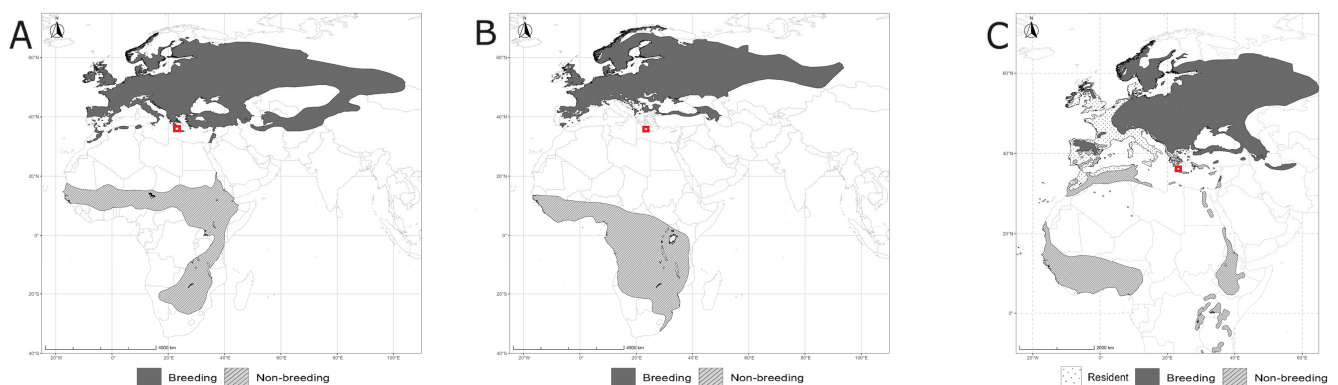


Figure 1. Distribution maps of (A) Whitethroat, (B) Garden Warbler and (C) Blackcap, shown from left to right. The maps depict the breeding, non-breeding and resident ranges. Data are from BirdLife International (2024, 2025) [37,38,43]. The red square indicates the approximate location of Antikythera Island, Greece, where all wing morphology data were collected.

2. Materials and Methods

2.1. Study Site

Fieldwork was conducted on the Greek island of Antikythera (35°51' N, 23°18' E). The island has an area of approximately 20 km² and is located in the Aegean Sea, roughly equidistant (31.5 km) between Kythera to the northwest and Crete to the southeast. The landscape is dominated by characteristic Mediterranean maquis and phrygana vegetation, while arable land covers only a small part of the island [44,45].

2.2. Data Collection

Data were collected during the autumn migration of 2022 at the Antikythera Bird Observatory as part of the long-term standardized ringing program for migrants run by the Hellenic Ornithological Society and the Hellenic Bird Ringing Centre. Birds were captured from 7:00 AM to 1:00 PM using 11 mist nets deployed at fixed locations in the island's center. Nets were checked at fixed one-hour intervals and were closed during adverse weather conditions, such as rain or strong winds, to ensure bird safety.

A total of 117 individuals from the family Sylviidae were measured, comprising 47 Garden Warblers (*Sylvia borin*), 40 Blackcaps (*Sylvia atricapilla*), and 30 Whitethroats

(*Curruca communis*). Trapped birds were identified to species. Age (adult/juvenile) and sex (male/female) were determined for those exhibiting sexual dimorphism, using standard morphological criteria [46,47]. Garden Warblers were not sexed, as the species lacks reliable external sexual dimorphism that can be assessed in the field. For individuals whose sex could not be reliably determined, it was recorded as unknown. From this sample, 111 individuals were used for geometric morphometric analysis of wing shape (43 Garden Warblers, 39 Blackcaps, and 29 Whitethroats).

2.2.1. Biometric Measurements

We recorded the following measurements: (a) *body mass* to the nearest 0.1 g using a portable digital scale [46]; (b) *wing length* (the length of the folded wing from the carpal joint to the tip of the longest primary) to the nearest 0.5 mm using a metal ruler [46]; (c) *wingspan* (the distance between the tips of the longest primaries on both wings); and (d) *Kipp's distance*, measured as the linear distance between the tips of the longest primary and the first secondary feather on the closed wing to the nearest 1 mm [25,48]. This index is a measure of wing pointedness (i.e., in pointed wings the longest primary is more distal) and is a known indicator of flight performance and dispersal ability [8,49].

To analyze wing shape in detail, we measured the lengths of primary feathers P9 to P1 (numbered distally to proximally; Figure 2) and the first secondary feather (S1), following Lockwood et al. [8]. The vestigial most-distal primary (P10) was excluded due to its minute size [50]. All feather lengths were measured from the tip to the point where they enter the skin with an accuracy of 1 mm. The relative lengths of specific primaries, such as a longer P9 and a shorter P5, are associated with a more pointed wing shape characteristic of long-distance migrants [51].

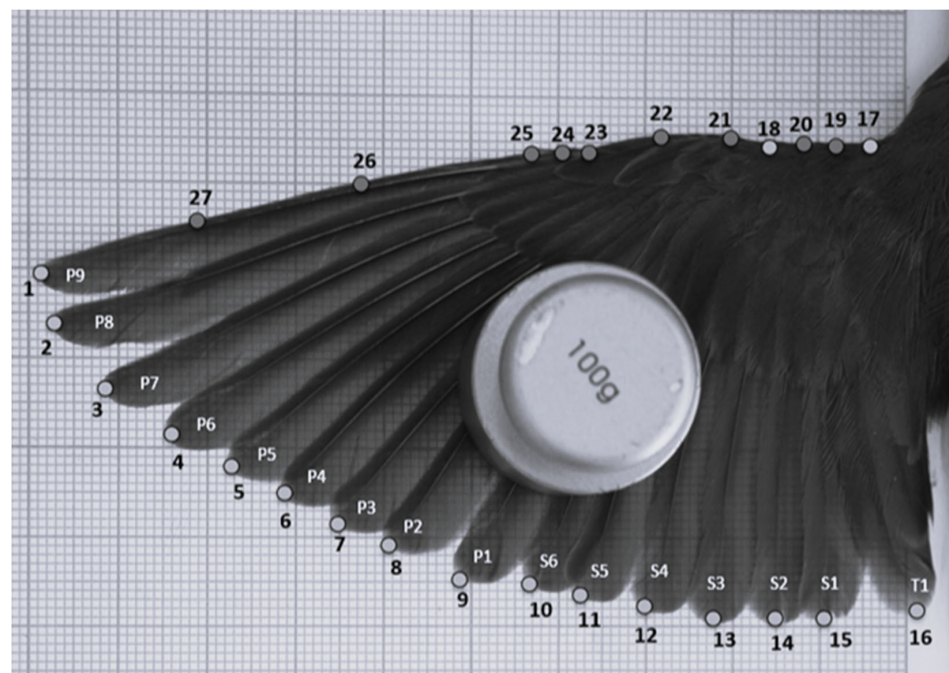


Figure 2. Depiction of the location of the 27 landmarks (LM) in a Blackcap wing for the purpose of landmark-based morphometric analysis. Primary feathers (P1–P9), secondary feathers (S1–S6), and the first tertial feather (T1) are indicated in white alphanumeric text.

To minimize bias, all measurements were taken by a single, experienced ringer, and only individuals not undergoing molt or exhibiting significant feather wear were included. Upon completion of all procedures, all birds were released unharmed at their capture site.

2.2.2. Geometric Morphometrics: Imaging and Digitization

Image Acquisition

To analyze wing shape, we obtained a digital image of the fully extended left wing of each bird using a Canon EOS 1300D camera. The camera was mounted on a tripod, positioned approximately 40 cm perpendicular to the wing with a $0.55\times$ magnification, ensuring the lens was parallel to the dorsal wing surface. The wing was gently stabilized in a fully outstretched position using a small metallic magnet. Each image included scaled graph paper (1 mm accuracy) for subsequent calibration and the bird's unique ringing code for identification. Only images from individuals without active molt or significant feather wear were analyzed.

Landmark Digitization

The wing shape was characterized using 27 two-dimensional landmarks (Figure 2), digitized using tpsDIG software, version 2.32 [52]. The landmark set was designed following the protocol of Provinciati et al. [14] to adequately capture the overall wing shape while adhering to the criterion of minimizing bending energy [53]. It comprised 18 homologous (*Type I/II*) landmarks placed at discrete anatomical structures: the shoulder joint (i.e., the anteroproximal point of the humerus; LM17), the wrist joint (i.e., the articulation of the ulna with the carpometacarpus; LM18), the tips of the rachis of the nine primary (LM1–LM9) and six secondary feathers (LM10–LM15), and the tip of the tertial feather (LM16). The vestigial distal primary was excluded. Additionally, nine semi-landmarks (*Type III*) placed along curved regions to capture proportional variation: two between the shoulder and wrist (LM19, LM20), two along the anterior vane of the ninth primary (LM25–LM27), three on the alula (LM21–LM23), and two on the vestigial (P10) primary feather (LM24, LM25). The alula region was included due to its aerodynamic role as a vortex generator, which influences lift and maneuverability [54,55]. The most-distal (P10) primary feather was included as its reduction varied among the three species, allowing additional variation in wing shape to be captured.

All landmarks were manually and consistently placed at corresponding positions across all scaled images by a single observer. This final set of digitized landmarks constituted the dataset for the wing morphospace used in subsequent statistical analyses.

2.2.3. Functional Indices

To complement the traditional measurements and geometric morphometric analysis, we calculated three functional wing indices: Kipp's Index (obtained directly in the field), aspect ratio, and wing loading. The latter two describe the shape and size of the wings, respectively, and are widely used in both aeronautical engineering and studies of animal flight [6].

Wing area was quantified from the digital images using ImageJ software, version 1.54g [56]. The area of the single extended wing was measured, and this value was doubled to estimate the total wing area. All image analyses were performed by a single observer to ensure consistency.

Aspect ratio, which reflects wing shape and thus aerodynamic efficiency, was calculated as the square of the wingspan divided by the total wing area [57]. Wing loading, an indicator of the force supported per unit of wing area, was calculated by dividing body mass by the total wing area [22].

Since wing loading can be sensitive to body mass variation, we tested for mass differences between age classes (adult vs. juvenile) within each species using independent t-tests. Levene's test confirmed homogeneity of variances in all cases. No significant differences in body mass were found (Garden Warbler: $t = -0.667$, d.f. = 45, $p = 0.507$;

Blackcap: $t = -0.346$, d.f. = 38, $p = 0.731$; Whitethroat: $t = -0.227$, d.f. = 27, $p = 0.822$). We therefore concluded that age-related bias in our wing loading estimates was negligible.

2.3. Analyses

2.3.1. Statistical Analysis of Morphometric Variables

We began by calculating the mean values for all morphometric variables for each species. To assess interspecific differences, we employed a combination of parametric and non-parametric tests. All variables were first tested for normality and homogeneity of variances (Levene's test); where necessary, data were log-transformed to meet these assumptions [58].

For variables satisfying the assumption of homogeneity of variances ($p > 0.05$), we used a one-way Analysis of Variance (ANOVA) with species as the independent factor. This was applied to wing length, wing area, the length of the 5th and 9th primary feathers, and aspect ratio. Where the ANOVA was significant, Tukey's HSD post hoc test was used for pairwise comparisons between species.

For variables that violated the assumption of homogeneity of variances even after transformation, we used the non-parametric Kruskal–Wallis test. This was applied to body mass, Kipp's Index, and wing loading. A significant Kruskal–Wallis result was followed by pairwise Mann–Whitney U tests to identify specific species differences.

The significance level for all tests was set at $\alpha = 0.05$.

2.3.2. Landmark-Based Morphometric Analysis

Geometric morphometric analyses were conducted using MorphoJ software (v. 1.08.02; [59]). The landmark dataset was first screened for outliers to identify potential digitization errors.

Data Preprocessing and Allometry Correction

A Generalized Procrustes Analysis (GPA) was performed to superimpose landmark configurations, removing variation due to position, orientation, and scale, thus isolating pure shape information [53,60,61]. Centroid size (the square root of the sum of the squared distances between the center of the configuration of landmarks and each landmark) was calculated as a measure of overall wing size. A multivariate regression of Procrustes coordinates on centroid size revealed a significant allometric effect in all three species (all $p < 0.05$). Consequently, the regression residuals were used as size-corrected shape variables for all subsequent analyses to isolate size-independent shape variation [62].

Exploring and Comparing Wing Shape

The size-corrected shape variables were analyzed using Principal Component Analysis (PCA) to identify the major axes of wing shape variation. Principal components (PCs) were visualized using transformation grids and wireframe diagrams to illustrate shape changes associated with each axis [63]. The first two axes (PC1 and PC2) often account for the most meaningful variation in the data.

To further investigate shape differences and determine the most important features discriminating groups, we performed a Canonical Variate Analysis (CVA) with 'species' as the grouping factor. The significance of pairwise differences in mean shape was assessed using 10,000 permutation tests on Mahalanobis and Procrustes distances. A Discriminant Function Analysis (DFA) with cross-validation was used to determine classification accuracy, estimating the proportion of individuals correctly assigned to their species based on wing shape. The DFA also produced graphical displays of the mean wing outlines for each species. Finally, a Procrustes ANOVA was used to quantify and test the significance of wing shape differences among species.

3. Results

3.1. Measurements and Functional Indices

Descriptive statistics for all measurements are presented in Table 1. One-way ANOVA and Kruskal–Wallis tests revealed significant interspecific differences across multiple morphometric traits among the three Sylviid warblers.

Table 1. Mean Values ($\pm$ SD; N) of morphological traits for Garden Warbler, Blackcap and Whitethroat.

Morphological Traits	Garden Warbler	Blackcap	Whitethroat
Body mass (g)	19.80 ($\pm$ 3.34, 47)	17.48 ($\pm$ 1.36, 40)	17.83 ($\pm$ 1.40, 29)
Wing length (cm)	8.09 ($\pm$ 0.22, 46)	7.67 ($\pm$ 0.20, 40)	7.52 ($\pm$ 0.29, 30)
Ninth primary feather (cm)	5.93 ($\pm$ 0.21, 46)	5.19 ($\pm$ 0.17, 40)	5.46 ($\pm$ 0.23, 30)
Fifth primary feather (cm)	5.35 ($\pm$ 0.18, 46)	5.33 ($\pm$ 0.15, 40)	5.46 ($\pm$ 0.15, 30)
Wing area (cm ²)	40.70 ($\pm$ 2.38, 43)	38.41 ($\pm$ 1.89, 35)	39.10 ($\pm$ 1.66, 27)
Aspect ratio	6.03 ($\pm$ 0.31, 40)	5.77 ($\pm$ 0.31, 33)	5.49 ($\pm$ 0.24, 27)
Wing loading	0.245 ($\pm$ 0.041, 43)	0.228 ($\pm$ 0.020, 35)	0.229 ($\pm$ 0.019, 26)
Wing pointedness (i.e., Kipp's Index)	1.88 ($\pm$ 0.48, 43)	1.76 ($\pm$ 0.22, 40)	1.58 ($\pm$ 0.18, 30)

In particular, our analyses showed significant differences in wing length and ninth (P9) primary feather length among the three pairwise comparisons; Garden Warblers showed the greatest mean values for both traits. Whitethroats had the shortest mean wing length, and Blackcaps had the shortest ninth primary feather length. Fifth (P5) primary feather length was significantly longer in Whitethroats compared to the other two species, which did not differ significantly from each other.

Additionally, our results showed that Garden Warblers presented significantly higher body mass and greater wing area than both Blackcaps and Whitethroats, which did not differ significantly from each other in these measures.

Regarding functional indices, aspect ratio differed significantly among the three species, with all pairwise comparisons being statistically significant. Wing loading also differed significantly among species; however, post hoc comparisons revealed a significant difference only between Garden Warblers and Blackcaps. Wing pointedness (Kipp's Index) varied significantly among species, with Whitethroats showing significantly lower values compared to both Garden Warblers and Blackcaps, whereas no significant difference was detected between the latter two (Table 2, Figure 3).

Table 2. Results of interspecific comparisons of morphometric traits among Garden Warbler, Blackcap, and Whitethroat. Parametric variables were analyzed using one-way ANOVA (F statistic) followed by Tukey's HSD post hoc tests, while non-parametric variables were analyzed using Kruskal–Wallis tests (H statistic) followed by pairwise Mann–Whitney U tests. Significant results ($p < 0.05$) are shown in bold.

Species Pairwise Comparison	Statistic (F/H)	d.f.	p-Value
Wing length	64.826 (F)	2, 113	<0.001
Garden Warbler–Blackcap			<0.001
Garden Warbler–Whitethroat			<0.001
Blackcap–Whitethroat			0.018
Wing area	12.781 (F)	2, 102	<0.001
Garden Warbler–Blackcap			<0.001
Garden Warbler–Whitethroat			0.006
Blackcap–Whitethroat			0.385
P9 primary feather	151.914 (F)	2, 113	<0.001

Table 2. Cont.

Species Pairwise Comparison	Statistic (F/H)	d.f.	p-Value
Garden Warbler–Blackcap			<0.001
Garden Warbler–Whitethroat			<0.001
Blackcap–Whitethroat			<0.001
P5 primary feather	6.129 (F)	2, 113	0.003
Garden Warbler–Blackcap			0.718
Garden Warbler–Whitethroat			0.019
Blackcap–Whitethroat			0.003
Aspect ratio	28.018 (F)	2, 97	<0.001
Garden Warbler–Blackcap			<0.001
Garden Warbler–Whitethroat			<0.001
Blackcap–Whitethroat			0.001
Body mass	16.309 (H)	2, 112	<0.001
Garden Warbler–Blackcap			<0.001
Garden Warbler–Whitethroat			0.015
Blackcap–Whitethroat			0.259
Wing loading	6.544 (H)	2, 101	0.038
Garden Warbler–Blackcap			0.014
Garden Warbler–Whitethroat			0.099
Blackcap–Whitethroat			0.564
Kipp's Index	19.025 (H)	2, 114	<0.001
Garden Warbler–Blackcap			0.088
Garden Warbler–Whitethroat			<0.001
Blackcap–Whitethroat			0.007

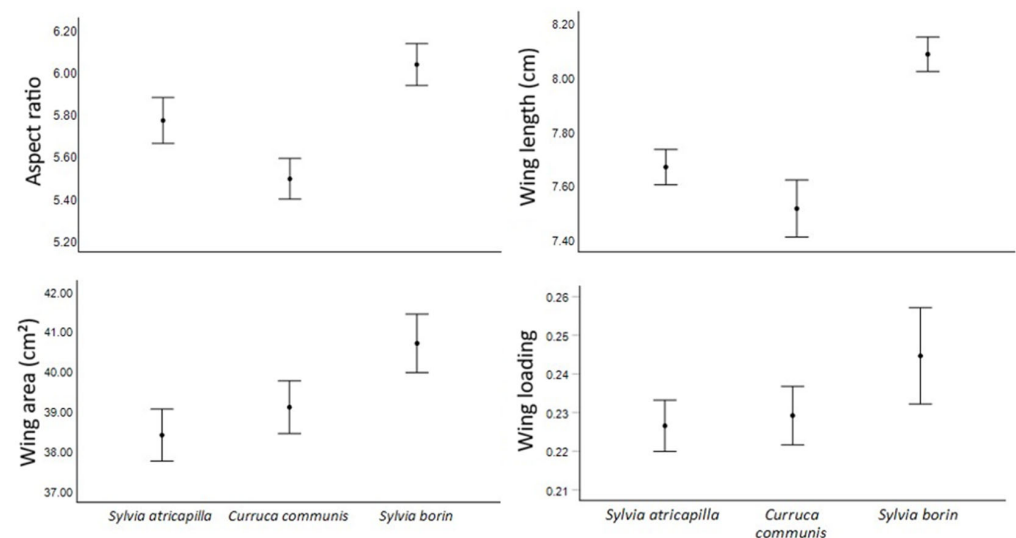


Figure 3. Interspecific comparison of key wing morphometric traits (aspect ratio, wing loading, wing length, and wing area) across Blackcap (*S. atricapilla*), Whitethroat (*C. communis*) and Garden Warbler (*S. borin*). Points represent species means; error bars indicate ± 1 standard error. Sample sizes vary among traits and species (see Table 1 for details).

3.2. Geometric Morphometrics

Landmark-based morphometric analysis revealed a good wing shape distinction between the three species. Representative wing images with digitized landmarks are shown in Figure 4A, while the Procrustes-superimposed landmark configurations for each species are presented in Figure 4B. In the latter, each larger point indicates the mean landmark position, and the surrounding scattered points reflect the individual variation.

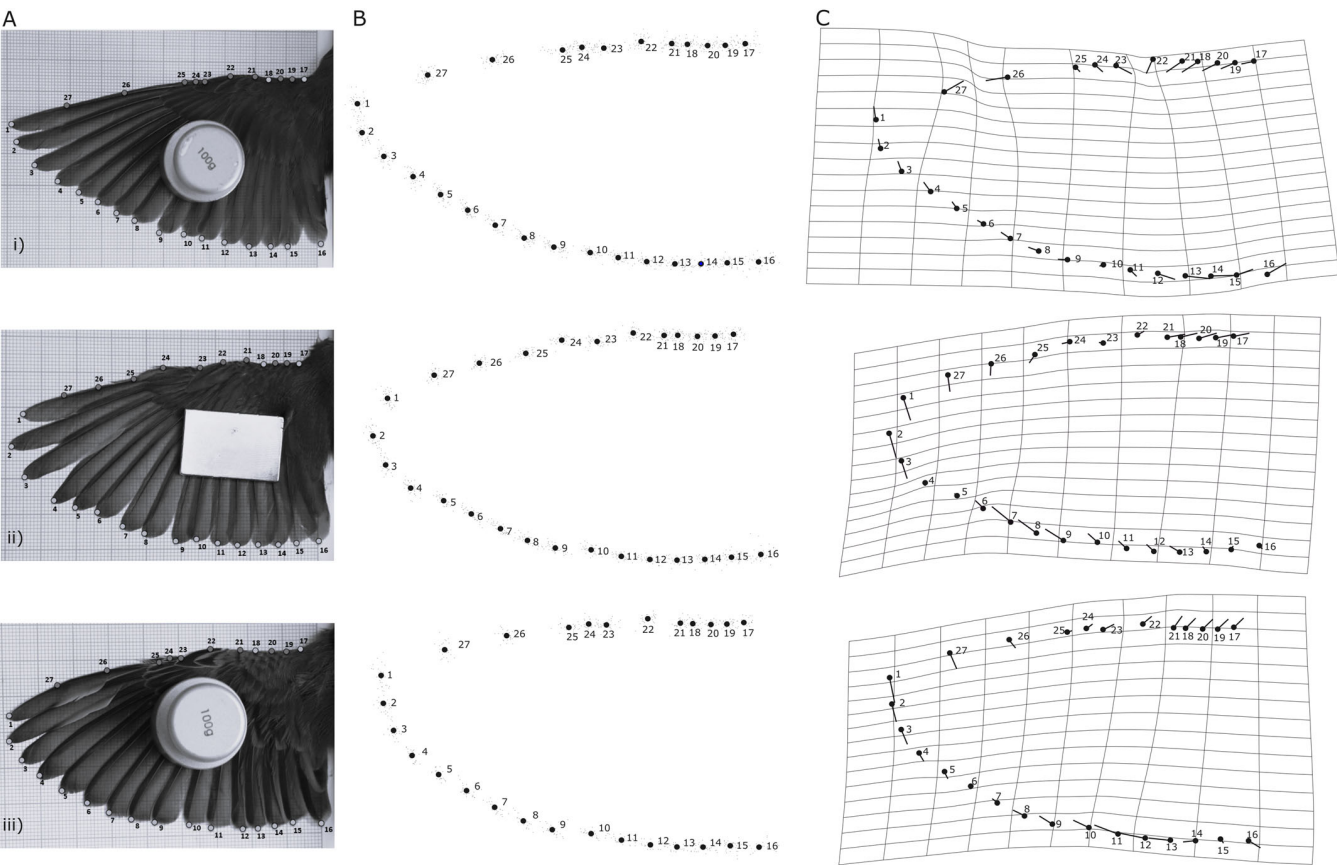


Figure 4. Geometric morphometric analysis of wing shape. **(A)** Dorsal view of a left wing for each species with all 27 landmarks. **(B)** Consensus wing shape for each species after Procrustes superimposition. **(C)** Transformation grid depicting shape changes along the first principal component (PC1) relative to the consensus. Species: **(i)** Garden Warbler, **(ii)** Blackcap, **(iii)** Whitethroat.

A Procrustes ANOVA confirmed significant interspecific differences in wing shape (Table 3). All pairwise comparisons were highly significant (all $p < 0.0001$), supported by high Goodall’s F-statistics and Pillai’s trace values (Table 3), confirming that each species possesses a distinct wing shape configuration.

Table 3. Procrustes ANOVA results for interspecific wing shape variation among the species. Significant results ($p < 0.05$) are in bold.

Interspecific Procrustes ANOVA	F	d.f.	Pillai’s Trace	p-Value
Garden Warbler–Blackcap	36.31	50	0.99	<0.0001
Garden Warbler–Whitethroat	11.66	50	0.98	<0.0001
Blackcap–Whitethroat	20.53	50	0.99	<0.0001

Principal Component Analysis (PCA) of wing shape generated 50 measures of relative deformations (Figure S1). The first three principal components (PCs) collectively explained 50% of the total shape variance, with PC1 and PC2 accounting for 21.01% and 17.28% of the variance, respectively. The distribution of individuals along PC1 and PC2 is shown in Supplementary Figure S2. The shape changes associated with PC1, visualized using a transformation grid, are shown in Figure 4C.

Canonical Variate Analysis (CVA) clearly separated the three species based on wing shape. The first two canonical variates (CVs) explained 100% of the between-group variation (CV1 = 77.07%, CV2 = 22.93%). The scatterplot of these CVs (Figure 5) shows three

distinct, non-overlapping clusters with 90% confidence ellipses. Wireframe graphs superimposed on the plot illustrate the mean wing shape configuration for each species.

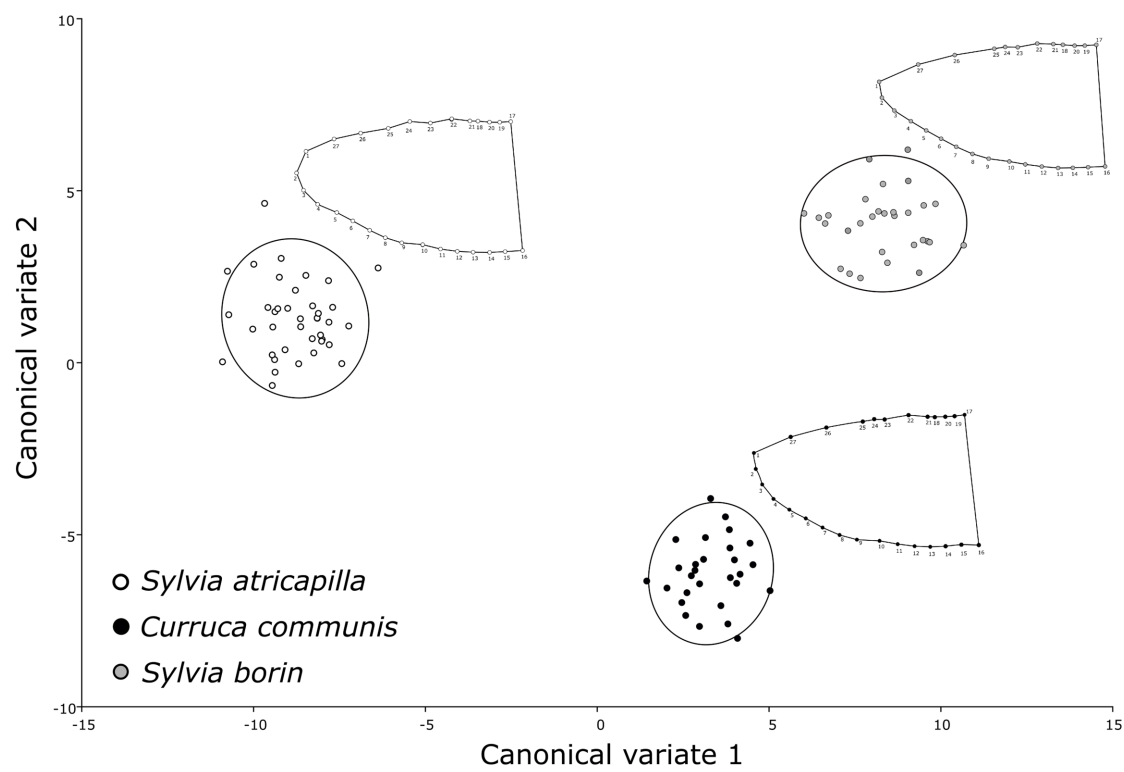


Figure 5. Canonical Variate Analysis (CVA) of wing shape. The scatterplot shows the distribution of individuals with 90% confidence ellipses along the first two canonical variates (CV1 and CV2). From left to right: Blackcap *S. atricapilla* (white), Whitethroat *C. communis* (black) and Garden Warbler *S. borin* (gray).

Pairwise comparisons confirmed these morphological distinctions. Both Mahalanobis and Procrustes distances revealed highly significant differences among all species pairs (10,000 permutations; $p < 0.0001$; Table 4). The greatest morphological separation was between Garden Warbler and Blackcap, which had the highest Mahalanobis distance (17.34).

Table 4. Pairwise wing shape differences among species after the CVA. Values above the diagonal are Procrustes distances, values below are Mahalanobis distances. All comparisons were significant ($p < 0.0001$; 10,000 permutations).

Wing Shape	Garden Warbler	Blackcap	Whitethroat
Garden Warbler	-	0.0716 ($p < 0.0001$)	0.0462 ($p < 0.0001$)
Blackcap	17.3373 ($p < 0.0001$)	-	0.0577 ($p < 0.0001$)
Whitethroat	11.3409 ($p < 0.0001$)	14.1908 ($p < 0.0001$)	-

The Discriminant Function Analysis (DFA) cross-validation test demonstrated a high classification success percentage, with over 96% of specimens correctly assigned to their species (Table 5). Blackcaps had the highest correct classification percentage (97.44%). All pairwise species comparisons showed highly significant differences in wing shape (all $p < 0.0001$), as confirmed by both Mahalanobis and Procrustes distances: Garden Warbler–Blackcap: Mahalanobis distance = 19.7239 ($p < 0.0001$), Procrustes distance = 0.07160 ($p < 0.0001$); Garden Warbler–Whitethroat: Mahalanobis distance = 37.2595 ($p < 0.0001$), Procrustes distance = 0.04616 ($p < 0.0001$); Blackcap–

Whitethroat: Mahalanobis distance = 22.1924 ($p < 0.0001$), Procrustes distance = 0.057646 ($p < 0.0001$).

Table 5. Discriminant Function Analysis (DFA) classification results. The bold diagonal represents the correct classification percentage (%) for each species.

Wing Shape	Garden Warbler	Blackcap	Whitethroat	In Total
Garden Warbler	96.67 (29/30)	-	3.33 (1/30)	100 (30)
Blackcap	-	97.44 (38/39)	2.56 (1/39)	100 (39)
Whitethroat	-	3.57 (1/28)	96.43 (27/28)	100 (28)

The wireframes derived from the DFA provided a complementary visual synthesis of wing shape differences among the species (Figure 6), adding further detail to the quantitative results.

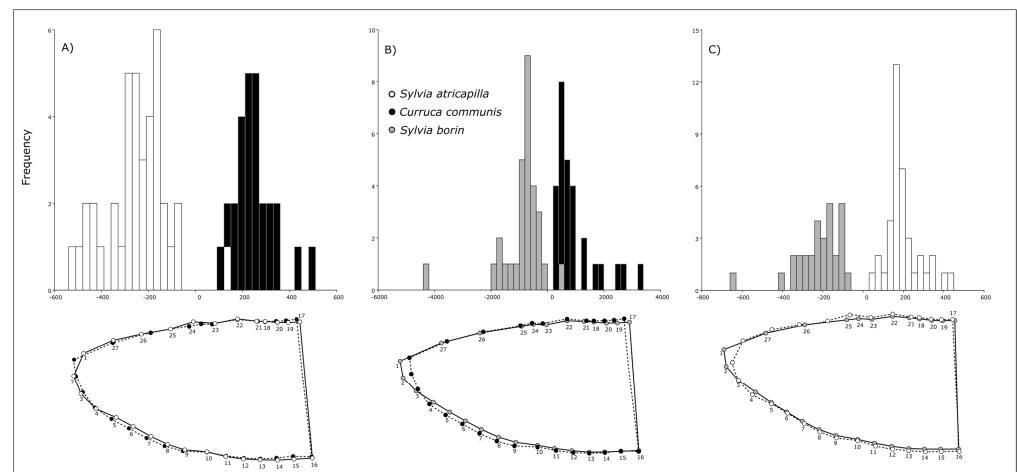


Figure 6. Frequency graph of cross-validation scores by groups and the pairwise wing shape comparison from Discriminant Function Analysis (DFA). Wireframe graphs overlay the mean wing shape of two species for each comparison, with landmarks numbered. Solid lines represent the first species listed, and dotted lines represent the second species listed. (A) Blackcap *S. atricapilla* vs. Whitethroat *C. communis*; (B) Garden Warbler *S. borin* vs. Whitethroat *C. communis*; (C) Garden Warbler *S. borin* vs. Blackcap *S. atricapilla*.

The most pronounced morphological divergence was between the Garden Warbler and Blackcap. The wings of the Garden Warbler were more swept, elongated, and pointed, tapering to a more slender tip (landmarks LM1–LM6). In contrast, the Blackcap exhibited a broader wing with a more rounded wingtip and greater convexity. Differences were also evident in the alula (LM21–LM23) and the vestigial primary (LM24, LM25), which were more curved and pronounced in the Blackcap, and in the inner wing base (LM10–LM16), which was narrower in the Garden Warbler.

While both the Garden Warbler and Whitethroat shared a pointed wingtip (LM27, LM1–LM3), they differed in the proximal primary region (LM4–LM10). The Garden Warbler maintained a more elongated and narrow profile, whereas the Whitethroat had a broader wing with a more convex outline.

The comparison between the Blackcap and Whitethroat revealed the greatest overall overlap, particularly in the wing base. However, the Whitethroat possessed a more pointed wingtip compared to the rounder tip of the Blackcap and a slightly broader curvature in the inner wing (LM4–LM9).

4. Discussion

Overall, our integrative morphometric approach, combining traditional biometrics, functional indices, and geometric morphometrics, revealed interspecific differences in wing morphology among the three migratory Sylviid warblers. Landmark-based analyses showed clearer separation in wing shape, whereas linear measurements and derived indices differentiated among several, but not all, species comparisons. The wing morphologies range from the elongated and pointed wings of the Garden Warbler to the shorter and rounder wings of the Blackcap, with the Common Whitethroat occupying an intermediate position. Our findings could possibly support the long-standing hypothesis that avian wing shape is a product of a functional trade-off, primarily between the need for aerodynamic efficiency during long-distance migration and the requirement for high maneuverability within specific breeding and foraging habitats [4,5,8].

4.1. Methodological Convergence and Divergence

The different morphometric approaches used in this study provided complementary perspectives on interspecific variation in wing morphology. Traditional linear measurements and derived indices captured broad differences among species, while geometric morphometric analyses offered an integrative representation of overall wing shape. However, some discrepancies were observed between methods, particularly in relation to wing pointedness. While both Kipp's Index and geometric morphometrics indicated that the Garden Warbler exhibits the most pointed wings, Kipp's Index suggested that Whitethroats had the most rounded wings, a pattern that was not evident in the landmark-based geometric morphometric analyses. Such differences likely arise from the contrasting nature of the methods, as biometric measurements reflect linear distances, whereas geometric morphometrics incorporates the spatial configuration of multiple landmarks, which allows for a much richer description of overall wing shape (e.g., [61]). Together, these results highlight the value of combining multiple morphometric approaches while also emphasizing that different methods may emphasize different facets of wing morphology.

4.2. Interpreting Wing Shape Variation in Relation to Migration Ecology

The correlation between wing morphology and migratory distance has been widely documented in avian ecomorphology [4,5]. Numerous studies have provided evidence that longer-distance migrants have longer and more pointed wings with higher aspect ratios [8,11,13,23], traits that are generally associated with reduced energetic expenditure during sustained flight [4,5]. Our results can be interpreted within this framework. The Garden Warbler, which undertakes the longest migration of the three (on average ~6550 km and a maximum migratory distance of ~11,700 km; [64]), exhibited the most profound adaptation toward this aerodynamically efficient phenotype, with the longest wings, highest aspect ratio, and most pronounced wing pointedness. This morphology reduces induced drag and wingtip vortices, lowering the cost of transport [26] and enabling sustained flight over ecological barriers like the Sahara Desert and the Mediterranean Sea. In addition, the higher wing loading and aspect ratio values observed in Garden Warblers are consistent with their migratory behavior, as increased wing loading is associated with higher flight speeds and shorter travel times [65], while higher aspect ratios are linked to lower transport costs during flight [4,6]. The Common Whitethroat, also a long-distance migrant (on average ~5550 km and a maximum of ~10,000 km; [64]), showed a relatively pointed wingtip combined with greater overall wing breadth. This suggests a different, perhaps more balanced, evolutionary compromise where aerodynamic efficiency is integrated with other performance needs.

The Blackcap presents a different morphological pattern compared to the other two species. The species shows highly polymorphic migratory behavior, encompassing long-distance, short-distance, and resident populations (short-distance migrants cover on average ~1700 km, long-distance migrants cover on average ~4550 km, and migratory distances are up to ~8950 km; [64]). Although some populations undertake substantial migrations, Blackcaps generally overwinter at more northerly latitudes than the strictly trans-Saharan Garden Warbler and Whitethroat [43], resulting in a shorter average migratory distance. In this context, the relatively shorter and rounder wings observed in this species may reflect reduced selective pressures for highly aerodynamically efficient wings optimized for sustained long-distance flight.

While a direct causal relationship cannot be inferred, these observed patterns are consistent with our a priori prediction and support the long-standing hypothesis that longer-distance migrants exhibit wing traits associated with greater aerodynamic efficiency.

4.3. Beyond Migration: Additional Ecological Pressures Shaping Wing Morphology

Wings are multifunctional structures and are subject to further selective pressures on functional traits related to flight [8,15,66]. Once migration is complete, wings must perform in the context of daily survival, such as foraging, escaping predators, and navigating complex habitats [9,17,29]. Adaptations toward broader, more rounded wings with lower aspect ratio and wing loading are generally associated with increased lift production, maneuverability, and acceleration, which are critical for rapid take-offs and tight maneuvers in cluttered environments [11,22,23]. A bird's wing loading strongly influences maneuverability, as the minimum turning radius is proportional to body mass and wing area [6]. The Blackcap's wing morphology may be interpreted within this framework. The species typically occupies woodlands with high vertical vegetation density, including both closed-canopy and dense understory [32], and builds its nests low in dense broadleaf shrubs or bush vegetation, making it particularly vulnerable to terrestrial predators [67,68]. Faster takeoff performance, associated with higher speed and acceleration capacity, facilitates predator escape [22,29], a fact of particular significance for birds susceptible to high ground predation rates [26]. Its rounded wings and lower wing loading are adaptations that could potentially maximize escape performance and foraging agility in such a three-dimensionally complex habitat, likely outweighing the benefits of a more efficient but less maneuverable wing.

The Garden Warbler, while sharing some broad habitat categories with the Blackcap [32], shows a subtle but ecologically significant divergence. It occupies more open-canopy woodland edges and scrub with dense undergrowth rather than dense forests [36]. This marginally more open structure may reduce the pressure for low-speed maneuverability, thereby permitting a greater degree of specialization for migratory flight. The Whitethroat's intermediate morphology, combining a pointed wingtip with a broader and more convex wing outline, may represent an adaptive compromise. The species typically occupies semi-open habitats, with low and dense vegetation [32,36] and builds its nests close to the ground within bushes or other fairly dense cover [38], potentially increasing exposure to terrestrial predators. In addition, compared to the other two species, Whitethroats forage mainly in bushes or other low vegetation, gleaning from leaves and twigs, while occasionally capturing insects in flight or on the ground [38,69]. In this ecological context, this intermediate morphology may provide sufficient aerodynamic efficiency for its long migration while retaining the enhanced lift and maneuverability beneficial for surviving in its preferred habitats, where predation risk remains a key concern.

While ecological variables were not directly measured in the present study and the interpretations above are based on species' natural-history information, they provide a

plausible ecological context for the observed morphological differences and highlight hypotheses that could be tested in future research.

4.4. Conclusions, and Future Directions

In conclusion, the wing morphology of these three warblers may be interpreted as a map of their ecological priorities. The Garden Warbler showed wing traits more closely associated with sustained, long-distance migration; the Blackcap exhibited features consistent with maneuverability and faster take-off, traits suited for structurally complex habitats; while the Whitethroat displayed an intermediate wing morphology. The study underscores that even among related and broadly sympatric species, subtle differences in life-history strategies may contribute to divergence in functional anatomy.

While some possible explanations that may account for the differences in species' wing morphologies were provided, further research is required to better understand the drivers underlying these phenotypical patterns. In particular, future studies could explore the influence of selective pressures associated with daily survival in both breeding and non-breeding areas within an ecological context. In addition, intraspecific variation in wing morphology could be further explored, as sex, age class, and population level differences are considered factors that may be associated with phenotypic variation. Previous work has documented morphological differences related to demographic and population-level variation in migratory passerines [14,19,22,70,71]. This may be particularly interesting for the Eurasian Blackcap, a species exhibiting a substantial variation in migratory strategies across different populations [40,72].

Analyses of external morphological traits have progressively improved our understanding of avian evolution, ecology, and dispersal processes [73]. However, integrating skeletal elements and pectoral muscle architecture could reveal how internal anatomy covaries with external wing form to produce integrated flight systems. Furthermore, employing phylogenetic comparative methods across the entire Sylviidae family would help disentangle evolutionary heritage from adaptive convergence and identify the macroevolutionary patterns underlying the microevolutionary differences we observed here. Wing morphology is often considered a proxy for dispersal capacity [74]. In an era defined by habitat fragmentation and climate change, species with wing morphologies specialized for efficient long-distance travel may have a greater inherent capacity to track shifting climatic niches. Conversely, species with morphologies specialized for resident agility in specific habitats may be more vulnerable if those habitats become fragmented. Thus, understanding these ecomorphological relationships could provide a crucial tool for predicting vulnerability and informing conservation strategies in a rapidly changing world.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/birds7010018/s1>, Figure S1. Diagram showing the relative percentage of variance explained by each principal component of the wing shape Principal Component Analysis (PCA) for the three migratory warbler species (Garden Warbler, Whitethroat and Blackcap); Figure S2. Principal Component analysis (PCA) of wing shape. The scatterplot shows the distribution of individuals with 90% confidence ellipses, along the first two principal components (PC1 = 21.01% of variance; PC2 = 17.28% of variance). Species are indicated by color: Garden Warbler *Sylvia borin* (red), Whitethroat *Curruca communis* (blue) and Blackcap *Sylvia atricapilla* (green); Table S1. Complete dataset of biometric measurements for the Garden Warbler (*Sylvia borin*) individuals sampled during autumn migration period on Antikythera Island, Greece; Table S2. Complete dataset of biometric measurements for the Eurasian Blackcap (*Sylvia atricapilla*) individuals sampled during autumn migration period on Antikythera Island, Greece; Table S3. Complete dataset of biometric measurements for the Common Whitethroat (*Curruca communis*) individuals sampled during autumn migration period on Antikythera Island, Greece; Table S4. Complete dataset of wing area and derived functional indices

(aspect ratio, wing loading) for the Garden Warbler (*Sylvia borin*) individuals included in the analyses. Blank cells indicate missing values resulting from incomplete measurements required for index calculation; Table S5. Complete dataset of wing area and derived functional indices (aspect ratio, wing loading) for the Eurasian Blackcap (*Sylvia atricapilla*) individuals included in the analyses. Blank cells indicate missing values resulting from incomplete measurements required for index calculation; Table S6. Complete dataset of wing area and derived functional indices (aspect ratio, wing loading) for the Common Whitethroat (*Curruca communis*) individuals included in the analyses. Blank cells indicate missing values resulting from incomplete measurements required for index calculation.

Author Contributions: Conceptualization, S.G., C.B. and A.A.; methodology, S.G., C.B. and A.A.; software, A.A. and S.G.; validation, S.G. and A.A.; formal analysis, A.A.; investigation, A.A. and C.B.; resources, C.B. and A.A.; data curation, A.A.; writing—original draft preparation, A.A., S.G. and C.B.; writing—review and editing, A.A., S.G. and C.B.; visualization, A.A.; supervision, S.G.; project administration, S.G. and C.B. All authors have read and agreed to the published version of the manuscript.

Funding: The A.G. Leventis Foundation funded the fieldwork conducted at the Antikythera Bird Observatory. Rings were supplied free of charge by the Hellenic Bird Ringing Centre.

Institutional Review Board Statement: Bird trapping, handling, ringing, and photography was done under the license YTIEN/ΔΔΔ/6117/170 issued from the Hellenic Ministry of Environment and Energy.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available upon request from the corresponding authors.

Acknowledgments: This is contribution No.45 from the Antikythera Bird Observatory, the Hellenic Ornithological Society/BirdLife Greece. We thank all the volunteers of Antikythera Bird Observatory for assisting in mist netting and ringing and the field owners who provided free access to their ground. Animal handling complied with the current laws of Greece.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Wainwright, P.C. Ecomorphology: Experimental Functional Anatomy for Ecological Problems. *Am. Zool.* **1991**, *31*, 680–693. [\[CrossRef\]](#)
2. Koehl, M.A.R. When Does Morphology Matter? *Annu. Rev. Ecol. Syst.* **1996**, *27*, 501–542. [\[CrossRef\]](#)
3. Pennycuik, C.J. Mechanics of Flight. In *Avian Biology*; Elsevier: Amsterdam, The Netherlands, 1975; pp. 1–75, ISBN 978-0-12-249405-5.
4. Rayner, J.M.V. Form and Function in Avian Flight. In *Current Ornithology*; Johnston, R.F., Ed.; Springer: Boston, MA, USA, 1988; pp. 1–66, ISBN 978-1-4615-6789-9.
5. Norberg, U.M. *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution*; Zoophysiology; Springer: Berlin/Heidelberg, Germany, 1990.
6. Lindhe Norberg, U.M. Structure, Form, and Function of Flight in Engineering and the Living World. *J. Morphol.* **2002**, *252*, 52–81. [\[CrossRef\]](#)
7. Hedenström, A. Adaptations to Migration in Birds: Behavioural Strategies, Morphology and Scaling Effects. *Phil. Trans. R. Soc. B* **2008**, *363*, 287–299. [\[CrossRef\]](#) [\[PubMed\]](#)
8. Lockwood, R.; Swaddle, J.P.; Rayner, J.M.V. Avian Wingtip Shape Reconsidered: Wingtip Shape Indices and Morphological Adaptations to Migration. *J. Avian Biol.* **1998**, *29*, 273. [\[CrossRef\]](#)
9. Huber, G.H.; Turbek, S.P.; Bostwick, K.S.; Safran, R.J. Comparative Analysis Reveals Migratory Swallows (Hirundinidae) Have Less Pointed Wings than Residents. *Biol. J. Linn. Soc.* **2016**, *120*, 228–235. [\[CrossRef\]](#)
10. Calmaestra, R.G.; Moreno, E. A Phylogenetically-Based Analysis on the Relationship between Wing Morphology and Migratory Behaviour in Passeriformes. *Ardea* **2001**, *89*, 407–416.
11. Kaboli, M.; Aliabadian, M.; Guillaumet, A.; Roselaar, C.S.; Prodon, R. Ecomorphology of the Wheatears (Genus *Oenanthe*). *Ibis* **2007**, *149*, 792–805. [\[CrossRef\]](#)
12. Baldwin, M.W.; Winkler, H.; Organ, C.L.; Helm, B. Wing Pointedness Associated with Migratory Distance in Common-garden and Comparative Studies of Stonechats (*Saxicola torquata*). *J. Evol. Biol.* **2010**, *23*, 1050–1063. [\[CrossRef\]](#)

13. Minias, P.; Meissner, W.; Włodarczyk, R.; Ożarowska, A.; Piasecka, A.; Kaczmarek, K.; Janiszewski, T. Wing Shape and Migration in Shorebirds: A Comparative Study. *Ibis* **2015**, *157*, 528–535. [\[CrossRef\]](#)
14. Carvalho Provinciano, I.C.; Araújo, M.S.; Jahn, A.E. Drivers of Wing Shape in a Widespread Neotropical Bird: A Dual Role of Sex-Specific and Migration-Related Functions. *Evol. Ecol.* **2018**, *32*, 379–393. [\[CrossRef\]](#)
15. Marchetti, K.; Price, T.; Richman, A. Correlates of Wing Morphology with Foraging Behaviour and Migration Distance in the Genus *Phylloscopus*. *J. Avian Biol.* **1995**, *26*, 177. [\[CrossRef\]](#)
16. Niemi, G.J. Patterns of Morphological Evolution in Bird Genera of New World and Old World Peatlands. *Ecology* **1985**, *66*, 1215–1228. [\[CrossRef\]](#)
17. Swaddle, J.P.; Lockwood, R. Morphological Adaptations to Predation Risk in Passerines. *J. Avian Biol.* **1998**, *29*, 172. [\[CrossRef\]](#)
18. Hahn, S.; Korner-Nievergelt, F.; Emmenegger, T.; Amrhein, V.; Csörgő, T.; Gursoy, A.; Ilieva, M.; Kverek, P.; Pérez-Tris, J.; Pirrello, S.; et al. Longer Wings for Faster Springs—Wing Length Relates to Spring Phenology in a Long-distance Migrant across Its Range. *Ecol. Evol.* **2016**, *6*, 68–77. [\[CrossRef\]](#) [\[PubMed\]](#)
19. De La Hera, I.; Pulido, F.; Visser, M.E. Longitudinal Data Reveal Ontogenetic Changes in the Wing Morphology of a Long-distance Migratory Bird. *Ibis* **2014**, *156*, 209–214. [\[CrossRef\]](#)
20. Thoma, C.T.; Makridou, K.N.; Bakaloudis, D.E.; Vlachos, C.G. Age-Specific Differences in Wing Pointedness and Wing Length of European Turtle Doves *Streptopelia turtur* Migrating through the Eastern Flyway. *Ring. Migr.* **2020**, *35*, 94–100. [\[CrossRef\]](#)
21. Van Oordt, F.; Torres-Mura, J.C.; Hertel, F. Ecomorphology and Foraging Behaviour of Pacific Boobies. *Ibis* **2018**, *160*, 313–326. [\[CrossRef\]](#)
22. Vanhooydonck, B.; Herrel, A.; Gabela, A.; Podos, J. Wing Shape Variation in the Medium Ground Finch (*Geospiza fortis*): An Ecomorphological Approach. *Biol. J. Linn. Soc.* **2009**, *98*, 129–138. [\[CrossRef\]](#)
23. Savile, O.B.O. Adaptive Evolution in the Avian Wing. *Evolution* **1957**, *11*, 212–224. [\[CrossRef\]](#)
24. Rayner, J.M.V. The Mechanics of Flight and Bird Migration Performance. In *Bird Migration*; Gwinner, E., Ed.; Springer: Berlin/Heidelberg, Germany, 1990; pp. 283–299. ISBN 978-3-642-74544-7.
25. Bowlin, M.S.; Wikelski, M. Pointed Wings, Low Wingloading and Calm Air Reduce Migratory Flight Costs in Songbirds. *PLoS ONE* **2008**, *3*, e2154. [\[CrossRef\]](#)
26. Swaddle, J.P.; Lockwood, R. Wingtip Shape and Flight Performance in the European Starling *Sturnus vulgaris*. *Ibis* **2003**, *145*, 457–464. [\[CrossRef\]](#)
27. Van Oorschot, B.K.; Mistick, E.A.; Tobalske, B.W. Aerodynamic Consequences of Wing Morphing during Emulated Take-off and Gliding in Birds. *J. Exp. Biol.* **2016**, *219*, 3146–3154. [\[CrossRef\]](#)
28. Norberg, U.M. Morphology of the Wings, Legs and Tail of Three Coniferous Forest Tits, the Goldcrest, and the Treecreeper in Relation to Locomotor Pattern and Feeding Station Selection. *Philos. Trans. R. Soc. London B Biol. Sci.* **1979**, *287*, 131–165. [\[CrossRef\]](#)
29. Noreau, F.; Desrochers, A. Combined Effects of Migration Distance, Foraging Method Vegetation Density, and Population Density on Wing Shapes of Boreal Songbirds. *BioRxiv* **2018**. BioRxiv:413351.
30. Blondel, J.; Catzefflis, F.; Perret, P. Molecular Phylogeny and the Historical Biogeography of the Warblers of the Genus *Sylvia* (Aves). *J. Evol. Biol.* **1996**, *9*, 871–891. [\[CrossRef\]](#)
31. Voelker, G.; Light, J.E. Palaeoclimatic Events, Dispersal and Migratory Losses along the Afro-European Axis as Drivers of Biogeographic Distribution in *Sylvia* Warblers. *BMC Evol. Biol.* **2011**, *11*, 163. [\[CrossRef\]](#) [\[PubMed\]](#)
32. Cody, M.L. Habitat Selection and Interspecific Territoriality among the Sylviid Warblers of England and Sweden. *Ecol. Monogr.* **1978**, *48*, 351–396. [\[CrossRef\]](#)
33. Bonte, D.; Provoost, S.; Hoffmann, M. Habitat and Territory Segregation within Sylviine Warblers of the Flemish Coastal Dunes. *Belg. J. Zool.* **2001**, *131*, 49–57.
34. Wilhelmsson, P.; Jaenson, T.G.T.; Olsen, B.; Waldenström, J.; Lindgren, P.-E. Migratory Birds as Disseminators of Ticks and the Tick-Borne Pathogens *Borrelia* Bacteria and Tick-Borne Encephalitis (TBE) Virus: A Seasonal Study at Ottenby Bird Observatory in South-Eastern Sweden. *Parasites Vectors* **2020**, *13*, 607. [\[CrossRef\]](#) [\[PubMed\]](#)
35. Moreau, R.E. *The Palaearctic–African Bird Migration Systems*; Academic Press: London, UK, 1972.
36. Cramp, S.; Brooks, D.J. *Handbook of the Birds of Europe, the Middle East, and North Africa: The Birds of the Western Palearctic*; Oxford University Press: Oxford, UK, 1992; Volume VI.
37. BirdLife International. *Species Factsheet: Garden Warbler Sylvia Borin*; BirdLife International: Cambridge, UK, 2024.
38. BirdLife International. *Species Factsheet: Common Whitethroat Curruca Communis*; BirdLife International: Cambridge, UK, 2024.
39. Berthold, P.; Terrill, S.B. Migratory Behaviour and Population Growth of Blackcaps Wintering in Britain and Ireland: Some Hypotheses. *Ring. Migr.* **1988**, *9*, 153–159. [\[CrossRef\]](#)
40. Delmore, K.; Illera, J.C.; Pérez-Tris, J.; Segelbacher, G.; Lugo Ramos, J.S.; Durieux, G.; Ishigohoka, J.; Liedvogel, M. The Evolutionary History and Genomics of European Blackcap Migration. *eLife* **2020**, *9*, e54462. [\[CrossRef\]](#)

41. Shirihai, H.; Gargallo, G.; Helbig, A. *Sylvia Warblers: Identification, Taxonomy and Phylogeny of the Genus Sylvia*; Christopher Helm Publishers Ltd.: London, UK, 2001.
42. Ożarowska, A.; Zaniewicz, G.; Meissner, W. Blackcaps *Sylvia atricapilla* on Migration: A Link between Long-Term Population Trends and Migratory Behaviour Revealed by the Changes in Wing Length. *Acta Ornithol.* **2016**, *51*, 211–219. [\[CrossRef\]](#)
43. BirdLife International. *Species Factsheet: Eurasian Blackcap Sylvia atricapilla*; BirdLife International: Cambridge, UK, 2025.
44. Dimaki, M.; Alivizatos, H. Ringing Studies of the Turtle Dove *Streptopelia turtur* (Aves: Columbidae during Passage through Antikythera Island, Southwestern Greece. *J. Nat. Hist.* **2015**, *49*, 419–427. [\[CrossRef\]](#)
45. Kassara, C.; Bairaktaridou, K.; Kakalis, E.; Tsiopelas, N.; Giokas, S.; Barboutis, C. Activity Patterns of Eleonora’s Falcons during the Pre-Breeding Period: The Role of Habitat Composition on the Island of Antikythera. *Avocetta* **2019**, *43*. [\[CrossRef\]](#)
46. Svensson, L. *Identification Guide to European Passerines*; British Trust for Ornithology: Norfolk, UK, 1992.
47. Jenni, L.; Winkler, R. *Moult and Ageing of European Passerines*; Bloomsbury Publishing: London, UK, 1994.
48. Milá, B.; Wayne, R.K.; Smith, T.B. Ecomorphology of Migratory And Sedentary Populations of the Yellow-Rumped Warbler (*Dendroica coronata*). *Condor* **2008**, *110*, 335–344. [\[CrossRef\]](#)
49. Claramunt, S.; Derryberry, E.P.; Remsen, J.V.; Brumfield, R.T. High Dispersal Ability Inhibits Speciation in a Continental Radiation of Passerine Birds. *Proc. R. Soc. B* **2012**, *279*, 1567–1574. [\[CrossRef\]](#) [\[PubMed\]](#)
50. Hernández, M.Á.; Campos, F.; Martín, R.; Santamaría, T. Usefulness of Biometrics to Analyze Some Ecological Features of Birds. In *Biometrics: Unique and Diverse Applications in Nature, Science, and Technology*; InTech: Rijeka, Croatia, 2011; pp. 1–22.
51. Hedenstrom, A.; Pettersson, J. Differences in Fat Deposits and Wing Pointedness between Male and Female Willow Warblers Caught on Spring Migration at Ottenby, SE Sweden. *Ornis Scand.* **1986**, *17*, 182. [\[CrossRef\]](#)
52. Rohlf, F.J. *tpsDig2*, version 2.32; Department of Ecology and Evolution, State University of New York at Stony Brook: Stony Brook, NY, USA, 2021; Available online: <http://sbmophometrics.org> (accessed on 29 December 2025).
53. Mitteroecker, P.; Gunz, P. Advances in Geometric Morphometrics. *Evol. Biol.* **2009**, *36*, 235–247. [\[CrossRef\]](#)
54. Lee, S.; Kim, J.; Park, H.; Jabłoński, P.G.; Choi, H. The Function of the Alula in Avian Flight. *Sci. Rep.* **2015**, *5*, 9914. [\[CrossRef\]](#)
55. Bao, H.; Song, B.; Yang, W.; Xuan, J.; Xue, D. The Progress of Aerodynamic Mechanisms Based on Avian Leading-Edge Alula and Future Study Recommendations. *Aerospace* **2021**, *8*, 295. [\[CrossRef\]](#)
56. Schneider, C.A.; Rasband, W.S.; Eliceiri, K.W. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **2012**, *9*, 671–675. [\[CrossRef\]](#) [\[PubMed\]](#)
57. Fiedler, W. Ecomorphology of the External Flight Apparatus of Blackcaps (*Sylvia atricapilla*) with Different Migration Behavior. *Ann. N. Y. Acad. Sci.* **2005**, *1046*, 253–263. [\[CrossRef\]](#) [\[PubMed\]](#)
58. Zar, J.H. *Biostatistical Analysis*, 5th ed.; Pearson Prentice-Hall: Upper Saddle River, NJ, USA, 2010.
59. Klingenberg, C.P. MORPHO J: An Integrated Software Package for Geometric Morphometrics. *Mol. Ecol. Resour.* **2011**, *11*, 353–357. [\[CrossRef\]](#)
60. Bookstein, F.L. *Morphometric Tools for Landmark Data: Geometry and Biology*; Cambridge University Press: Cambridge, UK, 1991.
61. Adams, D.C.; Rohlf, F.J.; Slice, D.E. Geometric Morphometrics: Ten Years of Progress Following the ‘Revolution’. *Ital. J. Zool.* **2004**, *71*, 5–16. [\[CrossRef\]](#)
62. Drake, A.G.; Klingenberg, C.P. The Pace of Morphological Change: Historical Transformation of Skull Shape in St Bernard Dogs. *Proc. R. Soc. B* **2008**, *275*, 71–76. [\[CrossRef\]](#)
63. Klingenberg, C.P. Visualizations in Geometric Morphometrics: How to Read and How to Make Graphs Showing Shape Changes. *Hystrix Ital. J. Mammal.* **2013**, *24*, 15–24. [\[CrossRef\]](#)
64. Doswald, N.; Willis, S.G.; Collingham, Y.C.; Pain, D.J.; Green, R.E.; Huntley, B. Potential Impacts of Climatic Change on the Breeding and Non-breeding Ranges and Migration Distance of European *Sylvia* Warblers. *J. Biogeogr.* **2009**, *36*, 1194–1208. [\[CrossRef\]](#)
65. Brewer, M.L.; Hertel, F. Wing Morphology and Flight Behavior of Pelecaniform Seabirds. *J. Morphol.* **2007**, *268*, 866–877. [\[CrossRef\]](#)
66. Norberg, U.M.; Rayner, J.M.V. Ecological Morphology and Flight in Bats (Mammalia; Chiroptera): Wing Adaptations, Flight Performance, Foraging Strategy and Echolocation. *Philos. Trans. R. Soc. London. B Biol. Sci.* **1987**, *316*, 335–427. [\[CrossRef\]](#)
67. Remeš, V. Nest Concealment and Parental Behaviour Interact in Affecting Nest Survival in the Blackcap (*Sylvia atricapilla*): An Experimental Evaluation of the Parental Compensation Hypothesis. *Behav. Ecol. Sociobiol.* **2005**, *58*, 326–332. [\[CrossRef\]](#)
68. Węgrzyn, E.; Leniowski, K. Nest Site Preference and Nest Success in Blackcaps *Sylvia atricapilla* in Poland. *Ardeola* **2011**, *58*, 113–124. [\[CrossRef\]](#)
69. Aymí, R.; Gargallo, G. Greater Whitethroat (*Curruca communis*). In *Birds of the World*; Billerman, S.M., Keeney, B.K., Rodewald, P.G., Schulenberg, T.S., Eds.; Cornell Lab of Ornithology: Ithaca, NY, USA, 2021.
70. Cabodevilla, X.; Moreno-Zarate, L.; Arroyo, B. Differences in Wing Morphology between Juvenile and Adult European Turtle Doves *Streptopelia turtur*: Implications for Migration and Predator Escape. *Ibis* **2018**, *160*, 458–463. [\[CrossRef\]](#)
71. Ożarowska, A.; Zaniewicz, G.; Meissner, W. Sex and Age-Specific Differences in Wing Pointedness and Wing Length in Blackcaps *Sylvia atricapilla* Migrating through the Southern Baltic Coast. *Curr. Zool.* **2021**, *67*, 271–277. [\[CrossRef\]](#)

72. Hiemer, D.; Salewski, V.; Fiedler, W.; Hahn, S.; Lisovski, S. First Tracks of Individual Blackcaps Suggest a Complex Migration Pattern. *J. Ornithol.* **2018**, *159*, 205–210. [[CrossRef](#)]
73. Tellería, J.L.; Hera, I.D.L.; Perez-Tris, J. Morphological Variation as a Tool for Monitoring Bird Populations: A Review: La Variación Morfológica Como Una Herramienta Para El Seguimiento De Las Poblaciones De Aves: Una Revision. *Ardeola* **2013**, *60*, 191–224. [[CrossRef](#)]
74. Desrochers, A. Morphological Response of Songbirds to 100 Years of Landscape Change in North America. *Ecology* **2010**, *91*, 1577–1582. [[CrossRef](#)] [[PubMed](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.