

ECOMORPHOLOGY OF MIGRATORY AND SEDENTARY POPULATIONS OF THE YELLOW-RUMPED WARBLER (*DENDROICA CORONATA*)

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Abstract. We contrast patterns of variation in morphological traits of migratory and sedentary forms of the Yellow-rumped Warbler (*Dendroica coronata*) to test functional predictions regarding the evolution of traits related to flight. Sedentary individuals are larger than migrants in all traits except bill width and depth. However, when traits are adjusted for body size differences using multivariate approaches, migrants have longer and more concave wings than do individuals from sedentary populations, suggesting selection for high—aspect ratio wings for fast, sustained flight. Subadults have relatively shorter and rounder wings than do adults of all subspecies except for the long-distance migrant *D. c. coronata*, and age-related differences are most pronounced in short-distance migrants. We propose a graphic model for the evolution of age-related differences in wing shape that is based on the role of antagonistic selective pressures imposed by migratory flight vs. maneuverability. Size-adjusted differences in tail length are not significant. Longer culmens and tarsi in the sedentary *D. c. goldmani* subspecies of Guatemala suggest differences in diet and foraging behavior compared to migratory groups. Our results strongly suggest that divergent natural selection has caused the morphological differentiation between migratory and sedentary subspecies.

Key words: *Dendroica*, ecomorphology, flight, ontogenetic shift, warbler, wing shape.

Ecomorfología de Poblaciones Migratorias y Sedentarias de *Dendroica coronata*

Resumen. Contrastamos los patrones de variación en caracteres morfológicos de poblaciones migratorias y sedentarias de *Dendroica coronata* para probar predicciones funcionales referentes a la evolución de caracteres relacionados con el vuelo. Los individuos sedentarios son más grandes que los migratorios en todos los caracteres, a excepción del ancho y alto del pico. Sin embargo, cuando los caracteres son corregidos por tamaño corporal utilizando métodos multivariados, las poblaciones migratorias tienen alas más largas y cóncavas que las sedentarias, lo cual sugiere el papel de la selección natural en producir alas puntiagudas para el vuelo rápido sostenido. Los subadultos tienen alas más cortas y más redondeadas que los adultos en todos los grupos excepto en la subespecie migratoria de larga distancia *D. c. coronata*, y las diferencias entre edades son más pronunciadas en las migratorias de corta distancia. Proponemos un modelo gráfico para la evolución de las diferencias en la forma del ala según la edad, que se basa en el papel de fuerzas selectivas antagónicas impuestas por el vuelo migratorio y la maniobrabilidad. Las diferencias en el tamaño de la cola ajustadas por tamaño corporal no son significativas. La mayor longitud del pico y el tarso de la subespecie sedentaria *D. c. goldmani* de Guatemala sugiere la existencia de diferencias en la dieta y la conducta de forrajeo con respecto a las migratorias. Nuestros resultados sugieren que la selección natural es la principal causa de la diferenciación morfológica entre poblaciones migratorias y sedentarias.

INTRODUCTION

Because sustained flight is a costly activity, migratory behavior is likely to exert strong selective pressures on the morphology of individuals (Winkler and Leisler 1992). Avian flight theory predicts that, compared to sedentary birds, long-distance migrants should have longer and more pointed wings of high aspect ratio, and shorter tails to minimize drag (Savile 1957,

Rayner 1988, Thomas and Balmford 1995). However, selective effects of migratory behavior on flight morphology can conflict with selective pressures exerted by other factors, including habitat type (Tellería and Carbonell 1999), foraging behavior (Norberg 1979, Hertel and Ballance 1999), antipredator behavior (Alatalo et al. 1984), and sexual selection (Hedenström and Møller 1992). For instance, long, pointed wings for fast, low-cost flight, and short tails to reduce drag are adaptations

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for long-distance migration, yet the dense vegetation often preferred by many migrant species should select for short, rounder wings and longer tails to favor slow, maneuverable flight and avoid collisions (Rayner 1988, Winkler and Leisler 1992).

Rayner (1988) predicted that selection for morphological adaptations for low-cost flight would be weak in small birds like passerines, which typically show adaptations for maneuverability in dense habitats and where conflicting selective pressures are combined with physical constraints due to size. However, although some studies have found no correlation between wing morphology and migratory distance (Keast 1980, Niemi 1985), evidence of morphological adaptations to migratory behavior has emerged from several interspecific studies of passerines (Gaston 1974, Leisler and Winkler 1985, Winkler and Leisler 1992, Yong and Moore 1994, Marchetti et al. 1995, Mönkkönen 1995, Kaboli et al. 2007), which have generally found a correlation between wing length or pointedness and migratory behavior and distance. Intraspecific analyses comparing migratory and sedentary populations of single species are less common. Several studies on Old World species have shown a significant relationship between migratory distance and wing length and pointedness (Gaston 1974, Senar et al. 1994, Copete et al. 1999, Tellería and Carbonell 1999, Pérez-Tris and Tellería 2001, Pérez-Tris et al. 2003), yet similar studies in New World passerine species have been limited to a few cases. Mulvihill and Chandler (1990) found no relationship between wing shape variation and migration distance among age and sex classes of the Dark-eyed Junco (*Junco hyemalis*), a medium distance migrant, though a comparison of migratory and resident subspecies revealed more pointed wings in migratory individuals (Mulvihill and Chandler 1991). Similarly, Egbert and Belthoff (2003) found that migratory House Finch (*Carpodacus mexicanus*) populations of eastern North America have reduced inner primary feathers and thus narrower wings than their sedentary ancestors in California, yet no differences in wing length were found. Finally, Wiedenfeld (1991) found that migratory Yellow Warblers in North America had longer wings relative to overall size than did sedentary populations in Central and South America, but he did not examine other variables related to wing shape.

Here we test the prediction that flight-related morphological traits will vary with respect to migratory distance in the Yellow-rumped Warbler (*Dendroica coronata*) subspecies that differ in their migratory behavior. The Yellow-rumped Warbler complex is composed of two common and widespread migratory forms, the Myrtle Warbler (*D. c. coronata*) and Audubon's warbler (*D. c. auduboni*) of North America, and two largely sedentary forms, the Black-fronted Warbler (*D. c. nigrifrons*) of the Sierra Madre Occidental of Mexico, and Goldman's Warbler (*D. c. goldmani*) of the highlands of western Guatemala (Hunt and Flaspohler 1998; Fig. 1). The Myrtle Warbler breeds in eastern and boreal North America and winters along the Atlantic and Pacific coasts of North America, southeastern

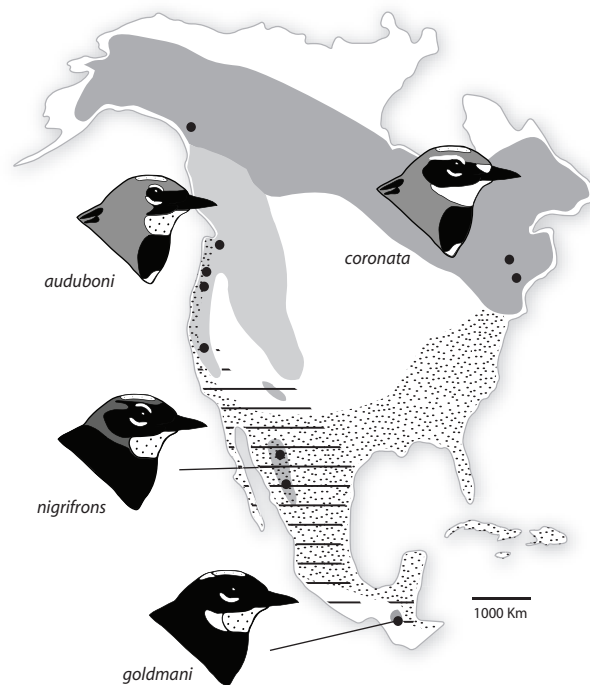


FIGURE 1. Breeding and wintering ranges, and basic plumage characteristics of males of the four main Yellow-rumped Warbler subspecies: *Dendroica coronata coronata* (Myrtle Warbler), *D. c. auduboni* (Audubon's Warbler), *D. c. nigrifrons* (Black-fronted Warbler) of western Mexico, and *D. c. goldmani* (Goldman's Warbler) of Guatemala. On the map, hatched area corresponds to wintering range of *D. c. auduboni*, and stippled area represents the wintering range of *D. c. coronata*. Stippled areas on bird schematics represent yellow plumage. Black dots represent sampling localities.

United States, and south along eastern Mexico to southern Central America and the Caribbean. Audubon's Warbler, which breeds in western North America, spends the nonbreeding season in the southwestern United States, Mexico and northern Central America (Howell and Webb 1995, Hunt and Flaspohler 1998). All four subspecies are fully diagnosable based on plumage coloration of the head, throat, dorsal and ventral areas, and the amount of white on greater coverts and rectrices (Hubbard 1970, Hunt and Flaspohler 1998), except along a narrow hybrid zone between *coronata* and *auduboni* groups in British Columbia and Alberta (Hubbard 1969). In contrast to the well-documented patterns of plumage variation in the complex, analysis of quantitative traits between groups has been superficial.

Here we contrast absolute and size-adjusted morphological variation in Yellow-rumped Warbler subspecific groups to assess the role of ecology and aerodynamics in driving morphological divergence among forms. Specifically, we predict that long-distance migratory individuals (*coronata* and *auduboni*) will be smaller and have relatively longer, more pointed wings, and shorter tails than sedentary individuals of *nigrifrons* and *goldmani* groups.

We also examine age-related differences in wing morphology and test the model proposed by Pérez-Tris and Tellería (2001), which predicts that juveniles should have shorter, more rounded wings than adults in migratory but not in sedentary populations. According to their model, selection should promote longer, more pointed wings in migrants to favor long-distance movements in adults. In contrast, inexperienced juveniles should benefit from shorter, more rounded wings to enable more maneuverable flight to avoid predators and forage more efficiently. In sedentary populations, where selection for long-distance flight morphology is absent, differences between juveniles and adults should be minimal or nonexistent.

Finally, while the emphasis of our study is on flight ecomorphology, we briefly examine differences in foraging-related morphology by comparing bill measurements and tarsus length between groups to infer potential differences in diet and foraging behavior among groups. Previous studies on the ecomorphology of warblers and other small passerines have documented associations among morphology, foraging method, and prey type (Miles and Ricklefs 1984, Winkler and Leisler 1985, Richman and Price 1992), and in particular, between bill morphology and foraging strategies (Eckhardt 1979, Price 1991), and between increased tarsus length and amount of ground feeding (Osterhaus 1962, Fitzpatrick 1985).

METHODS

FIELD SAMPLING AND MORPHOLOGICAL MEASUREMENTS

Birds from all four Yellow-rumped Warbler subspecies were captured in the field during the breeding season (April–July 2001–2004), using standard mist nets and song playbacks to attract individuals to the nets when necessary. Because of the sampling method, the number of females in most samples was small and insufficient to address sex-related morphological differences; thus, females were excluded from the analyses. Sampling localities and male sample sizes were as follows: *D. c. coronata* ($n = 24$), New Brunswick (43°53'N, 69°55'W) and Rangeley (44°58'N, 70°39'W), Maine; *D. c. auduboni* ($n = 28$), Naches (46°45'N, 120°54'W), Washington, and Malibu (34°01'N, 118°41'W), California; *D. c. nigrifrons* ($n = 24$), El Vergel (26°28'N, 106°23'W), Chihuahua, and San Diego Tenaenz (24°56'N, 105°55'W), Durango, Mexico; and *D. c. goldmani* ($n = 33$), Culchemical (15°31'N, 91°29'W) and Chichim (15°32'N, 91°33'W), Huehuetenango, and Ixchiguan (15°8'N, 91°54'W), San Marcos, Guatemala. Captured individuals were aged using plumage characteristics and degree of skull ossification (Pyle 1997). We classified individuals as adult if they had undergone at least one complete basic (post-nuptial) molt, and as subadult if they had undergone only a postnatal molt. All subadults in this study were second-year birds (hatched in the previous breeding season) and had thus

attained full size in morphological traits at the time of capture. No hatching-year (juvenile) birds were included in the analysis.

Individuals were each weighed and marked with a uniquely numbered aluminum band. A wing ruler was used to measure the unflattened wing chord (the distance from the carpal joint to the tip of the longest primary) to the nearest 0.5 mm. Dial calipers of 0.1-mm precision were used to measure tail length (from the uropygial gland to the tip of the longest rectrix), tarsus length (from the intertarsal joint to the most distal undivided scute on the tarsometatarsus), bill length (from the base of the bill at the cranium to the tip of the upper mandible), culmen length (from the anterior end of the nares to the tip of the upper mandible), and bill width and depth (both measured at the anterior end of the nares).

WING-SHAPE ANALYSIS

To examine wing shape, we used calipers to measure the length of each of the nine primary feathers, defined as the distance from the tip of the feather to the point where it enters the skin. Following convention, primaries were numbered p1 to p9 from proximal to distal. Several previous studies have used “primary distance,” defined as the distance from the tip of each primary to the tip of the longest primary. However, following recommendations by Lockwood et al. (1998) we used primary lengths to avoid statistical problems arising from measurement error, repeatability, and deviations from normality encountered when using the former measure. In addition, we used a metal ruler to measure the distance between the longest primary feather and the longest secondary feather on the folded wing, known as Kipp’s distance (Kipp 1959). Kipp’s distance has been identified as the most effective wing-tip index for measuring the overall proportions of the wing (Lockwood et al. 1998).

Most birds were measured early in the breeding season (April and May), about eight to nine months after the previous complete molt. Even though some wear was sometimes visible in the outermost primaries, accurate measurements of the total lengths of feathers were possible in most cases. When the tip of a feather had been worn off or was too frayed to be measured accurately, the feather was excluded. All measurements were taken by BM.

STATISTICAL ANALYSES

We used one- and two-way analysis of variance (ANOVA), with population and age as factors, to compare means of morphological traits of males among groups. To control for the effects of body size on morphological traits, we used a general linear model (GLM) to generate adjusted marginal trait means with population as the fixed factor, structural body size as the covariate, and a Bonferroni correction for multiple comparisons. Structural body size was assessed by means of a principal components analysis (PCA) on the covariance matrix of

TABLE 1. Coefficients of correlation (equivalent to factor loadings) between morphological variables used to assess structural body size and the derived principal components (PC1 and PC2) extracted by principal components analysis, from Yellow-rumped Warbler males of all ages and all subspecies ($n = 109$), measured between 2001 and 2004.

Variables	Factor loadings	
	PC1	PC2
Wing length	0.79**	0.34**
Tail length	0.79**	0.24*
Tarsus length	0.88**	0.06
Bill depth	0.55**	0.38**
Bill width	0.35**	0.66**
Culmen	0.80**	-0.48**
Bill length	0.92**	-0.25**
Variance explained	58%	16%

* = $P < 0.05$, ** = $P < 0.01$.

seven log-transformed morphological traits (wing length, tail length, tarsus length, bill length, culmen length, bill width, and bill depth) excluding weight (Rising and Sommers 1989). The PCA yielded high factor loadings on the first principal component (PC1; Table 1), and PC1 values were subsequently used as an index of overall size and introduced as the covariate in the GLM. To size-adjust the seven variables used to obtain the structural-size index, we modified our analysis to avoid having such variables both as dependent variables in the GLM and also as part of the PC1 values in the covariate. For these variables, we ran separate PCAs excluding each of the variables one at a time, then used the resulting PC1 values as the covariate in a GLM to obtain the size-adjusted marginal means of the excluded variable.

Finally, we obtained an additional assessment of wing shape by conducting a PCA on the covariance matrix of the eleven wing-related variables (wing length, p1–p9, and Kipp's distance). All analyses were carried out with SPSS Version 10.0. (SPSS Inc., Chicago, Illinois).

RESULTS

Sedentary Yellow-rumped Warbler males of the Mexican and Guatemalan subspecies (*D. c. nigrifrons* and *goldmani*, respectively) are heavier and have longer wings, tails, and tarsi, and deeper bills than their migratory counterparts (*D. c. coronata* and *auduboni*; mass: $F_{1,107} = 148.9$, $P < 0.001$; wing length: $F_{1,107} = 286.4$, $P < 0.001$; tail length: $F_{1,107} = 182.5$, $P < 0.001$; tarsus length: $F_{1,107} = 143.9$, $P < 0.001$; bill depth: $F_{1,107} = 43.0$, $P < 0.001$; Fig. 2). *D. c. goldmani* individuals also have significantly longer bills than do other subspecies (bill length: $F_{1,107} = 92.2$, $P < 0.001$; culmen length: $F_{1,107} = 102.0$, $P < 0.001$). These results are generally consistent with previous morphological studies of Yellow-rumped Warblers (Oberholser 1921, Hubbard 1970). However, because differences between traits

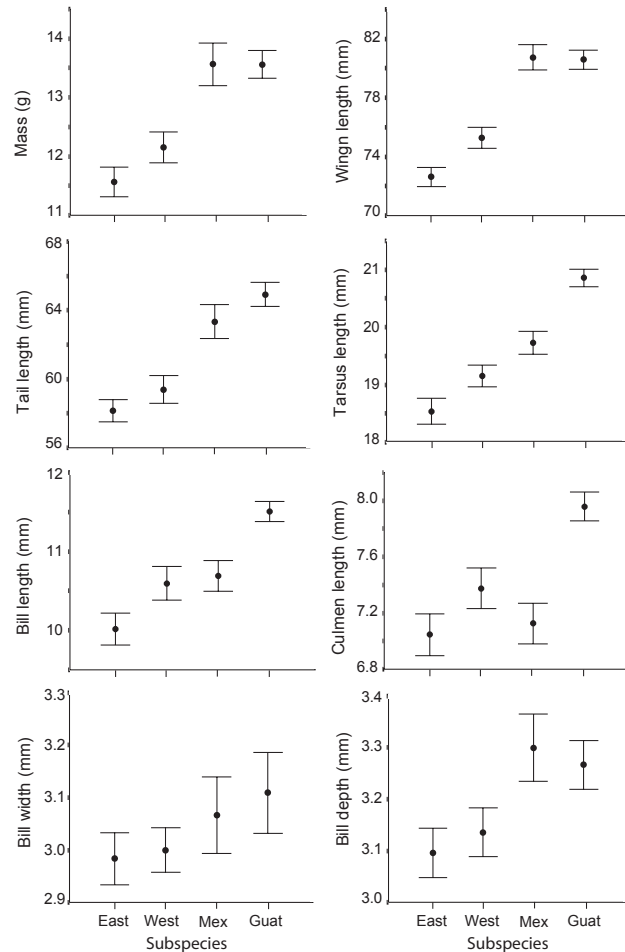


FIGURE 2. Means of morphological variables and mass in males of four Yellow-rumped Warbler groups (all ages): *Dendroica coronata coronata* (East), *D. c. auduboni* (West), *D. c. nigrifrons* (Mex) and *D. c. goldmani* (Guat), ordered from most to least migratory, measured between 2001 and 2004. Bars are Bonferroni-corrected 95% CI around the means (black dots). Lack of overlap between bars indicates statistical significance at the 0.05 level. P values for selected comparisons are indicated in the text.

can be affected by allometric scaling, we adjusted trait means for differences in overall body size (Rayner 1988, Lockwood et al. 1998). Size-adjusted means (Fig. 3) showed no significant differences in tail length ($F_{3,98} = 3.2$, $P = 0.07$) and bill depth among groups ($F_{3,98} = 2.2$, $P = 0.10$). *D. c. goldmani* individuals had significantly shorter wings than did individuals of the other subspecies when corrected for overall size ($F_{3,98} = 41.0$, $P < 0.001$), yet maintained significantly longer tarsi and culmens (tarsus: $F_{3,98} = 9.5$, $P < 0.001$; culmen: $F_{3,98} = 17.1$, $P < 0.001$).

Analysis of size-adjusted wing variables revealed significant differences in wing shape (relative to body size) among subspecies. The length of proximal primary feathers (p1–p5) showed a negative relationship with migratory distance, with *D. c. coronata* showing the shortest values and *D. c. goldmani* the longest values (Fig. 4). Distal primaries (p6–p9) showed

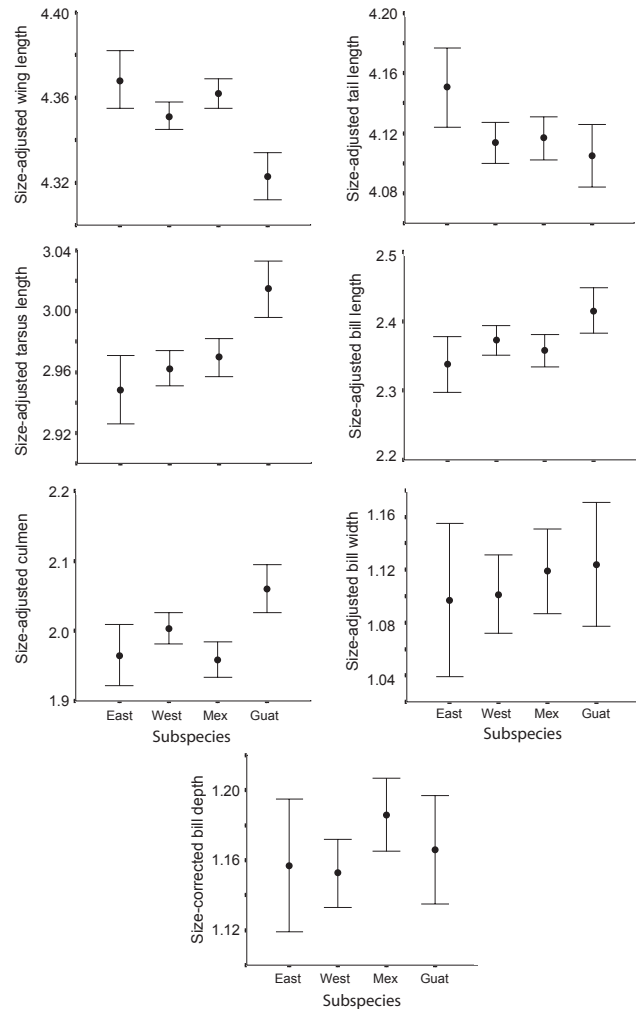


FIGURE 3. Size-adjusted means of morphological variables in males of four Yellow-rumped Warbler populations *Dendroica coronata coronata* (Myrtle Warbler), *D. c. auduboni* (Audubon's Warbler), *D. c. nigrifrons* (Black-fronted Warbler) of western Mexico, and *D. c. goldmani* (Goldman's Warbler) of Guatemala, all ages included, ordered from most (East) to least (Guatemala) migratory, measured between 2001 and 2004. Bars are Bonferroni-corrected 95% CI around the marginal means (black dots) estimated from a general linear model using principal component 1 values from a principal components analysis of structural body size variables (Table 1) as the covariate. Lack of overlap between bars indicates statistical significance at the 0.05 level. *P* values for selected comparisons are indicated in the text.

the opposite pattern, being longer in migrants and shorter in sedentary groups relative to body size, though the differences were not significant except for primary 6 (the longest primary in this species), which was significantly shorter in *goldmani*. This marked difference in proximal vs. distal primary lengths results in more concave and pointed wings in the longest-distance migrants (*D. c. coronata* and *auduboni*), and more convex and rounded wing shape in the fully sedentary group *D. c. goldmani*, with *nigrifrons* showing an intermediate pattern

(Fig. 5). Kipp's distance was shortest in *D. c. goldmani* and largest in *coronata*, and the trait showed strong negative allometry as revealed by the inverse pattern of absolute and size-adjusted Kipp's distances (Fig. 6), indicating that size-adjusted distances decrease with increasing overall size.

Results from an analysis of wing-shape variables using PCA are consistent with the GLM results (Table 2). PC1 represents an axis of increasing length of all variables, indicating that PC1 is correlated with size. PC2 is an axis of increasing proximal primaries and decreasing Kipp's distance, and describes wing concavity. The difference between migrants and residents in wing concavity as measured by PC2 values was significant ($F_{1,102} = 4.6, P = 0.03$). Finally, PC3 is an axis of increasing distal primaries, representing wing pointedness, though factor loadings were low and not significant.

We detected a significant age effect in wing length and shape among groups (two-way ANCOVA—age: $F_{1,94} = 8.2, P = 0.046$; group: $F_{3,94} = 13.2, P = 0.006$; covariate structural size: $F_{1,94} = 242.0, P < 0.001$). In all groups except *D. c. coronata*, where no age effects were detected, subadults had shorter and less pointed wings than adults as a result of a reduction of distal primary lengths (Table 3). Age-related differences were most pronounced in *D. c. nigrifrons*, where highly significant differences between adults and subadults were evident in wing length, distal primary lengths and Kipp's distance (Table 3).

DISCUSSION

Latitudinal patterns in morphology have been widely documented in birds (Zink and Remsen 1986, James 1991), and a tendency towards larger size in colder climates in conformity with Bergmann's ecogeographic rule has been described in a number of largely sedentary species (Johnston and Selander 1964, James 1970). However, Zink and Remsen (1986) showed that Bergmann's rule does not generally apply to migrants, and Wiedenfeld (1991) documented a clear negative correlation between body size and latitude in Yellow Warbler populations from Canada to tropical South America. In our study of the Yellow-rumped Warbler, individuals from southern populations (*D. c. nigrifrons* of Mexico and *goldmani* of Guatemala) were larger than migratory North American groups, a pattern that is consistent with these other studies and with the prediction that the demands of migratory flight select for smaller, lighter body configurations (Winkler and Leisler 1985, Wiedenfeld 1991, Winkler and Leisler 1992).

The unique selective pressures acting on the morphology of migratory birds explain the poor correlation between wing length and body size in this group (Freeman and Jackson 1990, Wiedenfeld 1991). This weak association not only cautions against the use of wing length as a proxy for overall body size, but also underscores the importance of separating size from shape using multivariate methods in order to reveal geographic patterns of natural selection (Mosimann and James 1979, Darroch and Mosimann 1985, Aldrich and James 1991), an approach that has been

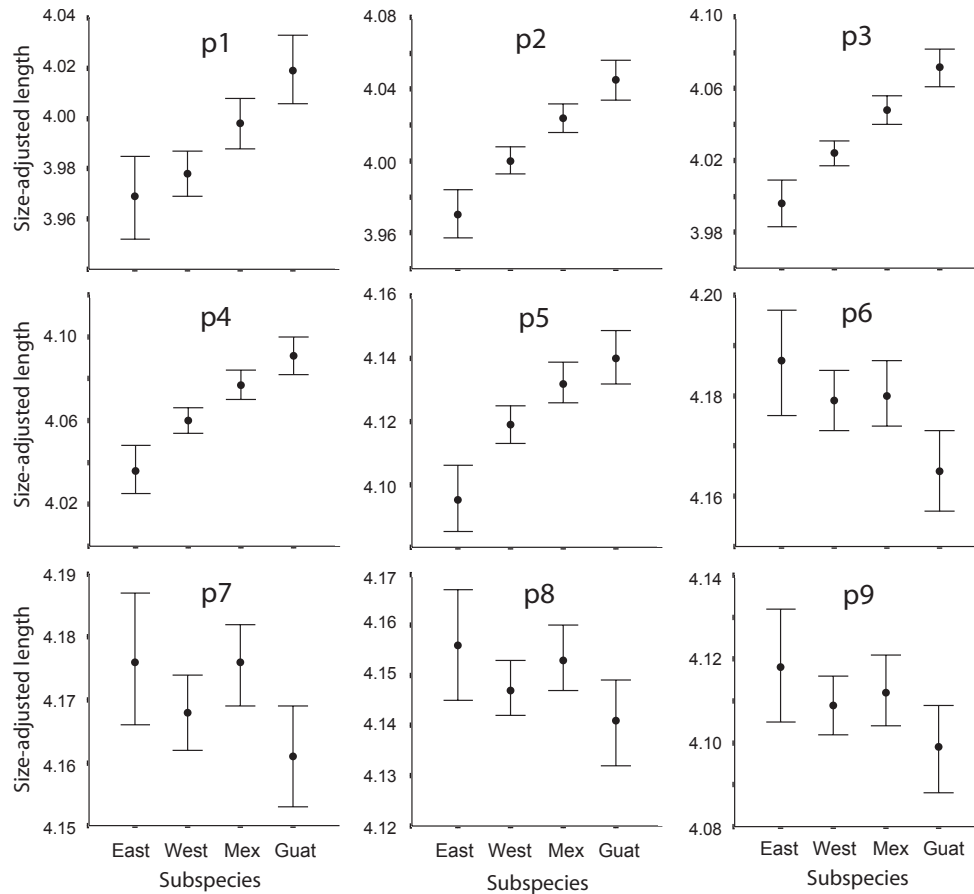


FIGURE 4. Size-adjusted primary-feather lengths (p1–p9) in adult males of Yellow-rumped Warbler subspecies (all ages), measured between 2001 and 2004. Bars are Bonferroni-corrected 95% CI around the marginal means (black dots) estimated from a general linear model using principal component 1 values from a principal components analysis of structural body size variables (Table 1) as the covariate. Lack of overlap between bars indicates statistical significance at the 0.05 level.

particularly useful in detecting adaptations in flight morphology. In the Yellow-rumped Warbler, size-adjustment of trait means revealed marked differences in wing shape between populations. As predicted, migratory forms (*D. c. coronata* and *auduboni*) had higher—**aspect ratio wings than did sedentary forms**. Migrants had relatively narrower and more pointed wings due to reduced inner primary (p1–p5) lengths and longer outer primary (p6–p9) lengths. This pattern was most pronounced in *D. c. coronata*, which on average is thought to migrate farther than other subspecies (Hunt and Flaspohler 1998). Sedentary *D. c. goldmani* and *nigrifrons* had relatively rounder and less concave wings due to their relatively long inner primaries and short outer primaries. Kipp's distance appears to be a strong predictor of wing pointedness in our study, revealing significant differences between groups when corrected for body size, and a strong positive relationship with migratory distance.

Size-adjusted wing length was significantly shorter in resident *D. c. goldmani* individuals. However, no significant difference was found between *D. c. coronata* and *auduboni*, and Mexican *nigrifrons* individuals had significantly longer wings

than *auduboni* individuals. Several studies have shown that wing shape is a more reliable predictor of migratory distance than is wing length (Winkler and Leisler 1992, Mönkkönen 1995, Egbert and Belthoff 2003), which suggests that selective pressures other than migration might be acting on wing length. An alternative explanation for the pattern of wing length in Mexico's *D. c. nigrifrons* is that this group might be a short-distance or partial migrant. While the group is typically described as sedentary (Howell and Webb 1995, Hubbard 1970), individuals have been recorded outside their breeding range in more southern latitudes of Mexico in the highlands of Michoacán during the nonbreeding season (Curson et al. 1994, Dunn and Garrett 1997, BM, pers. obs.), suggesting seasonal migratory movements. Some degree of migratory behavior in *D. c. nigrifrons* would also be consistent with its pattern of wing shape, which tends to be intermediate to that of fully sedentary *goldmani* and long- to short-distance migrant *auduboni*. Further study of the annual cycle of this poorly known Mexican group will be necessary to confirm the migratory tendencies suggested by our morphological data.

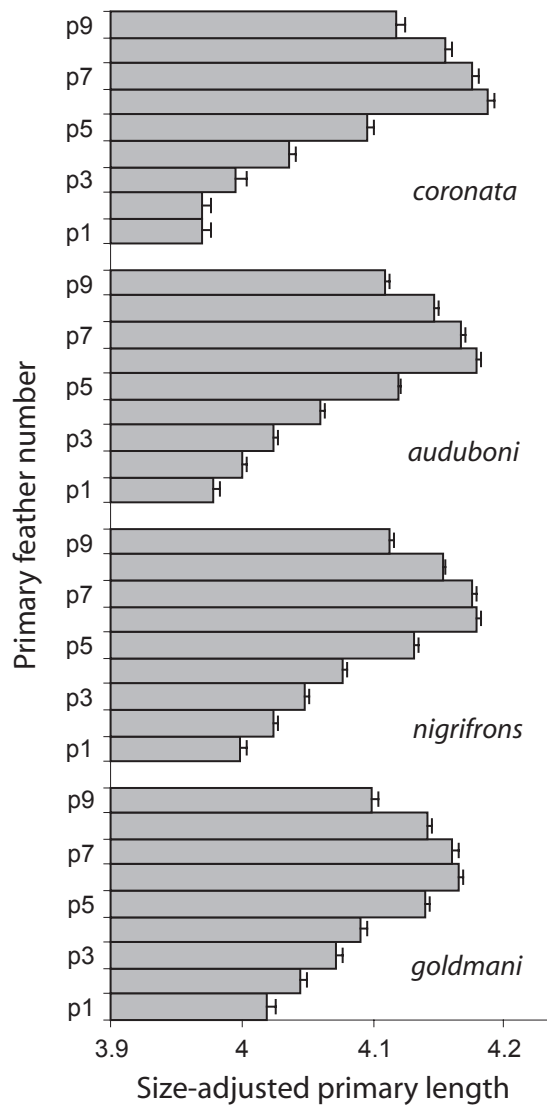


FIGURE 5. Size-adjusted means of primary feathers (p1–p9) of adult male Yellow-rumped Warblers (*Dendroica coronata*) measured between 2001 and 2004. Histograms represent adjusted means from a general linear model, and bars indicate SE. *D. c. coronata* is the longest-distance migrant and shows a narrower, more pointed wing. *D. c. goldmani* is fully sedentary and shows a more rounded wing.

The wings of subadult males were shorter and less pointed than those of adults in all subspecies except *D. c. coronata*, the longest-distance migrant. Interestingly, age-related differences were particularly strong in the *D. c. nigrifrons* group (a possible short-distance migrant, according to its wing morphology), for which differences between adults and subadults in wing length, distal primary lengths and Kipp's distance were all highly significant. We propose that this pattern of age-related morphology may reflect an evolutionary trade-off between antagonistic selective forces acting on wing morphology. Migratory birds reduce the cost of migration by elongating their wings but do so at the expense of maneuverability, which

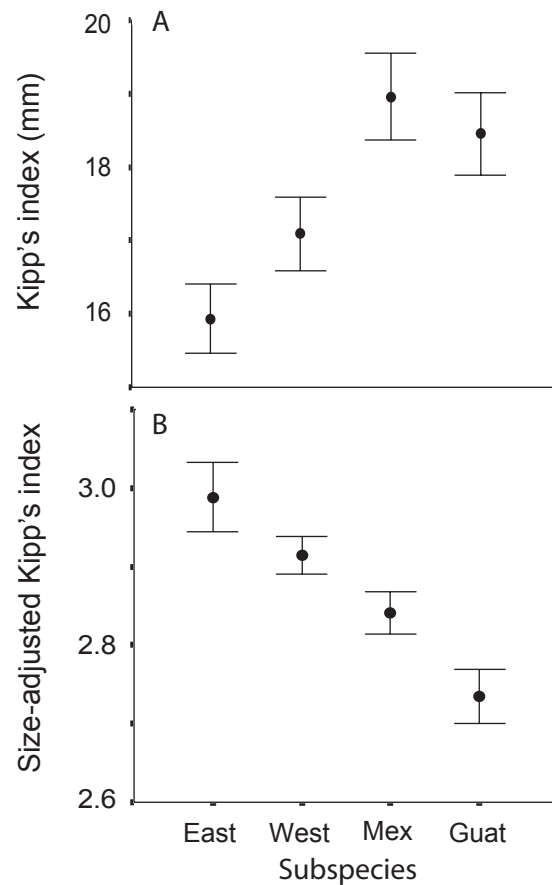


FIGURE 6. Wing shape differences among groups of adult male Yellow-rumped Warblers as measured by Kipp's distance (the distance between the longest primary and the longest secondary on the folded wing), measured between 2001 and 2004. Bars are 95% CI around the means (black dots). (A) Uncorrected Kipp's distance means, and (B) size-corrected marginal means estimated from a general linear model using principal component 1 values from a principal components analysis of structural body size variables (Table 1) as the covariate. Lack of overlap between bars indicates statistical significance at the 0.05 level.

instead favors more rounded and shorter wings (Pennycuik 1969, Leisler and Winkler 1985, Rayner 1988). However, increased survivorship over the first year of life might be favored by rounder, shorter wings that facilitate maneuverable flight to avoid predators and increase feeding efficiency (Alatalo et al. 1984, Pérez-Tris and Tellería 2001). In long-distance migrants, conflict between opposing selective forces on wing shape should be minimal. This is because selection for sustained fast flight likely overrides the countering selection towards maneuverable flight, resulting in net directional selection toward long, pointed wings in both juveniles and adults, and a small difference in wing shape between the two. In sedentary populations, age-related differences should again be small, as the release from migratory pressures should favor rounded wings for maneuverable flight in both juveniles and adults. In short- and medium-distance migrants, however, the antagonism between selective

TABLE 2. Coefficients of correlation (equivalent to factor loadings) between morphological variables related to wing shape and the derived principal components (PC1, PC2, and PC3) extracted by principal components analysis, from Yellow-rumped Warbler males of all ages and all subspecies ($n = 109$), measured between 2001 and 2004.

Variables	Factor loadings		
	PC1	PC2	PC3
Wing length	0.97**	0.01	0.18
Primary 1	0.91**	0.31**	-0.21*
Primary 2	0.94**	0.28**	-0.14
Primary 3	0.94**	0.27**	-0.10
Primary 4	0.96**	0.23*	-0.06
Primary 5	0.97**	0.17	-0.04
Primary 6	0.98**	0.06	0.11
Primary 7	0.98**	0.05	0.16
Primary 8	0.98**	0.04	0.17
Primary 9	0.97**	0.03	0.19
Kipp's distance	0.83**	-0.56**	-0.07
Variance explained	86%	10%	2%

* = $P < 0.05$, ** = $P < 0.01$.

forces of migration and maneuverability should be maximal, and differences between juveniles and adults should be largest. Here, divergent selection favoring rounded wings in juveniles and pointed wings in adults should lead to an ontogenetic shift between juvenile and adult morphologies. The larger difference between adults and subadults in *D. c. nigrifrons*, a group likely to undergo short-distance migration, is consistent with

TABLE 3. Age effects on size-adjusted wing length and wing shape in Yellow-rumped Warbler (*Dendroica coronata*) subspecies, measured between 2001 and 2004, as reflected by the P values from F tests of the effect of age based on the linearly independent pairwise comparisons among the estimated marginal means from a general linear model. Where significant, means are always smaller for subadults than for adults. P value for Wilks's lambda corresponds to the F test of the multivariate effect of age in each group.

	<i>coronata</i>	<i>auduboni</i>	<i>nigrifrons</i>	<i>goldmani</i>
Primary 1	0.39	0.50	0.53	0.88
Primary 2	0.27	0.40	0.21	0.13
Primary 3	0.56	0.46	0.43	0.24
Primary 4	0.61	0.36	0.26	0.09
Primary 5	0.97	0.31	0.13	*
Primary 6	0.51	0.08	***	*
Primary 7	0.36	*	***	*
Primary 8	0.66	*	***	0.12
Primary 9	0.27	*	***	0.09
Kipp's distance	0.47	0.09	***	0.11
Wing length	0.07	*	***	*
Wilks's lambda	0.30	0.71	0.61	0.68
n (adults, subadults)	15, 8	14, 13	16, 7	20, 10

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

this prediction, as are the relatively smaller differences found in *D. c. auduboni* and *goldmani*, and the absence of any significant difference in long-distance migrant *coronata*.

Pérez-Tris and Tellería (2001) proposed a similar model to explain their observation that juvenile European Blackcaps (*Sylvia atricapilla*) had significantly shorter wings than adults in migratory but not sedentary populations. Their model predicts increasing age-related differences in wing length with migratory distance, reflecting the increasing antagonism between selective forces acting on flight-efficient wings in adults and short, maneuverable wings in juveniles. Based on our results, we propose a modified version of their model (Fig. 7), which

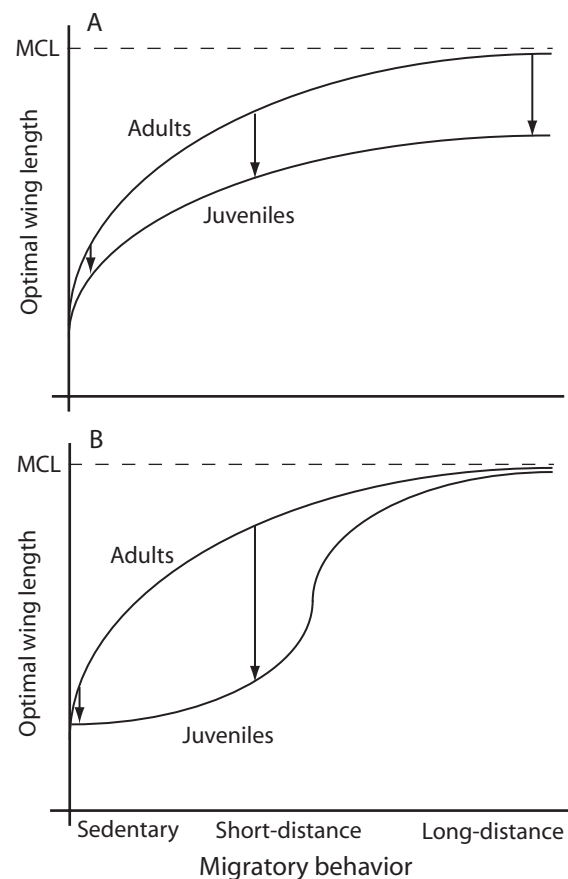


FIGURE 7. Graphical model of how differences in migratory distance affect age-related differences in wing morphology. (A) Model proposed by Pérez-Tris and Tellería (2001) for populations of the European Blackcap (*Sylvia atricapilla*). In their model, wing length increases with migratory distance, with this increase decelerating as wing length reaches a mechanical constraint limit (MCL) set by impaired maneuverability. Modified from Pérez-Tris and Tellería (2001). (B) Model proposed here based on Yellow-rumped Warbler data. Difference in wing-length between juveniles and adults is maximal for medium-distance migrants, where age-related trade-offs between migratory flight and maneuverability are most pronounced. Age-related differences in wing length for long-distance migrants are predicted to be low because selection favoring long, pointed wings overrides the advantages of rounder wings in juveniles.

predicts that differences between adults and subadults should be most pronounced not in long-distance migrants, where selection towards high-aspect ratio wings is likely to override adaptations for maneuverable flight in juveniles, but in short- to medium-distance migrants, where age-dependent selection on wing shape is likely to be strongest. Because Pérez-Tris and Tellería (2001) sampled migratory Blackcap populations in the Iberian peninsula wintering grounds, where populations from various European breeding populations mix, they were not able to separate long-distance from short-distance migrants in their analysis, and thus the applicability of our model to this species remains to be tested. In any case, detailed field observations of age-specific foraging efficiency and predator-avoidance behavior in populations of different migratory behaviors will be necessary to properly test our model and investigate the relative importance of the specific selective factors driving adaptive morphological divergence.

Though patterns of wing morphology were consistent with our predictions, we observed no significant differences in tail length among subspecies. Flight theory predicts that migrants should have shorter tails to minimize drag (Thomas and Balmford 1995), whereas sedentary birds should benefit from longer tails to increase maneuverability in dense vegetation. However, because migrants tend to also use dense vegetation, selection on relatively long wings might override the drag reduction conferred to migrants by shorter tails.

Significant differences in foraging-related morphology between fully sedentary *D. c. goldmani* and the other subspecies suggest differences in diet or foraging tactics. Individuals from the Guatemalan group had longer culmens and longer tarsi relative to body size. An elongated bill might reflect an adaptation to a predominantly invertebrate diet in contrast to migratory populations, which are known to be considerably frugivorous, at least during the nonbreeding season (Hunt and Flaspohler 1998), and the longer tarsi could well reflect ground-dwelling foraging behavior (Osterhaus 1962, Fitzpatrick 1985). In fact, individuals of both sexes were seen foraging mostly on the ground, gleaning invertebrates in short alpine grass (BM, pers. obs.). Further study of the ecology of *D. c. goldmani* in Guatemala will be needed to fully explain the morphological characteristics of the group.

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