Morphology of migration: Associations between wing, and bill morphology and migration in kingbirds (*Tyrannus*)

Short Title: Ecomorphology of migration in kingbirds (*Tyrannus*)

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Abstract

Morphology is closely linked to locomotion and diet in animals. In animals that undertake long-distance migrations, limb-morphology is under selection to maximize mobility and minimize energy expenditure. Migratory behaviors also interact with diet, such that migratory animals tend to be dietary generalists, while sedentary taxa tend to be dietary specialists. Despite a hypothesized link between migration status and morphology, phylogenetic comparative studies have yielded conflicting findings. We tested for evolutionary associations between migratory status and limb and bill morphology across kingbirds, a pan-American genus of birds with migratory, partially migratory, and sedentary taxa. Migratory kingbirds had longer wings, in agreement with expectations if selection favors improved aerodynamics for long-distance migration. We also found an association between migratory status and bill shape, such that more migratory taxa had wider, deeper, and shorter bills compared to sedentary taxa. However, there was no difference in intraspecific morphological variation among migrants, partial migrants, and residents, suggesting that dietary specialization has evolved independently of migration strategy. The evolutionary links between migration, diet, and morphology in kingbirds uncovered here further strengthen ecomorphological associations that underlie long-distance seasonal movements in animals.

Keywords: ecomorphology, flycatcher, migration, movement ecology, natural selection, partial migration, Tyrannidae

Introduction

Animal movement is linked to morphology at various taxonomic scales. At a macroevolutionary scale, streamlined or aerodynamic body shapes have been associated with the evolution of

long-distance migration in fish (Chapman *et al.*, 2015), insects (Johansson, Söderquist, & Bokma, 2009), and birds (Fiedler, 2005). Within species, migratory distance has also been associated with streamlined body shapes in fish (e.g., Crossin *et al.*, 2004) and aerodynamic shapes in birds (Voelker, 2001; Minias *et al.*, 2015; Vágási *et al.*, 2016). While certain taxa with long-distance movements exhibit strong selection for energy-efficient body shapes, this is not universal (Mulvihill & Chandler, 1990; Mönkkönen, 1995; Wang & Clarke, 2015). Thus, there is a persistent need to expand the taxonomic breadth of studies linking migration and morphology to better understand which lineages exhibit migration-morphology associations, and why these associations vary among taxa.

Morphology is also shaped by foraging strategies. For example, dietary niche is associated with head and body shape in fish (Knudsen *et al.*, 2011; Závorka *et al.*, 2020), birds (Felice *et al.*, 2019), and mammals (Swanson, Oliveros, & Esselstyn, 2019). Additionally, phenotypic plasticity is expected in dietary generalists, as shown in comparative common-garden experiments in stickleback minnows (Svanbäck & Schluter, 2012). In populations recently released from interspecific competition, such as island colonizers (Wilson, 1961; Clegg & Owens, 2002), phenotypic plasticity is thought to support increased morphological variation to limit intraspecific competition (i.e., 'niche variation hypothesis', Van Valen, 1965). Migratory lineages of dietary generalists may have strong preferences for food resources that are easiest to access (Sherry, 1984; Levey & Stiles, 1992; Bell, 2011) or that are superabundant (Moreau, 1952; Morse, 1971; Willis, 1974). In contrast, sedentary individuals may mitigate intra- and interspecific competition by seeking temporally stable food resources in microhabitats that are buffered from environmental fluctuation (e.g., temperature fluctuations; Bell, 2011). Comparisons across avian species (Levey & Stiles, 1992) and families (Chesser & Levey, 1998) have shown migratory taxa that forage on seasonally variable resources tend to exhibit more

48 morphological variation, presumably associated with opportunistic foraging across a wider
49 dietary breadth among or within individuals (Bell, 2011).

50 Testing how migration shapes morphological variation among taxa requires a
51 phylogenetic comparative framework with comprehensive inter- and intraspecific sampling.
52 Studies comparing migratory to sedentary birds support that long-distance migration favors
53 longer (Rayner, 1988; Wiedenfeld, 1991; Pérez-Tris & Tellería, 2001; Förschler & Bairlein,
54 2011; Tellería *et al.*, 2013), and more pointed (Carvalho Provinciato, Araújo, & Jahn, 2018;
55 Gómez-Bahamón *et al.*, 2020b) wings for increased aerodynamics. Hypotheses that link bill
56 morphology and migratory status are less well-studied, but hinge on differences in diet that
57 covary with migratory status (Bell, 2011; but see Cox, 1968; Herrera, 1978; Leisler, 1990).
58 Sedentary insectivorous taxa often have longer bills, presumably to improve closing speed for
59 capturing highly mobile prey (Leisler, 1990). In contrast, migratory taxa may have shorter bills
60 for capturing slow-moving prey like caterpillars to feed young during the breeding season and
61 small, abundant arthropods during winter (Thiollay, 1988; Leisler, 1990). Furthermore, studies
62 on bill size in relation to foraging strategies disagree, such that both narrow and wide bills are
63 associated with generalist diets (Tellería & Carbonell, 1999; Tellería *et al.*, 2013), and bill size
64 differs between isolated specialist populations of the same species (Alonso *et al.*, 2020).

65 Early assessments of morphological variation among migratory and sedentary avian
66 species did not account for their shared evolutionary history (Cox, 1968, 1985; Leisler, 1990).
67 Boyle and Conway (2007) advanced this approach by performing phylogenetically independent
68 contrasts to address selective pressures for the evolution of migration between species (see
69 also Gómez *et al.*, 2016; Vágási *et al.*, 2016). However, the literature on the role of migratory
70 status in shaping morphological phenotypes in birds draws predominantly from comparisons
71 among distantly related taxa (e.g., Rappole's 1995; critique of Herrera 1978). Thus, detailed
72 comparisons among taxa that differ in migratory status within a modern phylogenetic

comparative framework are necessary for a more comprehensive test of how migration is associated with morphology at different taxonomic scales (e.g., Bolnick *et al.*, 2007).

We used phylogenetic comparative methods to test for ecomorphological associations in wing and bill morphology among migratory, partially migratory, and sedentary kingbirds (*Tyrannus*; Fitzpatrick *et al.*, 2004). Kingbirds are flycatchers (Tyrannidae) with considerable variation in migration status and morphology within and among species, as well as a rich body of literature linking ecology and morphology (Fitzpatrick & Schauensee, 1980; Fitzpatrick, 1981; Sherry, 1984; Fitzpatrick, 1985; Cintra, 1997; Fitzpatrick *et al.*, 2004; Gabriel & Pizo, 2005; Carvalho Provinciato *et al.*, 2018; Gómez-Bahamón *et al.*, 2020b). As aerodynamic theory predicts that longer, more pointed wings and shorter tails are more efficient for long-distance migratory flights (Norberg, 1995; Pennycuick, 2008), we expected migratory taxa to have longer and more pointed wings compared to sedentary taxa (Kipp, 1942, 1958; Winkler & Leisler, 1992; Mönkkönen, 1995 and references therein; Lockwood, Swaddle, & Rayner, 1998). Tails of long-distance migrants should also be shorter than more sedentary individuals to reduce drag during long-distance flights (Rayner, 1988; Norberg, 1990; Winkler & Leisler, 1992; Förschler & Bairlein, 2011). However, tails are targets of sexual selection (Winquist & Lemon, 1994; Mobley, 2002), and tail lengths are often unassociated with migration strategy (e.g., Voelker, 2001; Neto *et al.*, 2013). Within-population variation in flight capability could be associated with migration (Fernández & Lank, 2007) or foraging ecology (Hromada & Tryjanowski, 2003), so we also tested whether more migratory taxa have more variable wing morphology compared to less migratory taxa.

Bill morphology is closely tied to foraging niche (Snow, 1953, 1954; Lack, 1971) and bill size and shape is typically related to broad dietary categories in birds (e.g., >50% insectivorous, granivorous, frugivorous etc.; e.g., Reaney *et al.*, 2020). We therefore predicted that there would be no relationship between migratory status and bill size because all kingbirds are primarily

insectivorous. Additionally, migration may impart an ‘ecological release’ associated with the evolution of a more variable, opportunistic diet (Bell, 2011). We thus predicted that more migratory taxa will have higher coefficients of variation in bill morphology compared to less migratory taxa.

Methods

Phylogeny construction

We extracted the clade of 15 kingbird taxa from the Harvey et al. (2020) suboscine phylogeny to construct a kingbird phylogeny that includes 28 operational taxonomic units (OTUs). Harvey et al. (2020) included all species (13/13) but only 15% of the subspecific diversity (3/20). We therefore added *T. savana* taxa following phylogenetic relationships and branch lengths estimated by Gómez-Bahamón (2020a). The remaining subspecies were added as polytomies assuming a most recent common ancestor (MRCA) of 0.5 million years from members of their species group (Figure 1A)**.** To test the sensitivity of analyses to this assumption, we tested a range of different dates for the MRCA for the added subspecies, which did not change the results (Supplementary Information 1).

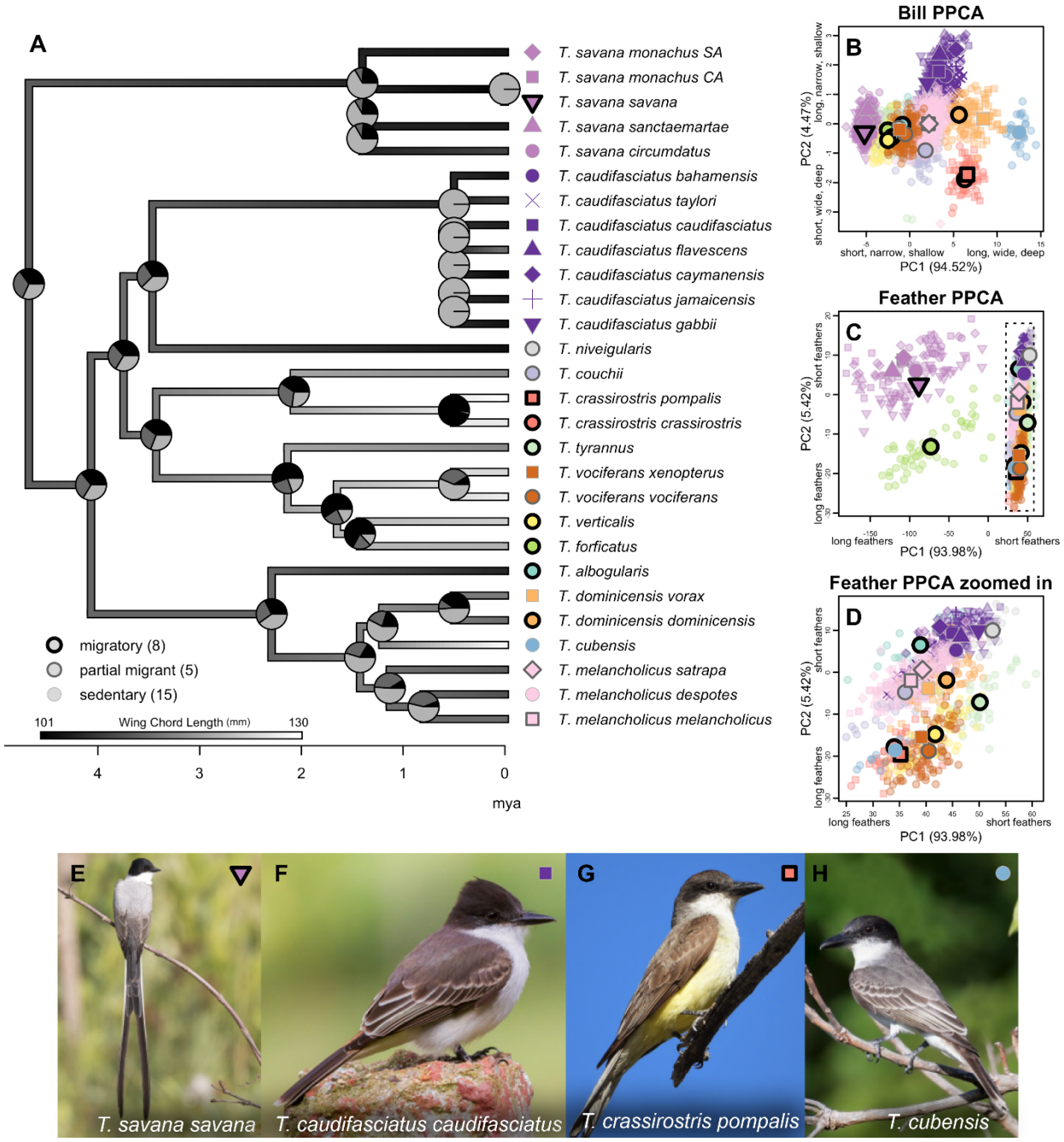

Figure 1. Ancestral state reconstruction of migration ecology category and wing chord length, as well as ordination of 28 kingbird OTUs for bill (length, width, depth) and feather (wing chord length, tail length, and Kipp's distance). A) Kingbird phylogeny showing ancestral state reconstruction of migration ecology strategy (pie charts at each node), and wing chord length (branch greyscale). B-D) PPCA plots showing individuals color-coded to species (identified at the tip labels of the phylogeny), shape-coded to subspecies, and their status as migratory, partially migratory, or sedentary is distinguished via the shape outline. Pie charts for each node in the phylogeny show the ancestral state reconstruction of migration type. E-H) photos of representative kingbird taxa with corresponding color- and shape-coded points in the top right of

each photo. Taxa are as follows: E) *Tyrannus savana savana* (photo credit: Rodrigo Conte), F) *Tyrannus caudifasciatus caudifasciatus* (photo credit: Yeray Seminario / Whitehawk), G) *Tyrannus crassirostris pompalis* (photo credit: Martin Molina), and H) *Tyrannus cubensis* (photo credit: Dubi Shapiro).

Morphological measurements

We measured bill length, width, and depth at the distal end of the nares. We also measured unflattened wing chord length, Kipp's distance (a measure of wing pointedness: the distance between the tip of the first secondary feather to the tip of the longest primary feather; Kipp, 1942, 1958; Baldwin *et al.*, 2010), tail length, and tarsus length on 2108 study skins from across the ranges of each species and subspecies (28 operational taxonomic units (OTUs); Figure 1A; Table S1.1). MM measured 2008 specimens, and identified all individuals to the lowest level of taxonomic identification (using Clements *et al.*, 2019) and classified each individual as migratory, partially migratory, or sedentary (*sensu* Fitzpatrick *et al.*, 2004). Partially migratory taxa are those in which individuals vary in migratory tendency (Boyle, 2008). JIGA (see Acknowledgements) measured 100 specimens to improve sampling of some taxa. Bill and tail measurements were taken twice and were confirmed to be within one mm of one another. Both right and left wing chords and tarsus lengths were measured and averaged. Measurements by JIGA were only taken once. We measured tail length as the longest rectrix to the nearest 0.1 cm (Pyle *et al.*, 1997). For most measurements, we used a Mitutoyo brand IP 67 digital calipers (part number 573-271) with a range of up to 15.24 cm, with 0.00127 cm resolution. For tails longer than 15.24 cm, we used a 30.48 cm stainless steel ruler placed between the two middle rectrices. When tails were longer than 30.48 cm photos were taken of the tails above a 0.64 x 0.64 cm square grid with the calipers measuring to their extent and ImageJ was used to calculate the full tail length (Supporting Information 2). We then averaged measurements across individuals within each OTU for downstream analyses. To test

150 associations between migratory strategy and intraspecific morphological variation, we also
151 calculated the coefficient of variation (mean/standard deviation) for each character and each
152 taxon. This provides a scaled measure of variance for each character and allows testing
153 whether migratory strategies differ in the amount of intraspecific variation.

154 We tested whether accounting for age (juvenile versus adult) and sex (female versus
155 male) classes improved linear models explaining morphological measurements among taxa. We
156 did this using the mulTree function of the mulTree package (Guillerme & Healy, 2020) in R,
157 which assesses intraspecific variation while accounting for phylogenetic relatedness (e.g.,
158 Nations *et al.*, 2019). We found that including age class improved model fit for all characters
159 except tarsus length and including sex class improved model fit for all characters except bill
160 length and tarsus length (Supporting Information 1). We subsequently omitted juveniles from our
161 analyses, but presented the results of both sexes combined in the main text because our results
162 did not differ when analyzing sexes independently (Supporting Information 3).

163

164 *Phylogenetic Principal Components Analysis*

165 We conducted a phylogenetic principal component analysis (PPCA) for bill measurements using
166 the phyl.pca function from the phytools package (Revell, 2009) because this gives information
167 on bill volume and shape that is not reflected in individual bill measurements (Table 1). Bill
168 PPCA scores were included in the following phylogenetic analysis of variance (see next
169 section). PPCA was also conducted for sexes separately (Supporting Information 3).

170

171 **Table 1**. Results of phylogenetic principal component analysis (PPCA) of bill measurements.
172 Percent variance explained by each eigenvector is in brackets for each principal component.

Loadings	Bill PPC1 (94.52%)	Bill PPC2 (4.47%)	lambda
Bill length	0.99	0.14	0.95
Bill width	0.93	-0.33	
Bill depth	0.94	-0.27	

173

174 *Phylogenetic Analysis of Variance*

175 We compared morphology between migratory, partially migratory, and sedentary taxa via a
176 phylogenetic analysis of variance (Garland *et al.*, 1993) with the phylANOVA function in the
177 phytools package (Revell, 2012). As differences in body size can account for much of the
178 variation among species (Albrecht, Gelvin, & Hartman, 1993; McCoy *et al.*, 2006; Revell, 2009;
179 Berner, 2011), we extracted phylogenetic residuals (Revell, 2009) for each dependent variable
180 (bill length, bill width, bill depth, wing chord, Kipp's distance, and tail length) with tarsus length
181 as an approximation of body size and the independent variable. We opted to use tarsus instead
182 of mass to adjust for body size (Rising & Somers, 1989; Senar & Pascual, 1997) because mass
183 can change seasonally (particularly in migratory birds; Lindström & Piersma, 1993) and also
184 varies by sex in some kingbirds (e.g., *T. melancholicus*, Jahn *et al.*, 2010; *T. savana*, Carvalho
185 Provinciato *et al.*, 2018; *T. tyrannus*, Murphy, 2007). To additionally support this decision, we
186 used the mulTree function of the mulTree package to test whether tarsus length had the highest
187 correlation among measurements while accounting for phylogeny, finding that tarsus length the
188 highest correlation with body mass among all variables for the individuals that had mass data
189 (Supporting Information 1). We then conducted a phylogenetic ANOVA for each character using
190 the residual values (with 1000 replicates) and reported mean P-values for pairwise, post-hoc
191 comparisons of mean values and coefficients of variation between migration categories. As
192 such, we conducted 51 tests of statistical significance, which raises the issue of multiple

hypothesis testing (Shaffer, 1995). Opinions differ on whether or not to adjust P-values when testing multiple hypotheses (Curran-Everett, 2000) and the 0.05 conventional threshold is ultimately arbitrary (Wasserstein, Schirm, & Lazar, 2019). Nonetheless, we report both uncorrected P-values and Bonferroni-corrected P-values (n = 3 tests for each set of pairwise comparisons of means or coefficients of variation). We also performed ancestral state reconstructions of wing chord length with the contMap function in the phytools package (Revell, 2012) and of migratory status with the fit.mle function in the diversitree package (FitzJohn, 2012). All statistical analyses were performed using program R version 4.0.3 (R Core Team, 2020).

Results

The mean values for each morphometric character +/- standard deviation for all adults in each OTU are reported in Table S1.1. We found that migratory taxa had longer wing chords (Figure 2F, Table 2) and pointier wings than sedentary taxa (Figure 2D, Table 2). However, we found no association between migratory status and coefficients of variation in bill morphology (Figure 2G-I, Table 2). In agreement with our prediction, we found no relationship between migratory status and bill length, width, depth, or bill PPC1 (Figure 2A-C, Figure 3A, Table 2). However, migratory taxa had shorter, wider, and deeper bills (bill PPC2) compared to sedentary taxa, which had longer, shallower, and more narrow bills (Figure 3B, Table 2).

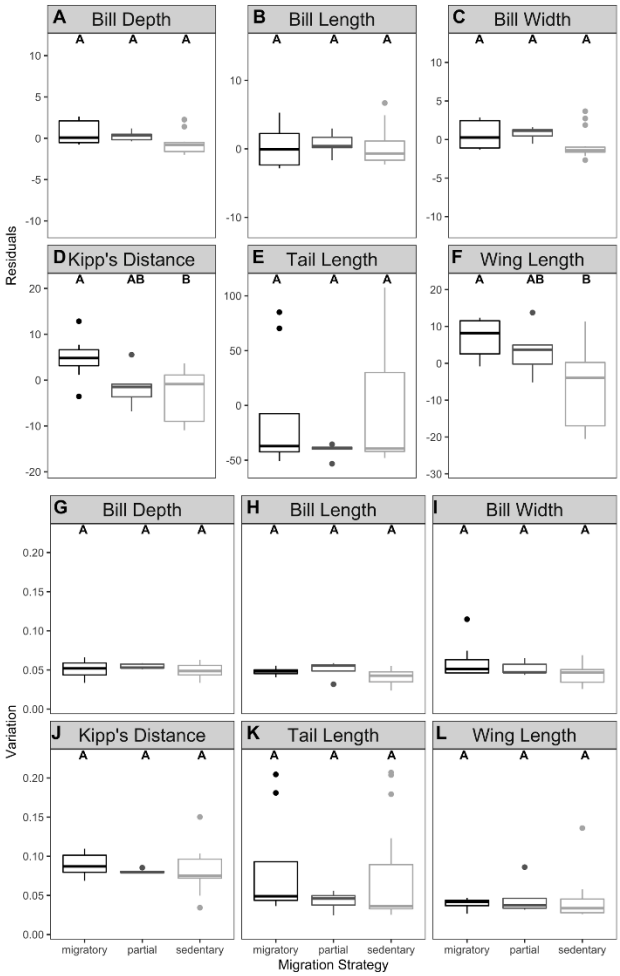

Figure 2. Phylogenetic ANOVA results comparing residuals of bill and feather morphometrics (A-F), and coefficient of variation in bill and feather morphometrics (G-L) across migratory, partially migratory, and sedentary kingbird OTUs. Note: although Kipp's distance was significantly different between migratory and sedentary taxa for all adults, this was not significantly different after Bonferroni correction when males were assessed separately (Supporting Information Table 3.6). Letters above each barplot show groupings resulting from post-hoc pairwise comparisons.

Table 2. T and P values from phylogenetic ANOVA analysis of adult *Tyrannus* flycatchers. Values shown in brackets are P values with Bonferroni adjustment (n = 3) to account for multiple hypothesis testing. Significant results are in bold. Model F and Pr(>F) values can be found in Table S1.4.

Morphometric	migratory v. partially migratory	migratory v. sedentary	partially migratory v. sedentary

	T	P (adj. p)	T	P (adj. p)	T	P (adj. p)
Bill length	0.32	0.73 (1.00)	0.06	0.96 (1.00)	0.30	0.82 (1.00)
CV Bill length	0.39	0.72 (1.00)	1.90	0.23 (0.66)	2.04	0.15 (0.39)
Bill width	0.20	0.82 (1.00)	1.68	0.30 (0.86)	1.65	0.24 (0.74)
CV Bill width	1.01	0.29 (0.99)	2.49	0.10 (0.33)	1.00	0.49 (1.00)
Bill depth	0.50	0.60 (1.00)	2.17	0.17 (0.49)	1.29	0.40 (1.00)
CV Bill depth	0.74	0.44 (1.00)	0.34	0.85 (1.00)	1.10	0.45 (1.00)
Bill PC1 (size)	0.07	0.94 (1.00)	0.62	0.70 (1.00)	0.45	0.74 (1.00)
CV Bill PC1 (size)	0.03	0.99 (1.00)	0.073	0.96 (1.00)	0.096	0.95 (1.00)
Bill PC2 (shape)	0.64	0.53 (1.00)	3.91	**0.01 (0.03)**	2.60	0.06 (0.18)
CV Bill PC2 (shape)	0.19	0.85 (1.00)	1.32	0.40 (1.00)	0.91	0.50 (1.00)
Kipp's distance	2.11	**0.05** (0.11)	3.73	**0.02 (0.04)**	0.83	0.57 (1.00)
CV Kipp's distance	0.71	0.43 (1.00)	0.79	0.62 (1.00)	0.12	0.94 (1.00)
Wing chord length	0.71	0.48 (1.00)	3.78	**0.02 (0.03)**	2.42	0.09 (0.20)
CV Wing chord length	0.56	0.54 (1.00)	0.28	0.87 (1.00)	0.39	0.78 (1.00)
Tail length	0.93	0.32 (1.00)	0.34	0.84 (1.00)	1.32	0.35 (1.00)
CV Tail length	1.15	0.23 (0.76)	0.35	0.83 (1.00)	0.98	0.49 (1.00)
CV Tarsus length	0.29	0.78 (1.00)	2.81	0.06 (0.16)	2.71	**0.04** (0.16)

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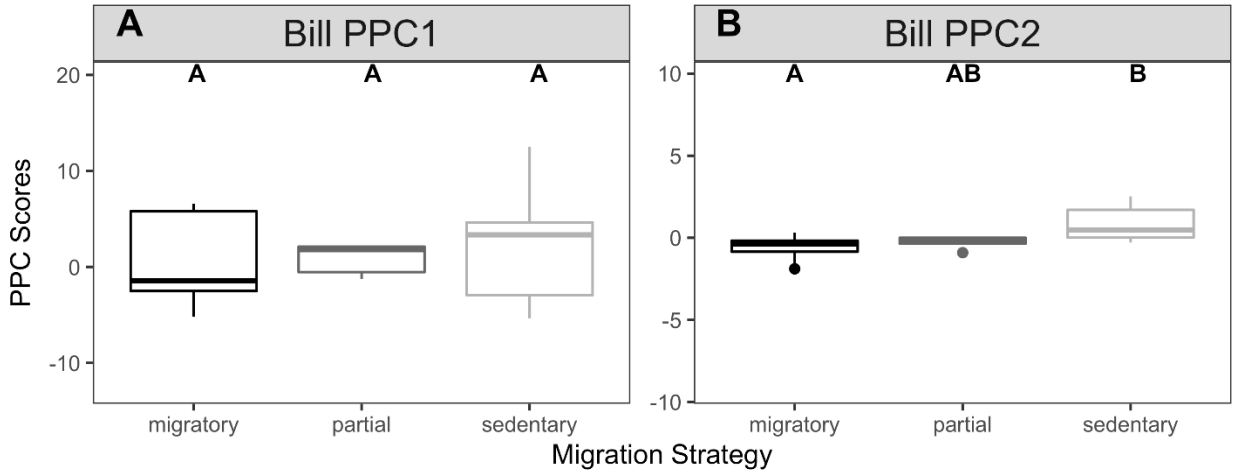

Figure 3. Phylogenetic ANOVA results comparing bill phylogenetic principal component (PPC) scores across For Peer Review migratory, partially migratory, and sedentary kingbird OTUs. Letters above each barplot show groupings resulting from post-hoc pairwise comparisons

Discussion

We found evidence of an association between migratory status and wing morphology in the kingbirds. This corroborates the idea that migratory birds have evolved morphological features that help in sustained, long-distance flight, such as longer wings (Winkler & Leisler, 1992; Milá, Wayne, & Smith, 2008; Neto *et al.*, 2013; Carvalho Provinciato *et al.*, 2018). There is a strong genetic component determining wing length (Böhning-Gaese & Oberrath, 1999; Tarka *et al.*, 2010), and among migratory taxa, wing length is positively associated with migratory distance (Förschler & Bairlein, 2011; Rönn, Shafer, & Wolf, 2016; Vágási *et al.*, 2016; Carvalho Provinciato *et al.*, 2018). Partial migration, wherein only some individuals migrate, is thought to be an evolutionary stepping-stone between sedentarism and obligate migration (Berthold, 1999; Bell, 2000; Chapman *et al.*, 2011). However, partial migration can also be sex and age-class dependent, as is the case for *T. melancholicus melancholicus* (Jahn *et al.*, 2010). Longer wings may allow for more flexibility in altering migration speeds according to conditions experienced

during migration (Hahn *et al.*, 2016), but there may be ecological limits and trade-offs imposed on wing length by other selective pressures, like shorter wings for aerial agility among arboreal species (Sheard *et al.*, 2020), for evading predators (Fernández & Lank, 2007), or for hovering flight (Marchetti, Price, & Richman, 1995).

Our finding of differences in bill shape between migratory and sedentary taxa suggests that bill shape is a potential target of selection pressures related to migration ecology. However, our comparisons of coefficients of variation did not support intraspecific competition as a driver of diversifying selection in bill morphology among generalist migratory kingbirds. The ratio of bill length/bill width holds potential significance in foraging behaviors in other tyrannids (Botero-Delgadillo & Bayly, 2012), but our findings disagree with other research across the Tyrannidae describing generalists as having intermediate bill morphologies (Fitzpatrick, 1985). We found that sedentary taxa had longer, narrower, and shallower bills compared to migratory taxa (Figure 1B; Table 1). Previous work has shown that directional selection increasing bill length in dietary specialists may be driven by interspecific competition, including from closely related taxa (Freed, Medeiros, & Cann, 2016). Thus, other selective pressures may be acting upon the bill shape and size. For example, bill morphology has been linked with thermoregulation in dietary generalists, and bill width and depth are adaptive for dissipating heat during migration for improved thermoregulation (Danner & Greenberg, 2015; Friedman *et al.*, 2017; Danner *et al.*, 2017). If convergence on bill shape is driven mainly by diet, future research integrating multivariate or nonlinear bill morphometrics (e.g., hooked bills, lateral and longitudinal bill curvature, bill surface area; Shao *et al.*, 2016) with degrees of intraguild dietary specialization and foraging behaviors would broaden our understanding of selection mechanisms shaping bill phenotypes.

The range of phenotypes shaped by migratory status is likely to be more varied than has been historically detectable using linear measurements of morphology alone. Divergence in bill

shape between migratory and sedentary taxa may define an important component of the suite of co-adaptations for migratory life histories (Bell, 2000). Morphology may be driven by selection related to migration itself, such as an increased need for heat dissipation or conservation in flight(see above). Alternatively, morphology may be shaped by a more complex competitive landscape that affects migratory and sedentary taxa differently. In taxa occupying tropical regions, like many kingbirds, the dry season is when both intra- and interspecific competition increase due to 'winter food limitation' and competition with migrants returning to wintering grounds, and competition with juvenile conspecifics (Hespenheide, 1975; Emlen, 1977; Orejuela, Raitt, & Álvarez, 1980; Stiles, 1980; Waide, 1980; Rappole, Ramos, & Winker, 1989; Rappole, 1995; Sherry, 2005; Danner *et al.*, 2013). Selection may favor longer bills among sedentary taxa to resolve both intra- and interspecific conflict (Table 1, Figure 3B), allowing access to more temporally stable food resources in microhabitats buffered from spatial and temporal environmental fluctuations (Bell, 2011).

Migratory and sedentary taxa may not differ in linear, individual bill metrics if a combination of characteristics (e.g., Table 1, Figure 3B) support a more generalist foraging strategy. For example, specific bill shapes could accommodate spatiotemporal changes in the competitive landscape (Navalón *et al.*, 2019) or provide increased stability for prey capture in perch-gleaning or hover-gleaning foraging techniques (Fitzpatrick, 1985; Fitzpatrick *et al.*, 2004; Botero-Delgadillo, 2011; Botero-Delgadillo & Bayly, 2012). The diversity of habitats that migratory taxa encounter during their annual cycle may shape phenotypes in more complex ways than previously thought, and techniques that incorporate more advanced characterizations of morphological variation may expose novel insight into how movement life history strategies shape phenotypes (e.g., Pol *et al.*, 2009; Mallarino *et al.*, 2011; Navalón *et al.*, 2019; Alonso *et al.*, 2020; Medina *et al.*, 2020).

Aspects of both wing and bill morphology appear to have evolved in association with migratory status in kingbirds that have migratory, partially migratory, and sedentary taxa. Our results suggest that migratory status has shaped wing morphology in a widespread avian genus, and that multivariate bill shape metrics may differ between sedentary and migratory lineages. Thus, adaptive phenotypes may be related to migratory status in more complex ways than previously understood. Assessments of the various mechanisms driving patterns in bill shape (e.g., heat dissipation, foraging strategy, and competitive landscape) across a broader range of taxonomic groups that differ in migration strategies would complement our refinement of the morphology of migration in kingbirds.

Data Availability

The data underlying the work, and the R code for all statistical analyses and results shared in tables and figures is available from the following public Github repository (https://github.com/mmacphe/Tyrannus_morphology). The voucher table and measurements of all individuals will also be made available at Dryad upon publication.

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Supporting Information

Supporting Information 1 – Supplementary Results

Supporting Information 2 – ImageJ protocol for measuring long *Tyrannus* tail lengths

Supporting Information 3 – Sex-specific results: means for each morphometric, phylogenetic principal components analysis (PPCA), and phylogenetic ANOVA