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

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

Authors & Affiliations
Maggie P. MacPherson [1,2,*], Alex E. Jahn [3,4], Nicholas A. Mason [2]
[1] Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA 70118
[2] Louisiana State University Museum of Natural Sciences, Louisiana State University, Baton Rouge, LA 70803
[3] Departamento de Zoologia, Universidade Estadual Paulista, Av. 24a No. 1515, Rio Claro, Brazil
[4] Environmental Resilience Institute, Indiana University, 717 E 8th St., Bloomington, IN 47408
[*]Corresponding author: Maggie P. MacPherson, E-mail: maggie.macpherson@gmail.com

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. In this study, 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. We found that migratory kingbirds had longer and more pointed 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 and deeper bills and sedentary taxa had longer bills. However, there was no difference in levels of intraspecific morphological variation among migrants, partial migrants, and residents, suggesting that dietary specialization has evolved independently of migration strategy. Evolutionary links between migration, diet, and morphology in kingbirds 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, more streamlined or aerodynamic body shapes have been associated with the evolution

of long-distance migration in fish (Common Roach (*Rutilus rutilus*); Chapman et al. 2015), insects (dragonflies; Johansson et al. 2009), and birds (Fiedler, 2005). Within species, migratory distance has also been associated with streamlined body shapes in fish (e.g., sockeye salmon (*Oncorhynchus nerka*); 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 (Arctic char (*Salvelinus alpinus*); Knudsen *et al.*, 2011, brown trout (*Salmo trutta*); 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 (*Gasterosteus aculeatus*; 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 more temporally-stable food resources in microhabitats that are more buffered from environmental fluctuation (e.g., temperature fluctuations; Bell, 2011). Comparisons across avian species (Levey & Stiles, 1992) and families (Chesser & Levey, 1998) have shown that migratory

taxa that forage on seasonally variable resources tend to exhibit more morphological variation, presumably associated with opportunistic foraging across a wider dietary breadth among or within individuals (Bell, 2011).

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

Early assessments of morphological variation among migratory and sedentary avian species did not account for their shared evolutionary history (Cox, 1968, 1985; Leisler, 1990). Although Boyle and Conway (2007) advanced this approach by performing phylogenetically independent contrasts to address selective pressures for the evolution of migration between species (see also Gómez *et al.*, 2016; Vágási *et al.*, 2016), the literature on the role of migratory status in shaping morphological phenotypes in birds draws predominantly from comparisons

among unrelated migratory and sedentary taxa (e.g., Rappole's (1995) critique of Herrera (1978)). Thus, detailed comparisons among taxa that differ in migratory status within a modern phylogenetic comparative framework are necessary for a more comprehensive test of whether and how migration is associated with morphology at different taxonomic scales (e.g., Bolnick *et al.*, 2007).

In this study, 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 tyrant flycatchers (family 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, 1985; Sherry, 1984; Cintra, 1997; Fitzpatrick *et al.*, 2004; Gabriel & Pizo, 2005; Carvalho Provinciato *et al.*, 2018; Gómez-Bahamón *et al.*, 2020a). 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 (e.g., 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, some species' tails are also 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, if migration ecology imparts an 'ecological release' that is associated with more variable, opportunistic diet (Bell, 2011), we expect 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) phylogeny of the suboscines 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), while the remaining subspecies were added as polytomies assuming a most recent common ancestor of 0.5 million years from members of their species group (Figure 1A)**.** To test the sensitivity of analyses to this assumption, we tried a range of different dates for the most recent common ancestor for the added subspecies and this did not change the results (see Output Files at https://github.com/mmacphe/Tyrannus_morphology).

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 Index (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); tail length, and tarsus length on 2108 kingbird 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 (following 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. A complete list of the specimens in this study and their associated metadata will be made available at Dryad data repository (doi to be provided upon acceptance). Bill and tail measurements were taken twice and were confirmed to be within one mm of one another. Both right and left wings and tarsi 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, and 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 (ImageJ protocol available in Supporting Information 2).

We used linear model comparisons to test whether accounting for age (juvenile versus adult) and sex (female versus male) classes improved model performance. We found that AIC values were lower in models that did not include age (except in tarsus length), and although AIC values were lower in some models that included sex (bill length, bill width, bill depth, and tarsus

length), we present the results of all adult individuals in the main text as our results did not differ when analyzing sexes independently (Supporting Information 3). To test associations between migratory strategy and morphology, we calculated the coefficient of variation (mean/standard deviation) for each taxon.

Phylogenetic Principal Components Analysis

As selection is thought to act independently on bill morphology compared to flight feather morphology, we conducted separate principal component analyses for bills and flight feathers to estimate their overall relative size and shape using the phyl.pca function from phytools package (Revell, 2009; Table 1). Because two species have extremely long tail feathers (*T. savana* and *T. forficatus*), we explored whether the PPCA would be substantially improved with their omission, but the amount of variance explained by PPC1 was similar regardless of whether these taxa were included or excluded (Table S1.2). The PPCA scores were included in the following phylogenetic analysis of variance (described in the next section). PPCA was also conducted for females and males separately and results can be found in Supplementary Material (Supporting Information 3).

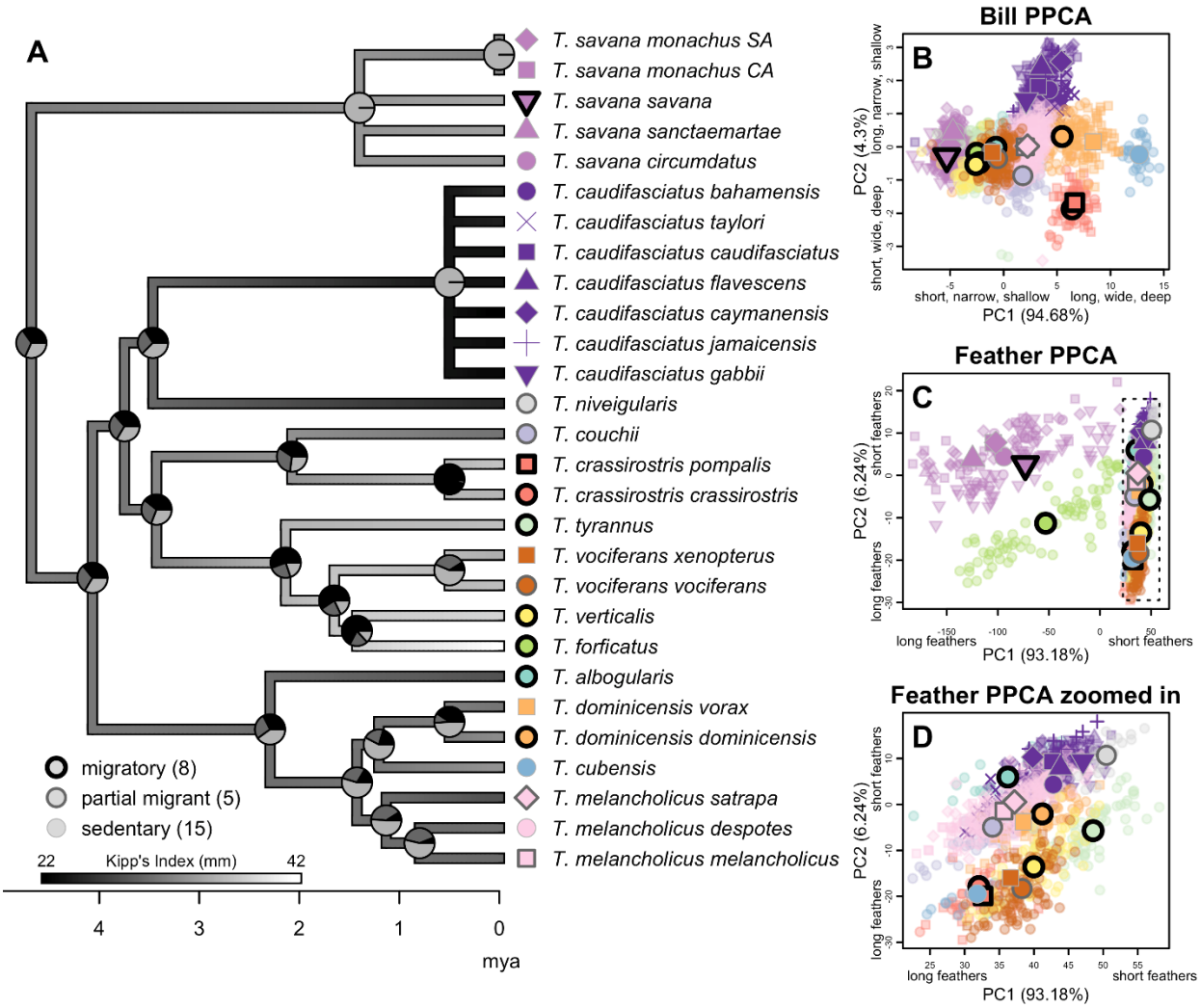

Figure 1. Ancestral state reconstruction of migration ecology category and Kipp's Index, and ordination of 28 kingbird OTUs for bill (length, width, depth) and feather (wing chord length and Kipp's Index) morphometrics. A) Kingbird phylogeny showing ancestral state reconstruction of migration ecology strategy (pie charts at each node), and Kipp's Index (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.

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

Loadings	**Bill PPC1 (94.68%)**	**Bill PPC2 (4.30%)**	**lambda**
Bill length	0.99	0.14	0.96
Bill width	0.93	-0.33	
Bill depth	0.94	-0.25	
	Feather PPC1 (93.18%)	**Feather PPC2 (6.24%)**	
Kipp's Index	-0.33	-0.64	0.96
Wing chord	-0.072	-0.99	
Tail length	-0.99	0.003	
	CV Bill PPC1 (80.17%)		
CV Bill length	0.92		0.03
CV Bill width	0.91		
CV Bill depth	0.82		
	CV Feather PPC1 (82.52%)		
CV Kipp's Index	-0.38		0.50
CV Wing chord	-0.42		
CV Tail length	-0.99		

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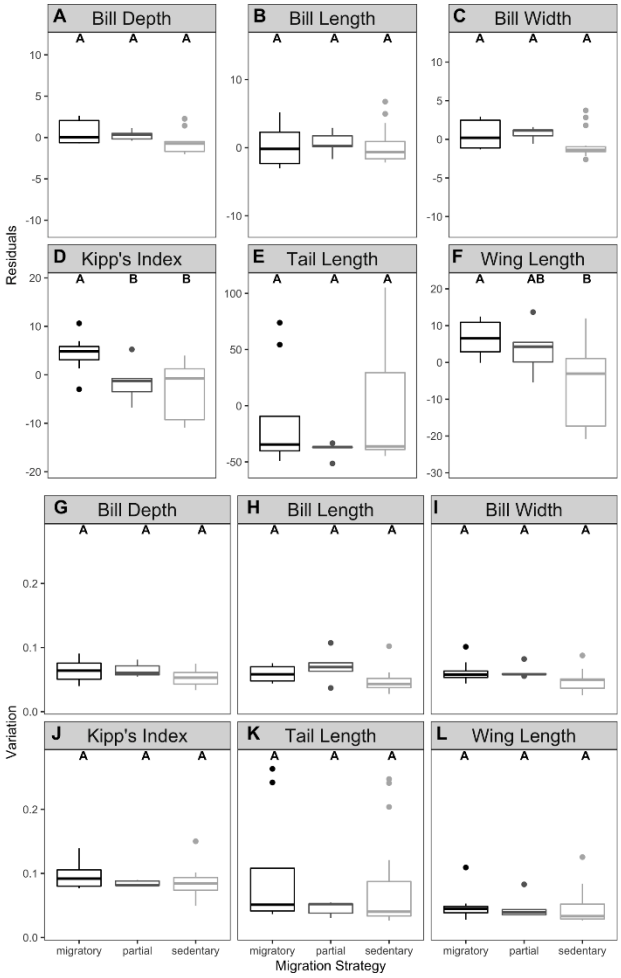
175 *Phylogenetic Analysis of Variance*

We compared morphology between migratory, partially migratory, and sedentary taxa via a phylogenetic analysis of variance (Garland *et al.*, 1993) with the phylANOVA function in the phytools package (Revell, 2012). As differences in body size can account for much of the variation among species (Albrecht, Gelvin, & Hartman, 1993; McCoy *et al.*, 2006; Revell, 2009; Berner, 2011), we extracted phylogenetic residuals (Revell, 2009) for each dependent variable (bill length, bill width, bill depth, wing chord, Kipp's Index, and tail length) with tarsus length as an approximation of body size and the independent variable. We opted to use tarsus instead of mass to adjust for body size (Rising & Somers, 1989; Senar & Pascual, 1997) because mass can change intra-annually (particularly in migratory birds; Lindström & Piersma, 1993), mass can also vary by sex in some kingbirds (e.g., *T. melancholicus*, Jahn *et al.*, 2010; *T. savana*, Carvalho Provinciato *et al.*, 2018; *T. tyrannus*, Murphy, 2007), and mass data were not available for many of the museum specimens we measured. We then conducted a phylogenetic ANOVA using the residual values, presenting the overall average value of P-values of 1000 replicates. Post-hoc comparisons identified differences in mean values between migration categories (a default setting in the phylANOVA function), which were subsequently displayed with boxplots (Figure 2 and 3). We performed an ancestral state reconstruction of Kipp's Index after finding it was associated with migration status via the phylANOVA, and we also performed an ancestral state reconstruction of migratory status. Specifically, we used the contMap function in the phytools package for continuous variables (Revell, 2012) and the fit.mle function in the diversitree package (FitzJohn, 2012; Figure 1A, Figure S1.1, Figure S1.2).

All statistical analyses were performed using program R version 4.0.3 (R Core Team, 2020). R code is provided for all analytical procedures undertaken in this manuscript at https://github.com/mmacphe/Tyrannus_morphology.

Results

The average lengths for each morphometric +/- standard deviation for each OTU are reported in Table S1.1. We found that migratory taxa had longer wings than sedentary taxa (Figure 2F, Table 2), and pointier wings than both partially migratory and 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 and partially 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).



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211 **Figure 2**. Phylogenetic ANOVA results comparing residuals of bill and feather morphometrics

212 (A-F), and coefficient of variation in bill and feather morphometrics (G-L) across migratory,

213 partially migratory, and sedentary kingbird OTUs. Significant differences are shown by different

214 letters: A versus B.

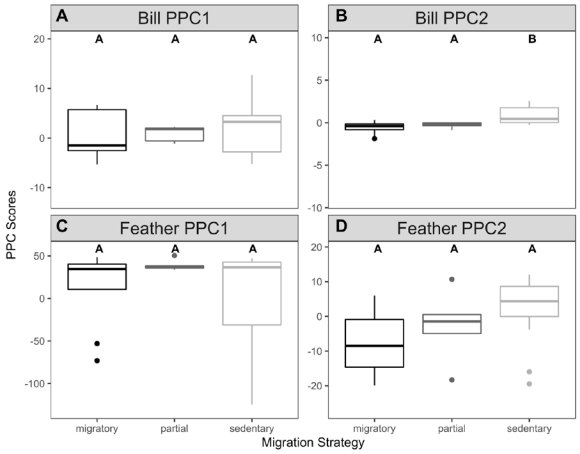

Figure 3. Phylogenetic ANOVA results comparing bill and feather phylogenetic principal component (PPC) scores across migratory, partially migratory, and sedentary kingbird OTUs. Letters above each barplot show groupings resulting from post-hoc pairwise comparisons.

Table 2. T and P values from phylogenetic ANOVA analysis. Significant results are in bold. Model F and Pr(>F) values can be found in Table S1.3.

Morphometric	**migratory v. partially migratory**		**migratory v. sedentary**		**partially migratory v. sedentary**	
	T	P	T	P	T	P
Bill length	0.31	0.72	0.09	0.96	0.26	0.86
CV Bill length	1.12	0.26	1.36	0.38	2.40	0.07
Bill width	0.19	0.84	1.62	0.31	1.58	0.27
CV Bill width	0.03	0.98	2.12	0.18	1.82	0.20
Bill depth	0.46	0.63	2.10	0.17	1.27	0.38
CV Bill depth	0.15	0.89	1.97	0.22	1.83	0.19
Bill PC1 (size)	0.08	0.92	0.66	0.69	0.46	0.74
CV Bill PC1 (size)	0.06	0.95	0.48	0.73	0.34	0.83

Bill PC2 (shape)	0.64	0.52	3.94	**<0.05**	2.63	**0.05**
CV Bill PC2 (shape)	0.59	0.55	2.89	0.09	1.79	0.20
Kipp's Index	1.99	**0.05**	3.57	**0.02**	0.83	0.54
CV Kipp's Index	1.08	0.29	1.24	0.42	0.15	0.91
Wing chord length	0.57	0.56	3.58	**0.02**	2.41	0.07
CV Wing chord length	0.18	0.86	0.39	0.82	0.14	0.92
Tail length	0.88	0.38	0.48	0.74	1.38	0.31
CV Tail length	1.18	0.23	0.48	0.81	0.90	0.57
Feather PC1 (size)	0.81	0.36	0.49	0.74	1.31	0.33
CV Feather PC1 (size)	0.85	0.40	0.40	0.80	1.28	0.37
Feather PC2 (shape)	0.92	0.31	2.45	0.12	1.06	0.44
CV Feather PC2 (shape)	0.16	0.87	1.54	0.32	1.48	0.28
CV Tarsus length	0.25	0.79	2.56	0.10	2.45	0.07

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; but not 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; but see 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). Interestingly, we found that migratory taxa had significantly pointier wings than partially migratory taxa and although not significant, partially migratory taxa appear to have intermediate wing chord lengths between sedentary and migratory taxa. 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 (e.g., shorter wings for agility in flight for arboreal species, or as an adaptation for evading predators, Fernández & Lank, 2007; or a consequence of year-round territoriality, Sheard *et al.*, 2020), or by foraging strategy (e.g., shorter wings for more efficient hovering flight; Marchetti, Price, & Richman, 1995).

Our finding of differences in bill shape between migratory and sedentary taxa suggest bill shape is a target of selection pressures related to migration ecology. However, our comparisons of coefficients of variation in the current study did not support that intraspecific competition has driven diversifying selection in bill morphology amongst generalist migratory kingbirds. A simple ratio of bill length/bill width has been shown to hold 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 (neither large or small) bill morphologies (Fitzpatrick, 1985). We found that sedentary taxa had longer, narrower, and shallower bills compared to migratory and partially 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 among migratory, partially migratory, and sedentary taxa. 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.

Aspects of kingbird ecology may partially explain the associations between migratory status and morphology that may or may not be present in other clades. Kingbirds are open-habitat foragers and thus may be predisposed to evolve migration under the 'evolutionary precursor hypothesis' (Fitzpatrick, 1985; Levey & Stiles, 1992). Furthermore, gains and losses of migration are common in this group (Gómez-Bahamón *et al.*, 2020a). As such, plasticity in migratory life history strategies of our study taxa could work in tandem with flexibility in wing and bill morphology. The difference in bill shape that we found seemed to be driven by the very short, thick, and deep bills present in two migratory *T. crassirostris* subspecies, and partially migratory *T. couchii* compared to very long, narrow, and shallow bills in sedentary *T. caudifasciatus* subspecies (six OTUs with island distributions distinct from one another, Mobley & de Juana, 2020; Figure S1.2). Thus, this trend could be the result of ecological release commonly experienced by island taxa (Wilson, 1961; Clegg & Owens, 2002; Cooney *et al.*, 2017). Tail length, and variation in wing chord length, and Kipp's Index could also be under sexual selection. This could particularly be the case in the kingbird species where tail length is suspected to be an honest indicator of mate quality (e.g., *T. forficatus,* Regosin & Pruett-Jones, 2001). Additionally, other forms of natural selection could be acting on flight morphology in species that use aerial courtship displays or engage in territorial encounters with conspecifics

(e.g., *T. savana*; Jahn & Tuero, 2020; Gómez-Bahamón *et al.*, 2020b), or in which sexual dimorphism may occur (e.g., *T. dominicensis*; Haberman, MacKenzie, & Rising, 1991). Additional studies spanning multiple genera will aid in further elucidating how morphology is shaped by migratory status.

Phenotypes shaped by migratory status may be more complex than has been historically assumed with linear measurements of morphology alone. Divergence in bill shape between migratory and sedentary taxa may define an important morphological feature that is a part of the suite of co-adaptations for migratory life histories (Bell, 2000). Morphology may be driven by selection related to migration itself such as increased needs of heat dissipation or conservation found in other studies (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 kingbird taxa, the dry season is when both intra- and interspecific competition increase due to 'winter food limitation' and competition with migrants returning to wintering grounds, in addition to 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 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).

Here we assessed the impact of variation in migration strategies on morphology in the kingbirds (genus *Tyrannus*). Aspects of both wing and bill morphology appear to evolve in association with migratory status in this group consisting of migratory, partially migratory, and sedentary taxa. Our results suggest that migratory status shapes wing morphology in a widespread avian genus, and that multivariate bill shape metrics (i.e., PPC2) may distinguish sedentary from migratory and partially 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

R code for all statistical analyses and results shared in tables and figures is available from our github repository (https://github.com/mmacphe/Tyrannus_morphology). The measurements of all individuals used in this research will be available at an online data repository upon acceptance (for now, this can be found here).

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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: averages for each morphometric, phylogenetic principal components analysis (PPCA), and phylogenetic ANOVA