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

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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 behaviours also interact with diet, such that migratory animals tend to be dietary generalists, whereas 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 that selection favours 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.

ADDITIONAL 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 *et al.*, 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). Although 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 *et al.*, 2019). Additionally, phenotypic plasticity is expected in dietary generalists, as shown in comparative common or garden experiments in stickleback minnows (Svanbäck & Schluter, 2012). In populations recently released from interspecific competition, such as island colonizers (Wilson,

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

Testing how migration shapes morphological variation among taxa requires a phylogenetic comparative framework with comprehensive inter- and intraspecific sampling. Studies comparing migratory to sedentary birds support that long-distance migration favours longer (Rayner, 1988; Wiedenfeld, 1991; Pérez-Tris & Tellería, 2001; Förschler & Bairlein, 2011; Tellería *et al.*, 2013) and more pointed (Carvalho Provinciato *et al.*, 2018; Gómez-Bahamón *et al.*, 2020b) wings for increased aerodynamics. Hypotheses that link bill morphology and migratory status are less well-studied, 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 like caterpillars to feed young during the breeding season and small, abundant arthropods during winter (Thiollay, 1988; Leisler, 1990). Furthermore, studies on bill size in relation to foraging strategies disagree, such that both narrow and wide bills are associated with generalist diets (Tellería & Carbonell, 1999; Tellería *et al.*, 2013), and bill size differs 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). 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). However, the literature on the role of migratory status in shaping morphological phenotypes in birds draws predominantly from comparisons among distantly related 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 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, 1985; Sherry, 1984; 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 *et al.*, 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 not associated 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.

MATERIAL AND 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 included 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 *Tyrannus 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 Myr from members of their species group (Fig. 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 (Supporting Information, Appendix S1).

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); Fig. 1A; Supporting Information, Table S1.1). M.M. 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). José Ignacio Giraldo Arango (see *Acknowledgements*) measured 100 specimens to improve sampling of some taxa. Bill and tail measurements were taken twice and were confirmed to be within 1 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 Mitutoyo 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 cm × 0.64 cm square grid with the calipers measuring to their extent and ImageJ was used to calculate the full tail length (Supporting Information, Appendix S2). We then averaged measurements across individuals within each OTU for downstream analyses. To test associations between migratory strategy and intraspecific morphological variation, we also calculated the coefficient of variation (mean/standard deviation) for each character and each taxon. This provides a scaled measure of

variance for each character and allows for testing whether migratory strategies differ in the amount of intraspecific variation.

We tested whether accounting for age (juvenile vs. adult) and sex (female vs. male) classes improved linear models explaining morphological measurements among taxa. We did this using the mulTree function of the mulTree package (Guillerme & Healy, 2020) in R, which assesses intraspecific variation while accounting for phylogenetic relatedness (e.g. Nations *et al.*, 2019). We found that including age class improved model fit for all characters except tarsus length and including sex class improved model fit for all characters except bill length and tarsus length (Supporting Information, Appendix S1, Table S1.2). We subsequently omitted juveniles from our analyses, but presented the results of both sexes combined in the main text because our results did not differ when analysing sexes independently (Supporting Information, Appendix S3).

PHYLOGENETIC PRINCIPAL COMPONENTS ANALYSIS

We conducted a phylogenetic principal component analysis (PPCA) for bill measurements using the phyl.pca function in the phytools package (Revell, 2009) because this gives information on bill volume and shape that is not reflected in individual bill measurements (Table 1). Bill PPCA scores were included in the following phylogenetic analysis of variance (see next section). PPCA was also conducted for the sexes separately (Supporting Information, Appendix S3).

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 *et al.*, 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 distance 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 seasonally (particularly in migratory birds; Lindström & Piersma, 1993) and also varies by sex in some kingbirds (e.g. *Tyrannus melancholicus*, Jahn *et al.*, 2010; *Tyrannus savana*, Carvalho Provinciato *et al.*, 2018; *Tyrannus tyrannus*, Murphy, 2007). To additionally support this decision, we used the mulTree function of the mulTree package to test whether tarsus length had the highest correlation
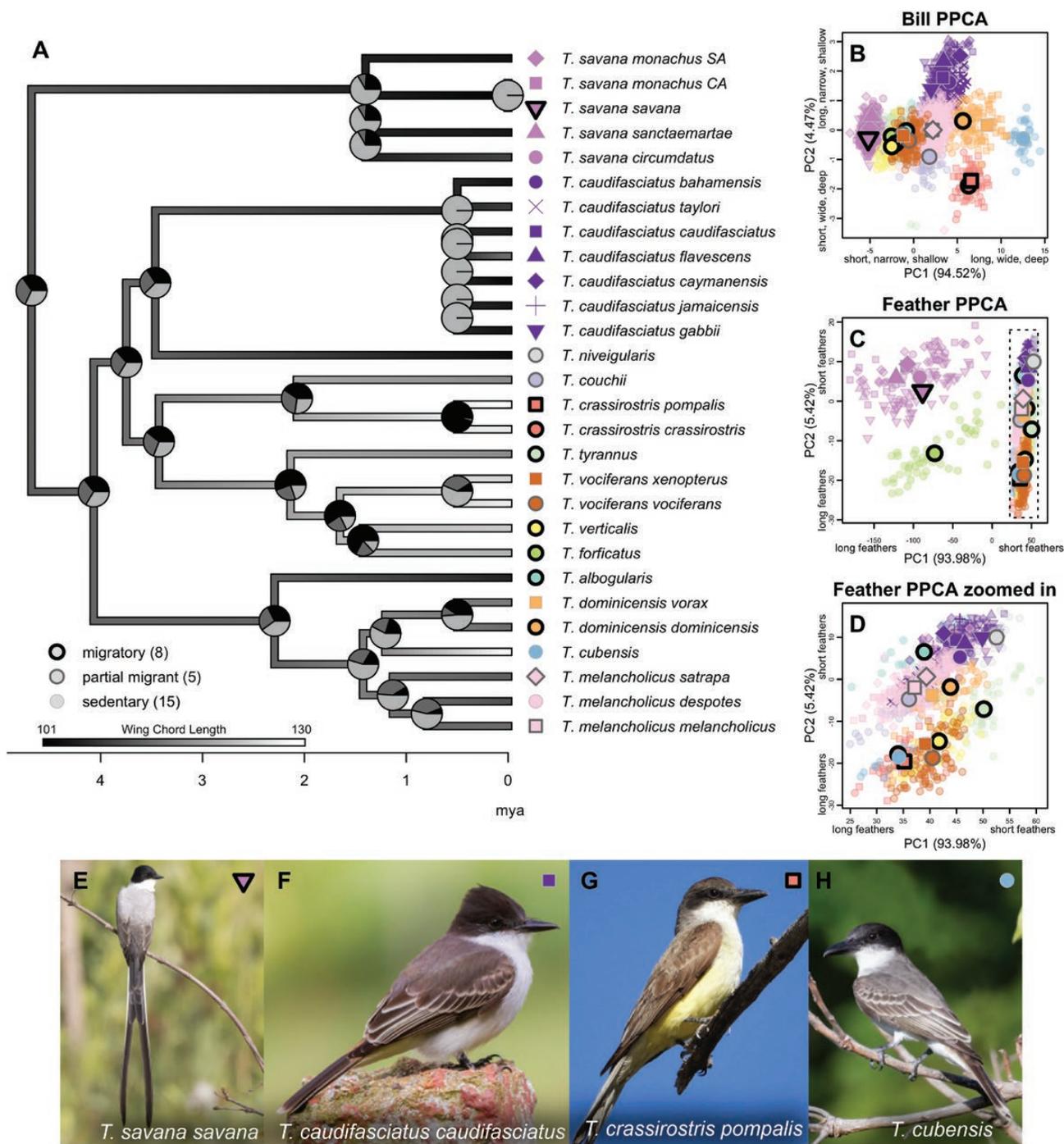
Figure 1. Ancestral state reconstruction of migration ecology category and wing chord length, as well as ordination of 28 kingbird OTUs for bill (length, width, depth) and feather (wing chord length, tail length and Kipp's distance). A, kingbird phylogeny showing ancestral state reconstruction of migration ecology strategy (pie charts at each node), and wing chord length (branch greyscale). B-D, PPCA plots showing individuals colour-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 colour- 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).

Table 1. Results of phylogenetic principal component analysis (PPCA) of bill measurements. Percent variance explained by each eigenvector is in parentheses 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	

among measurements while accounting for phylogeny, finding that tarsus length had the highest correlation with body mass among all variables for the individuals that had mass data (Supporting Information 1, Appendix S1, Table S1.3). We then conducted a phylogenetic ANOVA for each character using the residual values (with 1000 replicates) and reported mean P-values for pairwise, post-hoc comparisons of mean values and coefficients of variation between migration categories. As 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 *et al.*, 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 the program R v.4.0.3 (R Core Team, 2020).
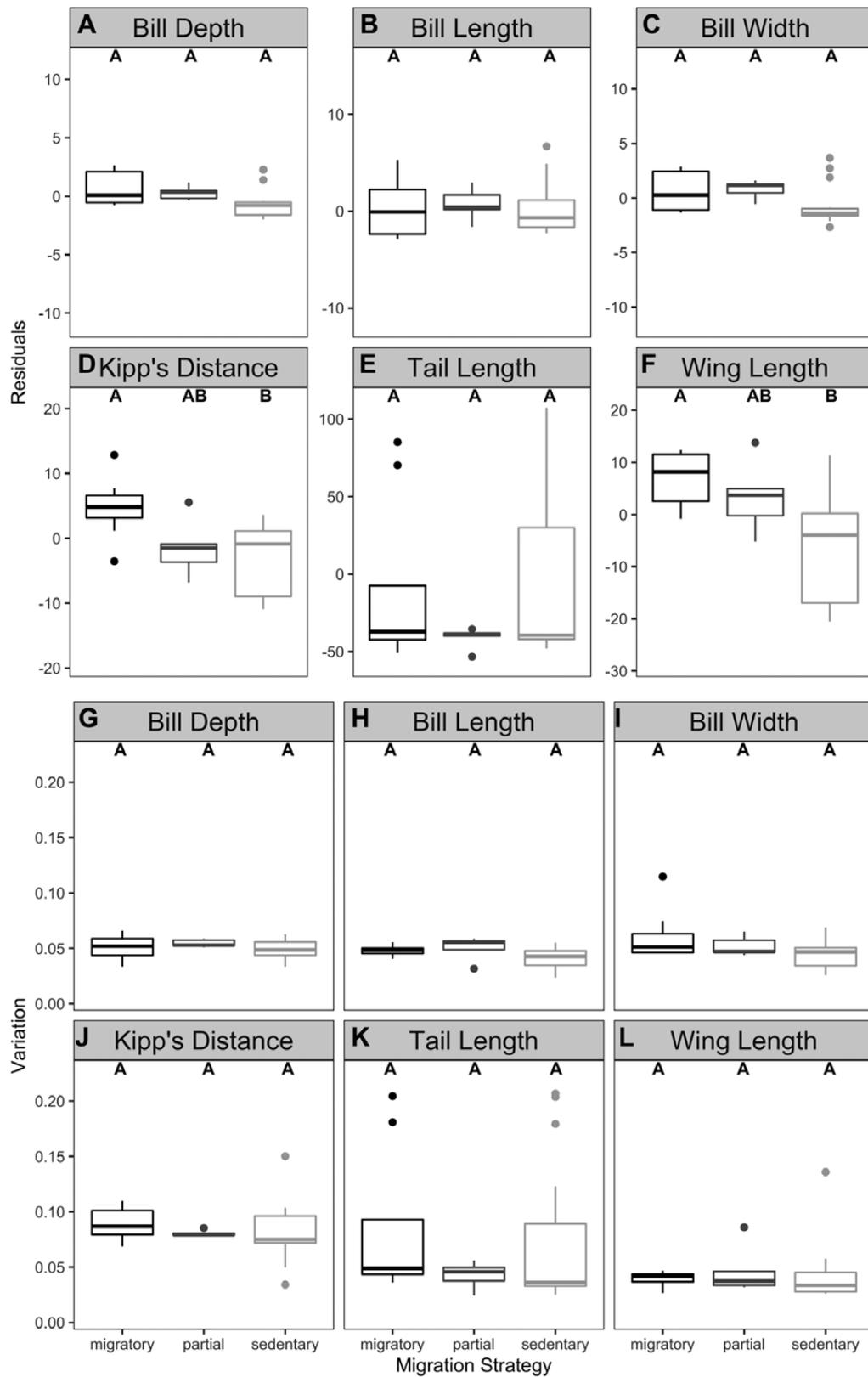
RESULTS

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

taxa, which had longer, shallower and narrower bills (Fig. 3B; Table 2).

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 *et al.*, 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 *et al.*, 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 *et al.*, 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 behaviours in other tyrannids (Botero-Delgadillo & Bayly, 2012); however, 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 (Fig. 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 *et al.*, 2016). Thus, other selective pressures may be acting upon bill shape and size. For example, bill morphology has been linked with thermoregulation in dietary generalists,

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.

Table 2. T and P values from phylogenetic ANOVA analysis of adult *Tyrannus* flycatchers. Values shown in parentheses 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 Supporting Information (Table S1.4)

Morphometric	Migratory vs. partially migratory		Migratory vs. sedentary		Partially migratory vs. 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)
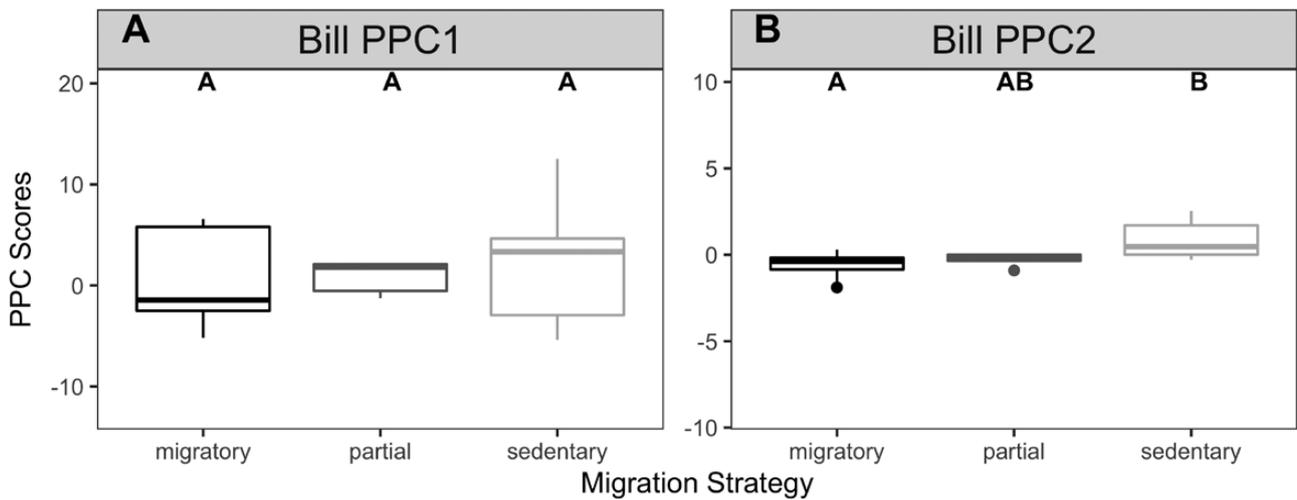
Figure 3. Phylogenetic ANOVA results comparing bill phylogenetic principal component (PPC) scores across migratory, partially migratory and sedentary kingbird OTUs. *A*, Bill PPC1 scores. *B*, Bill PPC2 scores. Letters above each bar plot show groupings resulting from post-hoc pairwise comparisons.

and bill width and depth are adaptive for dissipating heat during migration for improved thermoregulation (Danner & Greenberg, 2015; Danner *et al.*, 2017; Friedman *et al.*, 2017). If convergence on bill shape is driven mainly by diet, future research integrating multivariate or nonlinear bill morphometrics (e.g.

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 S3.6). Letters above each bar plot show groupings resulting from post-hoc pairwise comparisons.

hooked bills, lateral and longitudinal bill curvature, bill surface area; Shao *et al.*, 2016) with degrees of intraguild dietary specialization and foraging behaviours 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 *et al.*, 1980; Stiles, 1980; Waide, 1980; Rappole *et al.*, 1989; Rappole, 1995; Sherry, 2005; Danner *et al.*, 2013). Selection may favour longer bills among sedentary taxa to resolve both intra- and interspecific conflict (Table 1; Fig. 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; Fig. 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 public Github repository (https://github.com/mmacphe/Tyrannus_morphology). The voucher table and measurements of all individuals are available in the Dryad digital repository (MacPherson *et al.*, 2021).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Supplementary results.
Appendix S2. ImageJ protocol for measuring long *Tyrannus* tail lengths.
Appendix S3. Sex-specific results: means for each morphometric, phylogenetic principal components analysis (PPCA) and phylogenetic ANOVA.
Table S1.1. Morphological measurement means for adults of 28 *Tyrannus* OTUs (millimeters). All measurements are shown ± standard deviation and with the sample size in brackets. After *Tyrannus savana monachus*, 'CA' refers to Central America and 'SA' refers to South America.
Table S1.2. Tests of whether age or sex classes play a role in morphological measurements. We used the mulTree function in the mulTree library to test the role of age and sex classes on each morphological measurement.
Table S1.3. Test of whether tarsus length is the best morphological measurement to approximate body mass. We used the mulTree function in the mulTree library to assess the correlation of all measured morphologies with body mass for 438 individuals that had mass data on specimen tags (representing 18 taxa) while accounting for phylogeny.

Table S1.4. F and Pr(>F) values from phylogenetic ANOVA. Adjusted P-value after Bonferroni correction for multiple hypothesis testing is only shown for the instance using polytomies added with the most recent common ancestor at 0.5 Mya.

Figure S2.1. Image of a *T. savana* tail above 0.64 x 0.64 cm grid. Photos were taken directly above specimens using a RPS brand copy stand (https://www.amazon.com/gp/product/B003OAF2BA/ref=ppx_yo_dt_b_search_asin_title?ie=UTF8&psc=1), Canon Rebel T1i SLR, and Canon 18-55 mm image stabilizer lens. Mitutoyo brand digital calipers were placed between the middle rectrices to the base of the tail and extended. We prioritized showing the measurement on the digital calipers and the end of the tail for future tail length calculations.

Figure S2.2. Measuring the tail length.

Table S3.1. Summary of morphological measurements for **females** from 28 *Tyrannus* OTUs (millimeters).

Figure S3.1. Ancestral state reconstruction of migration ecology strategy and wing chord length, and ordination of 28 *Tyrannus* OTU adult **females** 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: Dubio Shapiro).

Table S3.2. Results of phylogenetic principal component analysis (PPCA) of bill morphometrics for adult **females**. Percent variance explained by each eigenvector is in brackets for each principal component.

Table S3.3. T and P values from phylogenetic anova analysis for adult **females**. Values shown in brackets are from phylogenetic ANOVA with Bonferroni correction to account for multiple hypothesis testing. No Bonferroni correction was done for the assessment of Tail length because it was analyzed alone with two taxa removed due to missing data (*T. savana sanctaemartae*, *T. caudfasciatus jamaicensis*). Significant results are in bold.

Figure S3.2. 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 *Tyrannus* OTU adult **females**. Significant differences are shown by different letters: A versus B.

Figure S3.3. Phylogenetic ANOVA results comparing bill phylogenetic principal component (PPC) scores across migratory, partially migratory, and sedentary *Tyrannus* OTU adult **females**. Significant differences shown by different letters: A versus B.

Table S3.4. Summary of morphological measurements for **males** from 28 *Tyrannus* OTUs (millimeters).

Figure S3.4. Ancestral state reconstruction of migration strategy and wing chord length, and ordination of 28 *Tyrannus* OTU adult **males** for bill (length, width, depth) and feather (wing chord length and Kipp's distance). A) Tyrannus phylogeny showing ancestral state reconstruction of migration 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: Dubio Shapiro).

Table S3.5. Results of phylogenetic principal component analysis (PPCA) of bill morphometrics for adult **males**. Percent variance explained by each eigenvector is in brackets for each principal component.

Table S3.6. T and P values from phylogenetic ANOVA for **males**. Significant results are in bold.

Figure S3.5. 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 *Tyrannus* OTU adult **males**. Significant differences are shown by different letters: A versus B.

Figure S3.6. Phylogenetic ANOVA results comparing bill phylogenetic principal component (PPC) scores across migratory, partially migratory, and sedentary *Tyrannus* OTU adult **males**. Significant differences shown by different letters: A versus B.

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