

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

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Received 6 April 2021; revised 29 July 2021; accepted for publication 2 August 2021

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; Pennycuik, 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 (Winqvist & 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 (MRCAs) 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

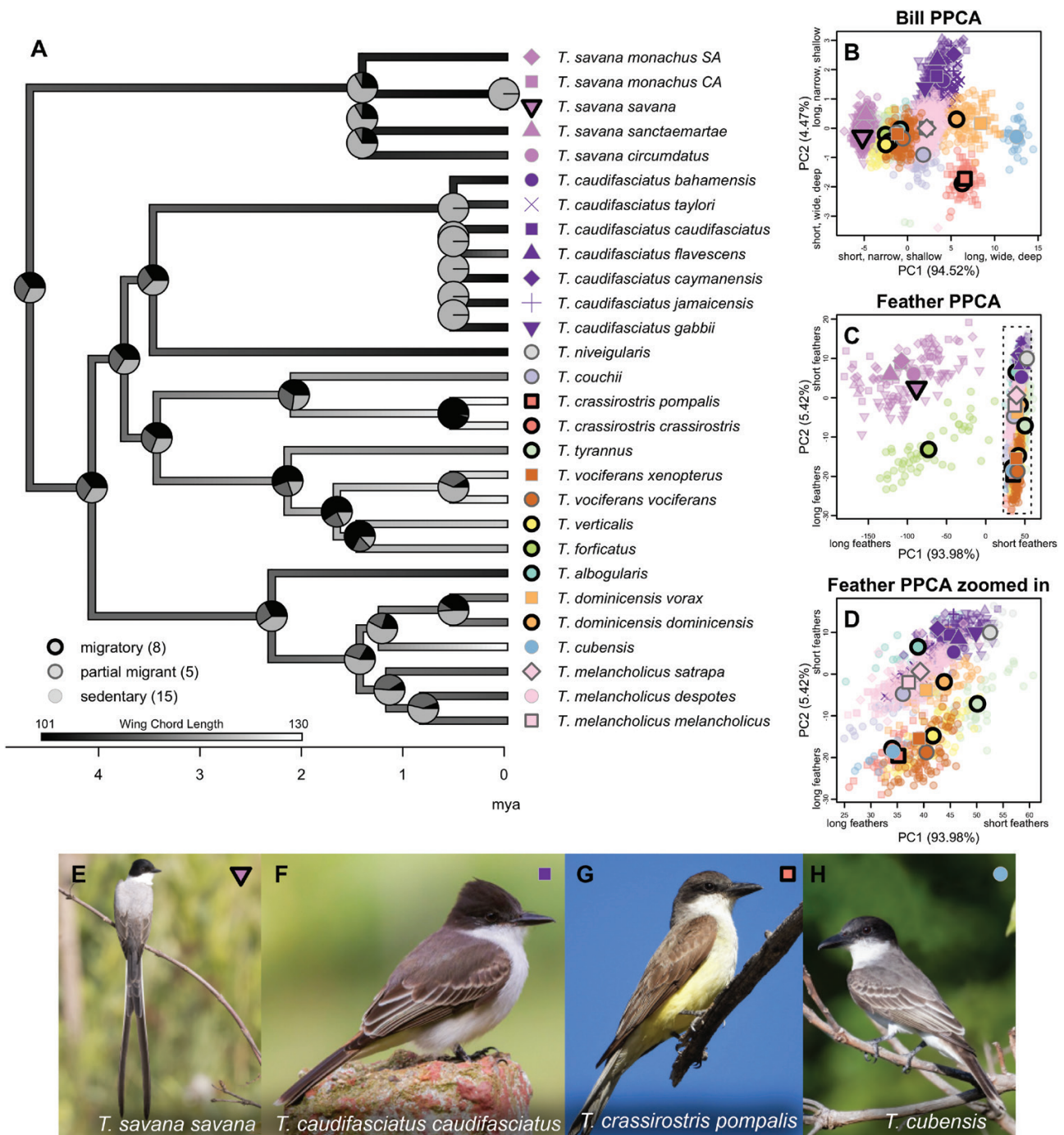


Figure 1. Ancestral state reconstruction of migration ecology category and wing chord length, as well as ordination of 28 kingbird OTUs for bill (length, width, depth) and feather (wing chord length, tail length and Kipp's distance). A, kingbird phylogeny showing ancestral state reconstruction of migration 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 sedentary 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-Delgado & 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,

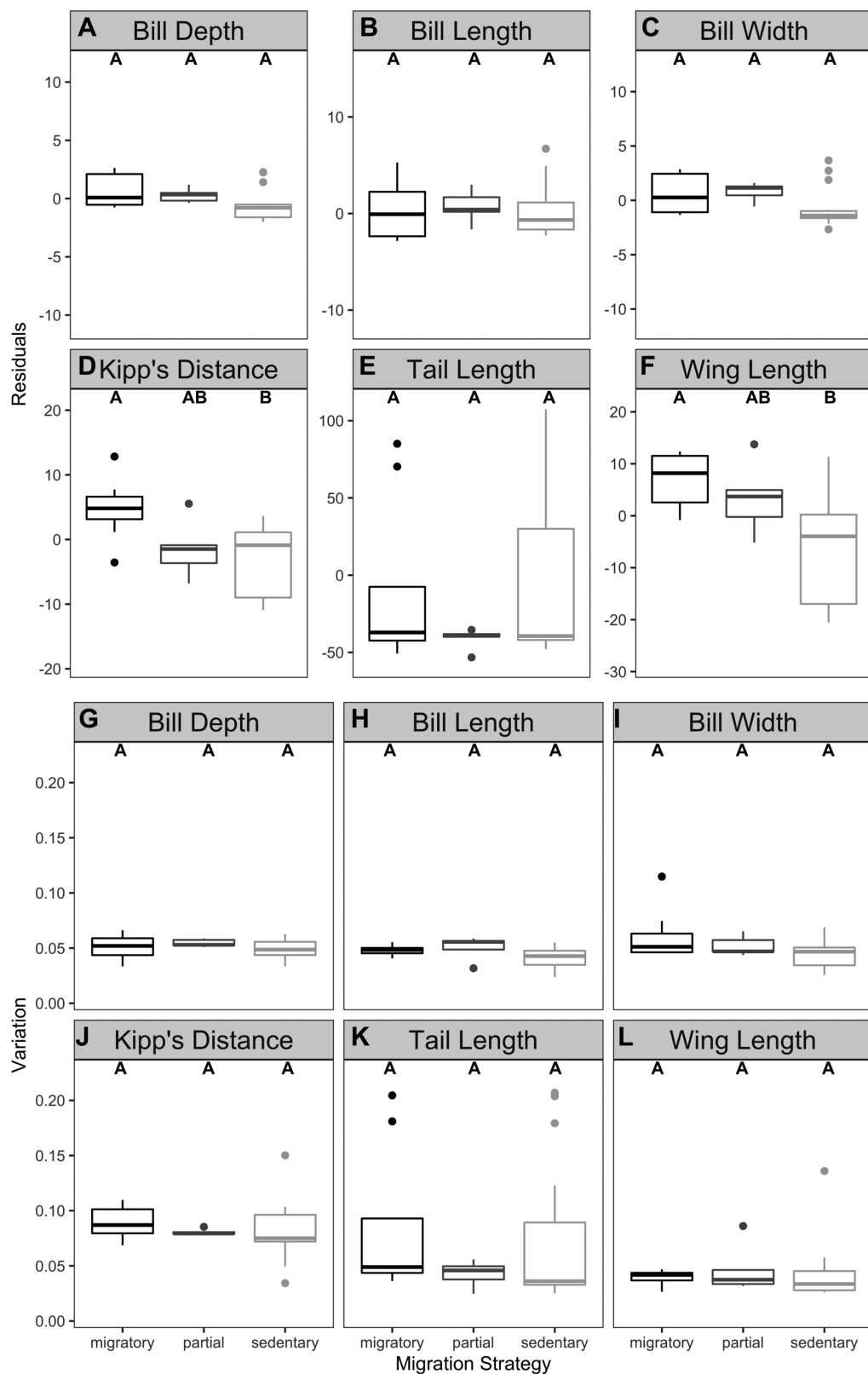


Figure 2. Phylogenetic ANOVA results comparing residuals of bill and feather morphometrics (A-F) and coefficient of variation in bill and feather morphometrics (G-L) across migratory, partially migratory and sedentary kingbird OTUs.

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)

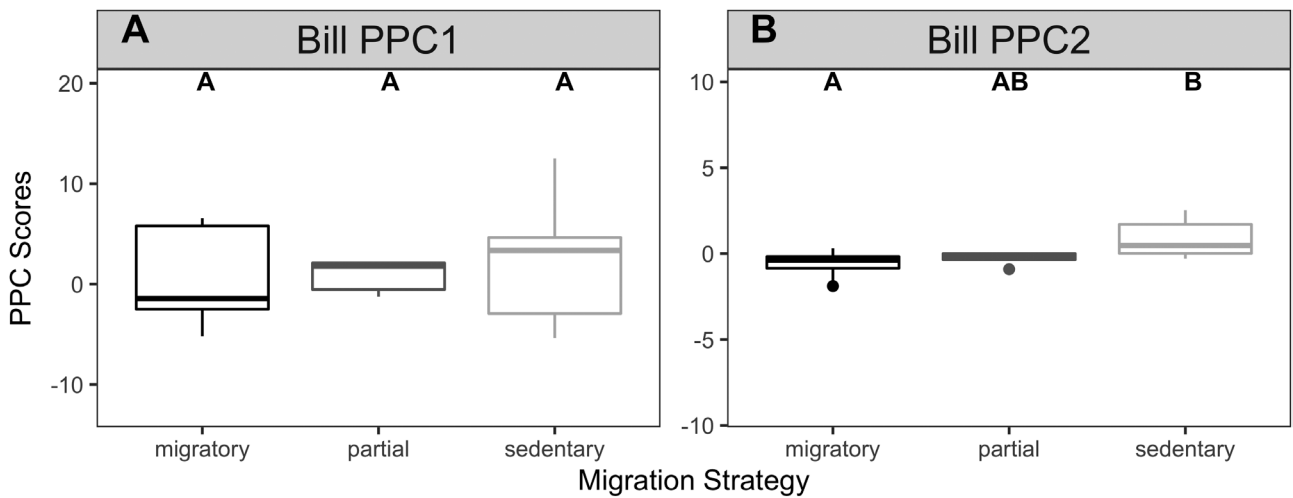


Figure 3. Phylogenetic ANOVA results comparing bill phylogenetic principal component (PPC) scores across migratory, partially migratory and sedentary kingbird OTUs. A, Bill PPC1 scores. B, Bill PPC2 scores. Letters above each bar plot show groupings resulting from post-hoc pairwise comparisons.

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.

(Figure 2. continued) 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-Delgado, 2011; Botero-Delgado & 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.

ACKNOWLEDGEMENTS

We thank José Ignacio ('Nacho') Giraldo Arango for measuring specimens, and Brenna and Michael Wells and Shelbey Hearn for their assistance measuring specimens used in this study. Ben Marks, Shannon Hackett and John Bates from the Field Museum of Natural History, Bradley Millen and Allan Baker from the Royal Ontario Museum, Gary Stiles from the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Jacob Saucier, Helen James and Gary Graves from the Smithsonian National Museum of Natural History, and Steven Cardiff and Van Remsen from the Louisiana State University Museum of Natural Science provided assistance in accessing the specimens used in this study. Thanks to Robb Brumfield and Michael Harvey for providing an early-access version of the suboscine phylogeny for our study. We also thank Calandra Stanley, Caleb McMahan, the Toronto MacPhersons and the Bogotá Acevedos for their special help aiding the lead author to visit collections. Travel to measure specimens was supported in part from a scholar award from the James S. McDonnell Foundation. Samantha Rutledge, David Vander Pluym and Subir Shakya provided helpful feedback on an earlier version of this manuscript, and we thank an anonymous reviewer and Prof. John A. Allen for their insightful peer review. We wish to acknowledge www.gbif.org for providing the ROM database (accessed September 30, 2020) and the Field Museum database (accessed October 20, 2020) online that was used to validate locality data previously recorded by hand. Amethys E'tessam, Clare Lister and Trey Hendrix also helped with georeferencing from locality data that was a part of this project.

FUNDING

AEJ is supported by Indiana University's Prepared for Environmental Change Grand Challenge Initiative and by FAPESP-São Paulo, Brazil (#2012/17225-2). Travel to measure specimens was funded in part from a scholar award from the James S. McDonnell Foundation.

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).

REFERENCES

- Albrecht GH, Gelvin BR, Hartman SE. 1993.** Ratios as a size adjustment in morphometrics. *American Journal of Physical Anthropology* **91**: 441–468.
- Alonso D, Fernández-Eslava B, Edelaar P, Arizaga J. 2020.** Morphological divergence among Spanish common crossbill populations and adaptations to different pine species. *Ibis* **162**: 1279–1291.
- Baldwin MW, Winkler H, Helm B. 2010.** Wing pointedness associated with migratory distance in common-garden and comparative studies of stonechats (*Saxicola torquata*). *Journal of Evolutionary Biology* **23**: 1050–1063.
- Bell C. 2000.** Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology* **31**: 258–265.
- Bell C. 2011.** Resource buffering and the evolution of bird migration. *Evolutionary Ecology* **25**: 91–106.
- Berner D. 2011.** Size correction in biology: how reliable are approaches based on (common) principal component analysis? *Oecologia* **166**: 961–971.
- Berthold P. 1999.** A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich* **70**: 1–11.
- Böhning-Gaese K, Oberrath R. 1999.** Phylogenetic effects on morphological, life-history, behavioural and ecological traits of birds. *Evolutionary Ecology Research* **1**: 347–364.
- Bolnick DI, Svanbäck R, Araújo MS, Persson L. 2007.** Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences* **104**: 10075–10079.
- Botero-Delgado E. 2011.** Cuantificando el comportamiento: estrategias de búsqueda y ecología de forrajeo de 12 especies sintópicas de Atrapamoscas (Tyrannidae) en la Sierra Nevada de Santa Marta, Colombia. *Revista Brasileira de Ornitologia* **19**: 343–357.
- Botero-Delgado E, Bayly NJ. 2012.** Does morphology predict behavior? Correspondence between behavioral and morphometric data in a tyrant-flycatcher (Tyrannidae) assemblage in the Santa Marta Mountains, Colombia. *Journal of Field Ornithology* **83**: 329–342.
- Boyle WA. 2008.** Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. *Journal of Animal Ecology* **77**: 1122–1128.
- Boyle WA, Conway CJ. 2007.** Why migrate? A test of the evolutionary precursor hypothesis. *The American Naturalist* **169**: 344–359.
- Carvalho Provinciato IC, Araújo MS, Jahn AE. 2018.** Drivers of wing shape in a widespread Neotropical bird: a dual role of sex-specific and migration-related functions. *Evolutionary Ecology* **32**: 379–393.
- Chapman BB, Brönmark C, Nilsson JÅ, Hansson LA. 2011.** The ecology and evolution of partial migration. *Oikos* **120**: 1764–1775.
- Chapman BB, Hulthén K, Brönmark C, Nilsson PA, Skov C, Hansson LA, Brodersen J. 2015.** Shape up or ship out: migratory behaviour predicts morphology across spatial scale in a freshwater fish. *Journal of Animal Ecology* **84**: 1187–1193.
- Chesser RT, Levey DJ. 1998.** Austral migrants and the evolution of migration in New World birds: diet, habitat, and migration revisited. *The American Naturalist* **152**: 311–319.
- Cintra R. 1997.** Spatial distribution and foraging tactics of tyrant flycatchers in two habitats in the Brazilian Amazon. *Studies on Neotropical Fauna and Environment* **32**: 17–27.
- Clegg SM, Owens PF. 2002.** The ‘island rule’ in birds: medium body size and its ecological explanation. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **269**: 1359–1365.
- Clements JF, Schulenberg TS, Iliff MJ, Billerman SM, Fredericks TA, Sullivan BL, Wood CL. 2019.** The eBird/Clements checklist of birds of the world: v2019. Available at: <https://www.birds.cornell.edu/clementschecklist/download/>.
- Cox GW. 1968.** The role of competition in the evolution of migration. *Evolution* **22**: 180–192.
- Cox GW. 1985.** The evolution of avian migration systems between temperate and tropical regions of the New World. *The American Naturalist* **126**: 451–474.
- Crossin GT, Hinch SG, Farrell AP, Higgs DA, Lotto AG, Oakes JD, Healey MC. 2004.** Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *Journal of Fish Biology* **65**: 788–810.
- Curran-Everett D. 2000.** Multiple comparisons: philosophies and illustrations. *American Journal of Physiology - Regulatory Integrative and Comparative Physiology* **279**: R1–R8.
- Danner RM, Greenberg R. 2015.** A critical season approach to Allen’s rule: bill size declines with winter temperature in a cold temperate environment. *Journal of Biogeography* **42**: 114–120.
- Danner RM, Greenberg RS, Danner JE, Kirkpatrick LT, Walters JR. 2013.** Experimental support for food limitation of a short-distance migratory bird wintering in the temperate zone. *Ecology* **94**: 2803–2816.
- Danner RM, Gulson-Castillo ER, James HF, Dzielski SA, Frank DC III, Sibbald ET, Winkler DW. 2017.** Habitat-specific divergence of air conditioning structures in bird bills. *The Auk* **134**: 65–75.
- Emlen JT. 1977.** Land bird communities of Grand Bahama Island: the structure and dynamics of an avifauna. *Ornithological Monographs* **24**: iii-129.
- Felice RN, Tobias JA, Pigot AL, Goswami A. 2019.** Dietary niche and the evolution of cranial morphology in birds. *Proceedings of the Royal Society B: Biological Sciences* **286**: 20182677.

- Fernández G, Lank DB. 2007.** Variation in the wing morphology of western sandpipers (*Calidris mauri*) in relation to sex, age class, and annual cycle. *The Auk* **124**: 1037–1046.
- Fiedler W. 2005.** Ecomorphology of the external flight apparatus of blackcaps (*Sylvia atricapilla*) with different migration behavior. *Annals of the New York Academy of Sciences* **1046**: 253–263.
- FitzJohn RG. 2012.** Diversitree: comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution* **3**: 1084–1092.
- Fitzpatrick JW. 1981.** Search strategies of tyrant flycatchers. *Animal Behaviour* **29**: 810–821.
- Fitzpatrick JW. 1985.** Form, foraging behavior, and adaptive radiation in the Tyrannidae. *Ornithological Monographs* **36**: 447–470.
- Fitzpatrick JW, Bates JM, Bostwick KS, Caballero IC, Clock BM, Farnsworth A, Hosner PA, Joseph L, Langham GM, Lebbin DJ. 2004.** Family Tyrannidae (tyrant-flycatchers). *Handbook of the Birds of the World*. In: del Hoyo J, Elliot A, Christie DA, Lynx E, Barcelona, Cotingas to Pipits and Wagtails. **9**: 170–462.
- Fitzpatrick W, Schauensee D. 1980.** Foraging behavior of Tyrant flycatchers. *The Condor* **82**: 43–57.
- Förschler MI, Bairlein F. 2011.** Morphological shifts of the external flight apparatus across the range of a passerine (northern wheatear) with diverging migratory behaviour. *PLoS One* **6**: e18732.
- Freed LA, Medeiros MCI, Cann RL. 2016.** Multiple reversals of bill length over 1.7 million years in a Hawaiian bird lineage. *The American Naturalist* **187**: 363–371.
- Friedman NR, Harmáčková L, Economo EP, Remeš V. 2017.** Smaller beaks for colder winters: thermoregulation drives beak size evolution in Australasian songbirds. *Evolution* **71**: 2120–2129.
- Gabriel V de A, Pizo MA. 2005.** Foraging behavior of tyrant flycatchers (Aves, Tyrannidae) in Brazil. *Revista Brasileira de Zoologia* **22**: 1072–1077.
- Garland T, Dickerman AW, Janis CM, Jones JA. 1993.** Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42**: 265–292.
- Gómez C, Tenorio EA, Montoya P, Cadena CD. 2016.** Niche-tracking migrants and niche-switching residents: evolution of climatic niches in New World warblers (Parulidae). *Proceedings of the Royal Society B: Biological Sciences* **283**: 20152458.
- Gómez-Bahamón V, Márquez R, Jahn AE, Miyaki CY, Tuero DT, Laverde-R O, Restrepo S, Cadena CD. 2020a.** Speciation associated with shifts in migratory behavior in an avian radiation. *Current Biology* **30**: 1312–1321.e6.
- Gómez-Bahamón V, Tuero DT, Castaño MI, Jahn AE, Bates JM, Clark CJ. 2020b.** Sonations in migratory and non-migratory fork-tailed flycatchers (*Tyrannus savana*). *Integrative and Comparative Biology* **60**: 1147–1159.
- Guillerme T, Healy K. 2020.** *multTree: performs MCMCglmm on multiple phylogenetic trees*. ZENODO. doi:10.5281/zenodo.12902.
- Hahn S, Korner-Nievergelt F, Emmenegger T, Amrhein V, Csörgő T, Gursoy A, Ilieva M, Kverek P, Pérez-Tris J, Pirrello S, Zehndtjiev P, Salewski V. 2016.** Longer wings for faster springs – wing length relates to spring phenology in a long-distance migrant across its range. *Ecology and Evolution* **6**: 68–77.
- Harvey M, Bravo G, Claramunt S, Cuervo A, Derryberry G, Battilana J, Seeholzer G, McKay JS, O'Meara BC, Faircloth BC, Edwards S, Pérez-Emán J, Moyle RG, Sheldon FH, Aleixo A, Smith BT, Chesser RT, Silveira LF, Cracraft J, Brumfield RT, Derryberry EP. 2020.** The evolution of a tropical biodiversity hotspot. *Science* **370**: 1343–1348.
- Herrera CM. 1978.** Ecological correlates of residence and non-residence in a Mediterranean passerine bird community. *Journal of Animal Ecology* **47**: 871–890.
- Hespenheide HA. 1975.** Selective predation by two swifts and a swallow in Central America. *Ibis* **117**: 82–99.
- Hromada M, Tryjanowski P. 2003.** Animals of different phenotype differentially utilise dietary niche - the case of the great grey shrike *Lanius excubitor*. *Ornis Fennica* **80**: 71–78.
- Jahn AE, Levey DJ, Hostetler JA, Mamani AM. 2010.** Determinants of partial bird migration in the Amazon Basin. *Journal of Animal Ecology* **79**: 983–992.
- Jahn AE, Tuero DT. 2020.** Fork-tailed flycatcher (*Tyrannus savana*). *Birds of the World*. Schulenberg TS, ed. Ithaca, NY, USA: Cornell Lab of Ornithology. Available at: <https://doi.org/10.2173/fotfly.01>.
- Johansson F, Söderquist M, Bokma F. 2009.** Insect wing shape evolution: independent effects of migratory and mate guarding flight on dragonfly wings. *Biological Journal of the Linnean Society* **97**: 362–372.
- Kipp F. 1942.** Über Flügelbau und Wanderzug der Vögel. *Biologisches Zentralblatt* **62**: 289–299.
- Kipp FA. 1958.** Zur geschichte des Vogelzuges auf der grundlage der Flügelanpassungen. *Vogelwarte* **19**: 233–242.
- Knudsen R, Siwertsson A, Adams CE, Garduño-Paz M, Newton J, Amundsen PA. 2011.** Temporal stability of niche use exposes sympatric Arctic charr to alternative selection pressures. *Evolutionary Ecology* **25**: 589–604.
- Lack D. 1971.** *Ecological isolation in birds*. Cambridge, Massachusetts: Oxford: Harvard University Press, and Blackwell.
- Leisler B. 1990.** Selection and use of habitat of wintering migrants. In: Gwinner E, ed. *Bird migration*. Berlin, Heidelberg: Springer, 156–174.
- Levey DJ, Stiles FG. 1992.** Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. *The American Naturalist* **140**: 447–476.
- Lindström Å, Piersma T. 1993.** Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* **135**: 70–78.
- Lockwood R, Swaddle JP, Rayner JMV. 1998.** Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology* **29**: 273–292.
- MacPherson MP, Jahn AE, Mason NA. 2021.** Morphology of migration: associations between wing shape, bill morphology and migration in kingbirds (*Tyrannus*). *Dryad, Dataset*. <https://doi.org/10.5061/dryad.4f4qrjcs>.
- Mallarino R, Grant PR, Grant BR, Herrel A, Kuo WP, Abzhanov A. 2011.** Two developmental modules establish

- 3D beak-shape variation in Darwin's finches. *Proceedings of the National Academy of Sciences* **108**: 4057–4062.
- Marchetti K, Price T, Richman A. 1995.** Correlates of wing morphology with foraging behaviour and migration distance in the correlates of wing morphology with foraging behaviour and migration distance in the genus *Phylloscopus*. *Journal of Avian Biology* **26**: 177–181.
- McCoy MW, Bolker BM, Osenberg CW, Miner BG, Vonesh JR. 2006.** Size correction: comparing morphological traits among populations and environments. *Oecologia* **148**: 547–554.
- Medina JJ, Maley JM, Sannapareddy S, Medina NN, Gilman CM, McCormack JE. 2020.** A rapid and cost-effective pipeline for digitization of museum specimens with 3D photogrammetry. *PLoS One* **15**: e0236417.
- Milá B, Wayne RK, Smith TB. 2008.** Ecomorphology of migratory and sedentary populations of the yellow-rumped warbler (*Dendroica coronata*). *The Condor* **110**: 335–344.
- Minias P, Meissner W, Włodarczyk R, Ożarowska A, Piasecka A, Kaczmarek K, Janiszewski T. 2015.** Wing shape and migration in shorebirds: a comparative study. *Ibis* **157**: 528–535.
- Mobley JA. 2002.** *Molecular phylogenetics and the evolution of nest building in kingbirds and their allies (Aves: Tyrannidae)*. Berkeley: University of California.
- Mobley JA, de Juana E. 2020.** Loggerhead kingbird (*Tyrannus caudifasciatus*). In: del Hoyo J, Elliott A, Sargatal J, DChristie DA, de Juana E, Eds. *Birds of the World*.
- Mönkkönen M. 1995.** Do migrant birds have more pointed wings?: a comparative study. *Evolutionary Ecology* **9**: 520–528.
- Moreau RE. 1952.** The place of Africa in the Palaearctic migration system. *Journal of Animal Ecology* **21**: 250–271.
- Morse DH. 1971.** The insectivorous bird as an adaptive strategy. *Annual Review of Ecology and Systematics* **2**: 177–200.
- Mulvihill RS, Chandler CR. 1990.** The relationship between wing shape and differential migration in the dark-eyed junco. *The Auk* **107**: 490–499.
- Murphy MT. 2007.** A cautionary tale: cryptic sexual size dimorphism in a socially monogamous passerine. *The Auk* **124**: 515–525.
- Nations JA, Heaney LR, Demos TC, Achmadi AS, Rowe KC, Esselstyn JA. 2019.** A simple skeletal measurement effectively predicts climbing behaviour in a diverse clade of small mammals. *Biological Journal of the Linnean Society* **128**: 323–336.
- Navalón G, Bright JA, Marugán-Lobón J, Rayfield EJ. 2019.** The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. *Evolution* **73**: 422–435.
- Neto JM, Gordinho L, Belda EJ, Marín M, Monrós JS, Fearon P, Crates R. 2013.** Phenotypic divergence among West European populations of reed hunting *Emberiza schoeniclus*: the effects of migratory and foraging behaviours. *PLoS One* **8**: e63248.
- Norberg UM. 1990.** *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*. Berlin: Springer.
- Norberg UM. 1995.** Wing design and migratory flight. *Israel Journal of Ecology and Evolution* **41**: 297–305.
- Orejuela JE, Raitt RJ, Álvarez H. 1980.** *Differential use by North American migrants of three types of Colombian forests*. In: Keast A, Morton ES, eds. *Migrant birds in the Neotropics: ecology, behavior, distribution and conservation*. Washington DC: Smithsonian Institution Press, 253–264.
- Pennycuik C. 2008.** The membrane wings of bats and pterosaurs. In: CJ Pennycuik, ed. *Modelling the flying bird*. London: Elsevier.
- Pérez-Tris J, Tellería JL. 2001.** Age-related variation in wing shape of migratory and sedentary blackcaps *Sylvia atricapilla*. *Journal of Avian Biology* **32**: 207–213.
- Pol MVD, Ens BJ, Oosterbeek K, Brouwer L, Verhulst S, Tinbergen JM, Rutten AL, Jong MD. 2009.** Oystercatchers' bill shapes as a proxy for diet specialization: more differentiation than meets the eye. *Ardea* **97**: 335–347.
- Pyle P, Howell SNG, Institute for Bird Populations, Point Reyes Bird Observatory. 1997.** *Identification guide to North American birds: a compendium of information on identifying, ageing, and sexing 'near-passerines' and passerines in the hand. Part I, Part I*. Bolinas: Slate Creek Press.
- R Core Team. 2020.** *R: a language and environment for statistical computing (4.0. 3)[Computer software]*. R Foundation for Statistical Computing. Available at: <https://www.R-project.org/>.
- Rappole JH. 1995.** *The ecology of migrant birds: a Neotropical perspective*. Washington, London: Smithsonian institution Press.
- Rappole JH, Ramos MA, Winker K. 1989.** Wintering wood thrush movements and mortality in Southern Veracruz. *The Auk* **106**: 402–410.
- Rayner JMV. 1988.** The evolution of vertebrate flight. *Biological Journal of the Linnean Society* **34**: 269–287.
- Reaney AM, Bouchenak-Khelladi Y, Tobias JA, Abzhanov A. 2020.** Ecological and morphological determinants of evolutionary diversification in Darwin's finches and their relatives. *Ecology and Evolution* **10**: 14020–14032.
- Revell LJ. 2009.** Size-correction and principal components for interspecific comparative studies. *Evolution* **63**: 3258–3268.
- Revell LJ. 2012.** phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.
- Rising JD, Somers KM. 1989.** The measurement of overall body size in birds. *The Auk* **106**: 666–674.
- von Rönn JAC, Shafer ABA, Wolf JBW. 2016.** Disruptive selection without genome-wide evolution across a migratory divide. *Molecular Ecology* **25**: 2529–2541.
- Senar JC, Pascual J. 1997.** Keel and tarsus length may provide a good predictor of avian body size. *Ardea* **85**: 269–274.
- Shaffer JP. 1995.** Multiple hypothesis testing. *Annual Review of Psychology* **46**: 561–584.
- Shao S, Quan Q, Cai T, Song G, Qu Y, Lei F. 2016.** Evolution of body morphology and beak shape revealed by a morphometric analysis of 14 Paridae species. *Frontiers in Zoology* **13**: 30.
- Sheard C, Neate-Clegg MHC, Alioravainen N, Jones SEI, Vincent C, MacGregor HEA, Bregman TP, Claramunt S,**

- Tobias JA. 2020.** Ecological drivers of global gradients in avian dispersal inferred from wing morphology. *Nature Communications* **11**: 2463.
- Sherry TW. 1984.** Comparative dietary ecology of sympatric, insectivorous Neotropical flycatchers (Tyrannidae). *Ecological Monographs* **54**: 313–338.
- Sherry TW. 2005.** Does winter food limit populations of migratory birds? In: Greenberg R, Marra, PP, eds. *Birds of two worlds: the ecology and evolution of migration*. Baltimore: Johns Hopkins University Press, 414–425.
- Snow DW. 1953.** Systematics and comparative ecology of the genus *Parus* in the Palaearctic region. Unpublished D. Phil. Thesis, Oxford University.
- Snow DW. 1954.** The habitats of Eurasian tits (*Parus* spp.). *Ibis* **96**: 565–585.
- Stiles FG. 1980.** Evolutionary implications of habitat relations between permanent and winter resident landbirds in Costa Rica. In: Keast A, Morton ES, eds. *Migrant birds in the Neotropics*. Washington DC: Smithsonian Institution Press, 421–435.
- Svanbäck R, Schluter D. 2012.** Niche specialization influences adaptive phenotypic plasticity in the threespine stickleback. *The American Naturalist* **180**: 50–59.
- Swanson MT, Oliveros CH, Esselstyn JA. 2019.** A phylogenomic rodent tree reveals the repeated evolution of masseter architectures. *Proceedings of the Royal Society B: Biological Sciences* **286**: 20190672.
- Tarka M, Åkesson M, Beraldi D, Hernández-Sánchez J, Hasselquist D, Bensch S, Hansson B. 2010.** A strong quantitative trait locus for wing length on chromosome 2 in a wild population of great reed warblers. *Proceedings of the Royal Society B: Biological Sciences* **277**: 2361–2369.
- Tellería JL, Carbonell R. 1999.** Morphometric variation of five Iberian blackcap *Sylvia atricapilla* populations. *Journal of Avian Biology* **30**: 63–71.
- Tellería LJ, Blázquez M, De La Hera I, Pérez-Tris J. 2013.** Migratory and resident blackcaps *Sylvia atricapilla* wintering in southern Spain show no resource partitioning. *Ibis* **155**: 750–761.
- Thiollay JM. 1988.** Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications. *Oikos* **53**: 17–30.
- Vágási CI, Pap PL, Vincze O, Osváth G, Erritzøe J, Møller AP. 2016.** Morphological adaptations to migration in birds. *Evolutionary Biology* **43**: 48–59.
- Van Valen L. 1965.** Morphological variation and width of ecological niche. *The American Naturalist* **99**: 377–390.
- Voelker G. 2001.** Morphological correlates of migratory distance and flight display in the avian genus *Anthus*. *Biological Journal of the Linnean Society* **73**: 425–435.
- Waide RB. 1980.** Resource partitioning between migrant and resident birds: the use of irregular resources. In: Keast A, Morton ES, eds. *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation*. Washington DC: Smithsonian Institution Press, 337–352.
- Wang X, Clarke JA. 2015.** The evolution of avian wing shape and previously unrecognized trends in covert feathering. *Proceedings of the Royal Society B: Biological Sciences* **282**: 20151935.
- Wasserstein RL, Schirm AL, Lazar NA. 2019.** Moving to a World Beyond $p < 0.05$. *The American Statistician* **73**: 1–19.
- Wiedenfeld DA. 1991.** Geographical morphology of male yellow warblers. *The Condor* **93**: 712–723.
- Willis EO. 1974.** Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecological Monographs* **44**: 153–169.
- Wilson EO. 1961.** The nature of the taxon cycle in the Melanesian ant fauna. *The American Naturalist* **95**: 169–193.
- Winkler H, Leisler B. 1992.** On the ecomorphology of migrants. *Ibis* **134**: 21–28.
- Winqvist T, Lemon RE. 1994.** Sexual selection and exaggerated male tail length in birds. *The American Naturalist* **143**: 95–116.
- Závorka L, Larranaga N, Lovén Wallerius M, Näslund J, Koeck B, Wengström N, Cucherousset J, Johnsson JI. 2020.** Within-stream phenotypic divergence in head shape of brown trout associated with invasive brook trout. *Biological Journal of the Linnean Society* **129**: 347–355.

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 \pm 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. caudifasciatus 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