



The evolution of sexually dimorphic tail feathers is not associated with tail skeleton dimorphism

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Sexual selection can influence the evolution of sexually dimorphic exaggerated display structures. Herein, we explore whether such costly ornamental integumentary structures evolve independently or if they are correlated with phenotypic change in the associated skeletal system. In birds, elongate tail feathers have frequently evolved in males and are beneficial as intraspecific display structures but impart a locomotor/energetic cost. Using the sexually dimorphic tail feathers of several passeriform species as a model system, we test the hypothesis that taxa with sexually dimorphic tail feathers also exhibit sexual dimorphism in the caudal skeleton that supports the muscles and integument of the tail apparatus. Caudal skeletal morphology is quantified using both geometric morphometrics and linear morphometrics across four sexually dimorphic passeriform species and four closely related monomorphic species. Sexual dimorphism is assessed using permutational MANOVA. Sexual dimorphism in caudal skeletal morphology is found only in those taxa that exhibit active functional differences in tail use between males and females. Thus, dimorphism in tail feather length is not necessarily correlated with the evolution of caudal skeletal dimorphism. Sexual selection is sufficient to generate phenotypic divergence in integumentary display structures between the sexes, but these changes are not reflected in the underlying caudal skeleton. This suggests that caudal feathers and bones evolve semi-independently from one another and evolve at different rates in response to different types of selective pressures.

Dimorphism in plumage in birds represents one of the most striking examples of sexual dimorphism, and indeed one that inspired Darwin's work on the topic (Darwin 1859, 1871). The males of numerous lineages exhibit elaborate tail feathers (rectrices) that are used as display structures, including species of quail (Brown and Gutierrez 1980), swallow (Park et al. 2001), duck, grouse, pheasant, parakeet, hummingbird, nightjar, kingfisher, and numerous passeriforms (Cuervo and Moller 2001). The evolution of ornamental rectrices is of particular interest because these tail feathers serve a dual role as both a display structure and as a critical component of the aerial locomotor apparatus. Indeed, evolution in tail morphology has been a major component of the diversification of birds. The tail represents a key component of the aerial locomotor apparatus, supplementing the role of the wings in flight by producing lift, reducing drag, and contributing to agility and maneuverability (Gatesy and Dial 1996, Thomas 1996). As an aerodynamic structure, the tail consists of a fan of tail feathers (rectrices) that can be spread or folded. Much like the wings or tail of an airplane, the shape of the tail fan in birds determines its aerodynamic properties, and thus a bird's aerial capabilities (Thomas 1993). As such, different flight behaviors are associated with characteristic tail fan shapes that provide advantageous aerodynamic properties for that behavior. For

example, birds that catch their prey on the wing typically exhibit a forked tail, a shape that is hypothesized to maximize agility (Thomas and Balmford 1995).

Aerodynamic theory predicts that natural selection should act to optimize the shape of the tail fan to meet aerodynamic demands (Norberg 1995, Thomas and Balmford 1995). Extremely long tails deviate from the aerodynamically 'optimum' shape, imposing a cost. This cost is manifested in several ways. Long tails increase drag and therefore result in a decreased flight performance, both in flight speed and energetic cost of flight (Evans and Thomas 1992, Balmford et al. 1993, Norberg 1995). In turn, maneuverability, foraging rates, and predator escape capability can all be affected negatively by the presence of a long tail (Evans 1998, Park et al. 2000, Rowe et al. 2001, Clark and Dudley 2009).

In cases where female mate choice has resulted in the evolution of elongate tail feathers in males, sexual selection may lead to the evolution of further morphological differences as males evolve ways to mitigate the performance costs of elongate tails. As one example, in species with sexually dimorphic tails, males also often exhibit longer wings as well (Evans and Thomas 1992, Andersson and Andersson 1994, Balmford et al. 1994). Longer wings produce more lift, compensating for the increased drag produced by an elongate tail (Evans

and Thomas 1992). Given the costs of locomotion associated with long tail feathers, it is reasonable to predict that other morphological features may evolve in junction with tail feather length (Balmford et al. 1994). This study tests whether the evolution of sexually dimorphic tail feathers is correlated with dimorphism in the underlying caudal skeleton that supports the tail fan.

Several lines of evidence suggest that caudal feather and caudal skeletal evolution may be linked. First, caudal feathers and bones are topologically and functionally closely associated. The fan of tail feathers is anchored to the pygostyle through bilateral fibroadipose structures known as rectricial bulbs (Gatesy and Dial 1996). Movements of the tail used in locomotion and display (e.g. fanning, elevation, depression, lateral deviation, rotation) are achieved through the action of muscles that attach to the pygostyle and free caudal vertebrae (Baumel 1988, Gatesy and Dial 1996). Second, in monomorphic species, pygostyle shape is correlated with tail fan shape (Felice 2014). Each tail fan shape (e.g. forked, graduated, square) is associated with characteristic pygostyle morphology. This relationship is strong enough that tail fan shape can be confidently predicted on the basis of pygostyle shape (Felice 2014). Such a correlation between skeletal and integumentary morphology suggests that the evolution in tail fan shape and caudal skeletal morphology are linked. Finally, in clades with highly specialized tails, rectricial and caudal skeletal morphology exhibit correlated trait evolution. Highly arboreal birds such as woodpeckers (Picinae) and the brown creeper *Certhia americana* utilize the tail as a prop during vertical climbing. These taxa are characterized by stiffened medial rectrices that are specialized for this function (Richardson 1942, Manegold and Töpfer 2012). The acquisition of reinforced tail feathers was accompanied by derived pygostyle morphology, including a larger area of surface attachment for the rectricial bulbs and for depressor muscles of the tail (Burt 1930, Richardson 1942, Clark and Dudley 2009, Manegold and Töpfer 2012). Coordinated modifications of both the rectrices and pygostyle morphology in this clade have been interpreted as evidence of correlated evolution of the feathers and bones of the tail (Manegold and Töpfer 2012).

If this general pattern is also present in taxa with sexually dimorphic tail feathers, then it is reasonable to predict that caudal skeletal morphology may also exhibit a sexually dimorphic signal. Herein, we test whether males and females of dimorphic species exhibit distinct caudal skeletal morphology. Several aspects of caudal vertebral morphology will be evaluated. First, the shape of the free caudal vertebrae is expected to change in conjunction with tail fan shape, facilitating movements of heavy, drag-inducing display feathers. Second, because pygostyle shape is correlated with differences in tail fan shape among monomorphic taxa, males and females of dimorphic taxa may also exhibit dimorphism in pygostyle shape. Finally, the evolution of larger tail feathers in males may require larger pygostyle surface area for the attachment of the medial rectrices, as observed in trunk foraging birds. The degree of sexual dimorphism in each of these skeletal features was assessed in a variety of passeriform taxa to investigate whether skeletal morphology evolves in a coordinated manner with sexually selected rectrices.

Material and methods

Caudal skeletal and integumentary morphology was quantified in four species that exhibit sexually dimorphic tail feathers (Fig. 1; Bancroft 1984, Cuervo and Moller 2000, 2001, Regosin and Pruett-Jones 2001). These taxa include the boat-tailed grackle *Quiscalus major*, pin-tailed whydah *Vidua macroura*, scissor-tailed flycatcher, *Tyrannus forficatus*, and white-rumped shama *Copsychus malabaricus*. As a basis for comparison, caudal morphology was also quantified in a monomorphic congener for each of the four dimorphic species. These are the common grackle *Q. quiscula*, village indigobird *V. chalybeata*, gray kingbird *T. dominicensis*, and oriental magpie-robin *C. saularis*, respectively. The latter four taxa are predicted to be sexually monomorphic in caudal skeletal morphology. A total of 329 skeletal specimens (191 male, 139 female) were measured representing these eight taxa. These data were collected from specimens housed in the following museum collections: AMNH, American Museum of Natural History, New York, NY; CM, Carnegie Museum of Natural History, Pittsburgh, PA; FMNH, Field Museum of Natural History, Chicago, IL; KU, Univ. of Kansas Museum of Natural History, Lawrence, KS; LACM, Natural History Museum of Los Angeles County, Los Angeles, CA; LSUMZ, LSU Museum of Natural Science, Baton Rouge, LA; NMNH, National Museum of Natural History, Washington, DC; OUVC, Ohio Univ. Vertebrate Collection, Athens, OH; UMMZ, Univ. of Michigan Museum of Zoology, Ann Arbor, MI; YPM, Yale Peabody Museum, New Haven, CT.

These focal taxa represent a suitable sample for studying patterns of caudal dimorphism as they exhibit a wide range of rectricial phenotypes, breeding behaviors, and body sizes. *Vidua macroura* are polygynous with highly territorial males in which the medial two rectrices are extremely elongate (Shaw 1984). The contrast, *V. chalybeata* exhibits sexually monomorphic tail feathers and utilizes a 'dispersed lek' courtship behavior (Shaw 1984). Both *V. macroura* and *V. chalybeata* are brood parasites that utilize the nests of waxbills (Savalli 1995). Patterns of sexual dimorphism are particularly well studied in the monogamous *Tyrannus forficatus*. Males of this species have elongate outermost rectrices and the length of the tail feathers in both sexes is correlated with fitness traits such as increased clutch size (Regosin and Pruett-Jones 2001). Similar to *T. forficatus*, the dimorphic *Copsychus malabaricus* and monomorphic *C. saularis* are considered monogamous (Aguon and Conant 1994, Siddique 2014). Unlike *T. forficatus*, the sexually dimorphic ornament found in *C. malabaricus* consists of an elongate graduated (diamond shaped) tail fan, with medial rectrices longer than lateral rectrices (Balmford et al. 1994). Finally, species within *Quiscalus* are polygynous to variable degrees. The level of polygyny is positively correlated with the magnitude of sexual dimorphism, with highly polygynous species (e.g. *Q. major*) exhibiting dimorphism in both body size and tail length, and less polygynous species (e.g. *Q. quiscula*) exhibiting low-to-absent dimorphism (Bjorklund 1991). Moreover, these taxa exhibit variation in foraging behavior. *Quiscalus* spp. are omnivorous ground foragers. *Copsychus malabaricus* is similarly a ground forager, but specializes on insects (Fan et al. 2015). Its congener,

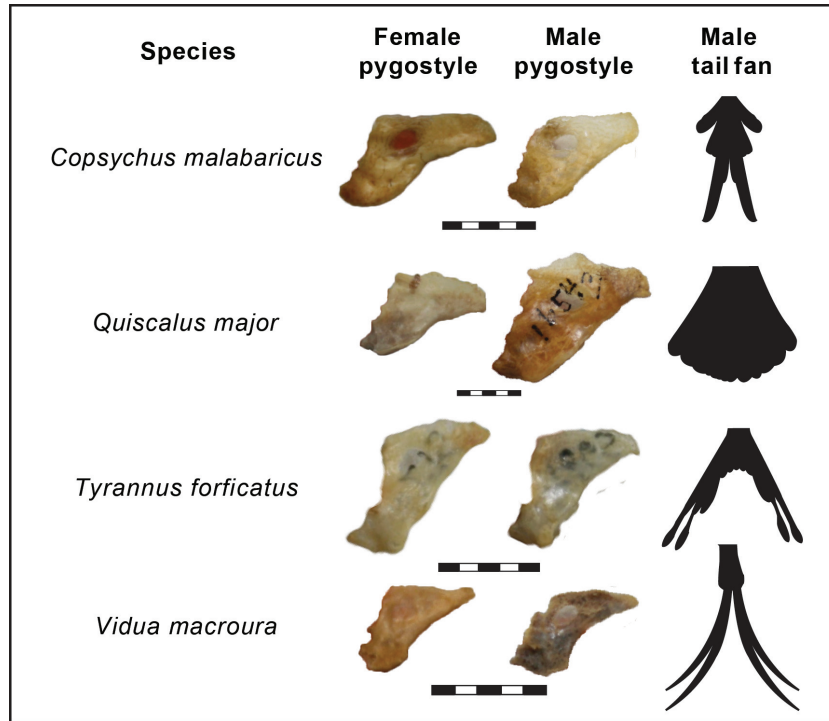


Figure 1. Caudal morphological variation. Specimens: *Copsychus malabaricus*: YPM 104000, female; AMNH 255552, male. *Tyrannus forficatus*: KU 15275, female; KU 19665, male. *Quiscalus major*: KU 39022, female; AMNH 16543, male. *Vidua macrocra*: FMNH 313258, female; UMMZ 136012, male. Scale bars = 5 mm. Far right column illustrates generalized male ornament of each species.

C. saularis is also insectivorous, foraging primarily in the lower branches of trees (Zann and Darjono 1992). *Vidua* spp. are granivorous (Savalli 1995). Both *Tyrannus forficatus* and *T. dominicensis* are insectivorous air-salliers (i.e. launching from a perch to pursue aerial prey), but *T. dominicensis* occasionally feeds on fruits (De Graaf et al. 1985). Given that the focal taxa are variable in ecology, rectricial phenotype and in the mating system under which the ornament evolved, if sexually dimorphic tail feathers are associated with sexually dimorphic skeletal morphology then this pattern should be detected across the entire sample.

The morphology of the free caudal vertebrae was quantified using methods described previously (Felice and O'Connor 2014). Briefly, digital calipers (Mitutoyo Model 573-731, Plymouth, MI) were used to collect the following metrics: centrum length (craniocaudal), centrum width, centrum height, spinous process length, spinous process width, spinous process height, transverse process length, transverse process width, ventral process length, ventral process width, ventral process height (Fig. 2). Because the number of free caudal vertebrae varies among individuals and taxa, a basis for making homologous comparisons of morphology among

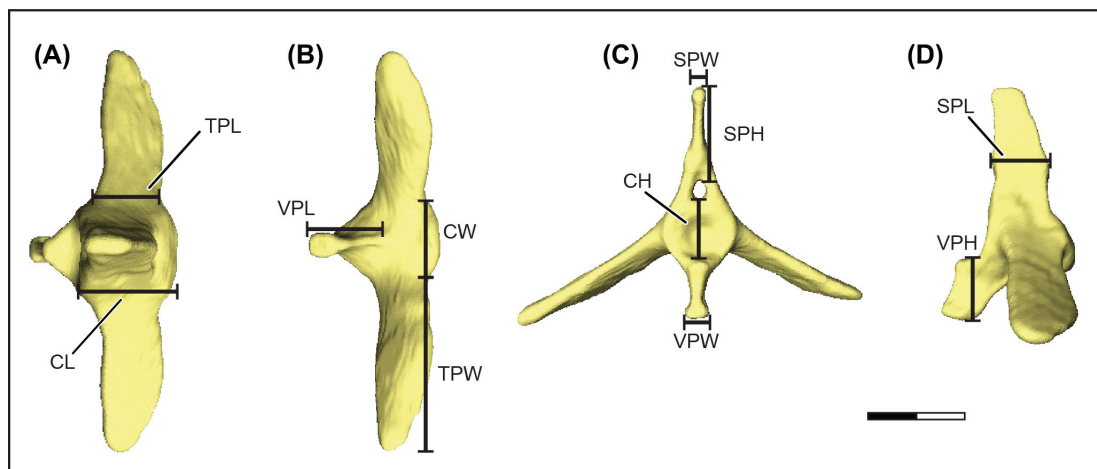


Figure 2. Free caudal vertebra: skeletal metrics. Free caudal vertebra in dorsal (A), ventral (B), anterior (C), and left lateral (D) views. Skeletal metrics collected: centrum length (CL), centrum width (CW), centrum height (CH), transverse process length (TPL), transverse process width (TPW), spinous process length (SPL), spinous process width (SPW), spinous process height (SPH), ventral process length (VPL), ventral process width (VPW), ventral process height (VPH).

individuals is required. As such, metrics were assessed for both the first (postsynsacral) and last (propygostylar) free caudal vertebrae, as well as the vertebra halfway along the free caudal series. In individuals with an even number of free caudal vertebrae, the morphology of the middle two vertebrae was quantified and the average of each measurement was used. Additionally, a body size proxy was calculated for each skeletal specimen. The body size proxy used herein consists of the geometric mean of several skeletal dimensions: femur length, sternal length, sternal width, sternal keel height, and synsacral length (Mosimann and James 1979, Simons 2010, Felice and O'Connor 2014). To mitigate the effects of body size on free caudal vertebral dimensions, the logarithm of each vertebral metric was divided by the logarithm of the body size proxy for that individual (Jungers et al. 1995). The resulting values were used as the free caudal vertebral dataset for the subsequent analyses. The complete dataset of all free vertebral measurements and body size proxy data is available as online supporting information.

Some skeletal specimens had incomplete caudal series. In these cases, pygostyle shape (see below) was quantified but not free caudal vertebral morphology. In most taxa, this decreased the sample size for free caudal vertebral morphology by 6.5–19%. However, for *V. chalybeata* and *V. macroura*, incomplete specimens were more common (20–62% incomplete), decreasing the sample size to a level whereby it was not feasible to incorporate either taxon into MANOVA approaches. Thus, this analysis was omitted for both species of *Vidua*.

Pygostyle shape was quantified using elliptical Fourier analysis (EFA), a geometric morphometric technique that is suitable for data with few clearly defined homologous landmarks (Rohlf and Archie 1984, Crampton 1995). With EFA, the outline of a shape is subjected to a Fourier decomposition, which summarizes the shape as a series of sine and cosine equations, termed harmonics. The coefficients of these harmonics describe a portion of the detail of the original shape. The harmonics are normalized to remove the effects of size, position, and rotation (Crampton 1995, Claude 2008). Harmonic coefficients can then be used as multidimensional data in statistical analyses, analogous to the Procrustes-aligned coordinates used in landmark based geometric morphometrics (Bonhomme et al. 2013).

Each pygostyle specimen was photographed in left lateral perspective in front of white graph paper. Specimens were secured with clay such that the lamina pygostyli was parallel with the camera lens. Using Adobe Photoshop, A) a lens correction filter was applied to mitigate the effects of geometric distortion introduced by the camera and B) background of each photo was then removed, leaving only the specimen and a 5 cm² scale bar. The outline of each specimen was automatically digitized using the ChainCoder function of the SHAPE software package (Iwata and Ukai 2002). The same software package was then used to apply Fourier decomposition and normalization. The Fourier power equation was used to determine that 95% of the total power to reconstruct the outline shapes in the sample is described by the first five harmonics (Crampton 1995). Thus, five harmonics were retained for all subsequent analyses of pygostyle shape. Finally, in order to evaluate differences in pygostyle size between sexes, the lateral surface area of

each pygostyle was measured using ImageJ (Abràmoff et al. 2004). Pygostyle size then was corrected for body size using the same method used for free caudal vertebral metrics.

The presence of sexual dimorphism in caudal skeletal morphology was evaluated using two different analytical approaches. First, for the free caudal vertebral morphology and pygostyle shape data sets, a permutational MANOVA (multivariate analysis of variance) was used (Anderson 2006). This analytical approach was chosen to accommodate significance testing utilizing the geometric morphometric (GMM) data describing pygostyle shape, which contains a high number of trait dimensions (variables) relative to the number of observations. In such cases, it is preferable to use distance-based (Q-mode) statistics such as permutational MANOVA rather than traditional parametric (R-mode) tests of significance, such as Wilk's lambda and Pillai–Bartlett trace (Adams 2014). Permutational MANOVAs were carried out using the vegan package in R (Oksanen et al. 2013). Because some of the Fourier coefficients are negative values, Kulczynski distance was selected as the most suitable distance metric (Legendre and Legendre 2012), and significance was tested using 1000 permutations. This method was also used to test the significance of the interaction between pygostyle shape and body size (i.e. static allometry). Second, a one-tailed t-test was used to test whether males of species with dimorphic tail feathers exhibit a larger pygostyle than females.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.1q2s5>> (Felice and O'Connor 2015).

Results

Sexual dimorphism was assessed for three aspects of the caudal vertebral morphology in each of the eight taxa examined: free caudal vertebral morphology, pygostyle shape, and pygostyle size. An examination of free caudal vertebrae reveals no significant difference in morphology between males and females in either the taxa with monomorphic rectrices or those with dimorphic rectrices (Table 1), with the exception of *Quiscalus major*. Likewise, permutational MANOVA reveals that pygostyle shape is not significantly different between males and females in any of the eight taxa (Table 2). However, a difference in pygostyle size between the sexes was detected in *Quiscalus quiscula*, *Q. major*, and *Vidua macroura* (Table 3). In each case, males exhibit a larger pygostyle than females. All other taxa were found

Table 1. Results of permutational MANOVA, free caudal vertebral morphology sexual dimorphism. Shaded rows exhibit sexually dimorphic tail feathers. Note that negative sum of squares and F numbers are allowable in pt-MANOVA when using non-Euclidean distance metrics (Gower 1985, Chapman and Underwood 1999).

Species	Sum of squares	F number	R ²	p-value
<i>Copsychus malabaricus</i>	−40.05	−6.91	−0.26	0.99
<i>Copsychus saularis</i>	1.18	4.09	0.20	0.12
<i>Quiscalus major</i>	0.13	6.18	0.09	<0.001
<i>Quiscalus quiscula</i>	0.13	0.92	0.02	0.61
<i>Tyrannus dominicensis</i>	0.12	1.57	0.04	0.16
<i>Tyrannus forficatus</i>	0.06	0.73	0.02	0.69

Table 2. Results of permutational MANOVA, pygostyle shape sexual dimorphism. Shaded rows exhibit sexually dimorphic tail feathers.

Species	Sum of squares	F number	R ²	p-value	Number of males	Number of females
<i>Copsychus malabaricus</i>	0.03	0.59	0.02	0.74	28	18
<i>Copsychus saularis</i>	0.037	0.51	0.03	0.78	13	7
<i>Quiscalus major</i>	0.08	1.55	0.02	0.16	38	33
<i>Quiscalus quiscula</i>	0.05	0.85	0.01	0.51	47	19
<i>Tyrannus dominicensis</i>	0.04	1.06	0.02	0.37	20	28
<i>Tyrannus forficatus</i>	0.03	0.53	0.01	0.81	24	15
<i>Vidua chalybeata</i>	0.05	0.75	0.05	0.62	11	4
<i>Vidua macroura</i>	0.14	1.83	0.08	0.12	10	14

to be monomorphic for this trait. Finally, pygostyle shape and body size exhibit a significant interaction in *Tyrannus dominicensis* and *T. forficatus* only (Table 4). For all other taxa, allometry does not influence pygostyle shape.

Discussion

An assessment of skeletal shape and size variation in a sample of sexually dimorphic species and closely related sexually monomorphic taxa within Passeri and Tyranni reveals little evidence for correlated variation in bony morphology and feather morphology. No single pattern explaining skeletal morphology was detected across all four genera examined here. First, no differences were detected between males and females in pygostyle shape. Similarly, each comparison reveals that free caudal vertebral morphology is also monomorphic between sexes, with the exception of *Quiscalus major*. Five of the eight taxa are monomorphic in pygostyle size. The three taxa with sex-specific differences in pygostyle size are *Quiscalus quiscula*, *Q. major* and *Vidua macroura*. These findings are interesting in light of recent evidence that pygostyle shape and tail fan shape are correlated across a wide range of Aequornithes and Charadriiformes (Felice 2014). Comparing patterns of caudal evolution and use among these clades suggests that functional variation, rather than skeleton-integumentary interactions, is the primary cause of caudal skeletal evolution.

Clades that support the hypothesis of pygostyle-tail fan covariation are also highly variable in locomotor behavior and ecology (Felice 2014, Felice and O'Connor 2014). Specifically, within Aequornithes and Charadriiformes, species that exhibit major differences in foraging behavior exhibit significantly different pygostyle morphology, supporting the hypothesis that locomotor function of the tail is a major force driving morphological evolution in the caudal skeleton

(Felice and O'Connor 2014). Although the passeriform taxa in this study are also variable in ecology, foraging style, and reproductive behavior, males and females within each species are not expected to differ drastically in these traits, even in cases where parental care differs between the sexes (De Graaf et al. 1985, Zann and Darjono 1992, Savalli 1995, Fan et al. 2015). One exception is *Vidua*, the lone genus in this analysis that supports the hypothesis that males and females with different tail fan shapes also exhibit different caudal skeletal morphologies (Table 3). In *Vidua macroura* there is a critical difference in tail function between males and females: males actively display to potential mates by hovering and performing rapid upward flicking of the elongate tail (Shaw 1984). Its monomorphic congener, *V. chalybeata*, also hovers during courtship displays, but does not utilize tail flicking (Payne 1973). This difference in tail function between the two species could explain why this is the only one of the examined pairs that exhibits the predicted pattern of skeletal dimorphism. In this case, it seems that in addition to tail ornament size, tail function and behavior is shaped by sexual selection in *V. macroura*. Together with previous evidence between pygostyle morphology and tail function (Richardson 1972, Manegold and Töpfer 2012, Felice and O'Connor 2014), these findings suggest that evolution of caudal skeletal diversity is shaped more by functional variation than by any strict association between the caudal skeleton and the integument.

Quiscalus quiscula and *Q. major* were also found to have sex differences in pygostyle size (but not shape). In *Quiscalus*, males have larger pygostyles in both the species with monomorphic rectrices (*Q. quiscula*) and the species with dimorphic rectrices (*Q. major*). This is contrary to the prediction that sexual dimorphism in the caudal skeleton would reflect dimorphism in the rectrices. *Quiscalus* is alone among the genera examined here in that sexual dimorphism is expressed as a size difference in the entire tail fan, compared to the

Table 3. Results of t-test, pygostyle size dimorphism. Shaded rows exhibit sexually dimorphic tail feathers.

Species	T-statistic	Degrees of freedom	p-value
<i>Copsychus malabaricus</i>	0.82	26.36	0.21
<i>Copsychus saularis</i>	0.61	17.93	0.27
<i>Quiscalus major</i>	4.47	59.78	<0.001
<i>Quiscalus quiscula</i>	3.44	33.39	<0.001
<i>Tyrannus dominicensis</i>	0.42	43.69	0.34
<i>Tyrannus forficatus</i>	-0.43	24.90	0.66
<i>Vidua chalybeata</i>	1.01	4.79	0.16
<i>Vidua macroura</i>	2.78	21.11	<0.01

Table 4. Results of multivariate regression of pygostyle shape on body size. Shaded rows exhibit sexually dimorphic tail feathers.

Species	Sum of squares	F number	R ²	p-value
<i>Copsychus malabaricus</i>	0.05	0.99	0.03	0.42
<i>Copsychus saularis</i>	0.05	0.66	0.04	0.70
<i>Quiscalus major</i>	0.10	1.99	0.02	0.06
<i>Quiscalus quiscula</i>	0.09	1.5	0.02	0.17
<i>Tyrannus dominicensis</i>	0.15	3.99	0.08	<0.01
<i>Tyrannus forficatus</i>	0.14	2.29	0.06	0.04
<i>Vidua chalybeata</i>	0.02	0.30	0.02	0.94
<i>Vidua macroura</i>	0.15	1.87	0.08	0.13

other taxa in which ornaments are only one or two pairs of rectrices. For this reason, it is possible that among the species examined here that only *Quiscalus* exhibit a significant difference in tail mass between males and females (although rectricial mass was not quantified here). A large difference in rectricial mass could necessitate a larger pygostyle surface area to allow for a larger bulbi rectricium and thus deeper 'rooting' of the rectricial calimi. Such a function for an increase in lamina pygostyli size has been previously suggested (Manegold and Töpfer 2012). Perhaps more interesting is that both species of *Quiscalus* exhibit dimorphism in pygostyle size, although this pattern was only predicted to be present in *Q. major*. This pattern may be attributed to the degree of monomorphism present in *Q. quiscula*. Although *Q. quiscula* was considered monomorphic for the purposes of this study, it may show some dimorphic features. Dimorphism in body size and tail length is present to variable degrees throughout *Quiscalus*, with *Q. major* being among the most dimorphic species and *Q. quiscula* among the least (Bjorklund 1991). Pygostyle dimorphism may reflect an overall pattern of dimorphism occurring throughout this genus (Bjorklund 1991). *Quiscalus major* (but not *Q. quiscula*) is also the only species with a significant difference in free caudal vertebral morphology between males and females (Table 3). However, the goodness-of-fit is very low ($R^2 = 0.09$), which indicates that whereas the relationship between sex and free caudal vertebral morphology is statistically significant in this taxon, sex differences explain very little of the total variation in free caudal vertebrae.

It is significant to note that pygostyle morphology was quantified in only two dimensions for the purposes of this study. Thus, phenotypic variation in the mediolateral dimension of pygostyle or the morphology of the propygoistylar joint were not assessed. Recent advances in 3D surface based morphometric techniques (Boyer et al. 2015) provide an opportunity to evaluate such components of skeletal morphology in the future. In addition, a key future effort will be to investigate the functional morphology of tail display behaviors in order to better understand how biomechanical and neuromuscular mechanisms shape the tail skeleton, complementing previous research emphasizing that caudal skeletal morphology is shaped primarily by tail function (Richardson 1972, Manegold and Töpfer 2012, Felice and O'Connor 2014).

Ultimately, no overarching pattern of dimorphism in caudal skeletal morphology was observed in passeriform taxa with sexually dimorphic tail feathers, refuting the hypothesis that the evolution of costly tail feathers necessitates correlated changes in the tail skeleton. None of the examined taxa exhibited significant sex differences in free caudal vertebral morphology or pygostyle shape. Only a minority of the taxa examined exhibit pygostyle size dimorphism, most notably *V. macroura*. Pygostyle shape is influenced by body size in just one genus, *Tyrannus*. Together, these findings illustrate that the factors that influence morphological evolution of the caudal skeleton in passeriform birds are highly complex and variable among even closely related taxa. Moreover, this highlights that disparity in ecology, foraging behavior, and reproductive biology (as is present in this sample) can have profound effects on patterns of phenotypic evolution and trait interactions.

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