

RESEARCH ARTICLE

Allometry, sexual selection and evolutionary lines of least resistance shaped the evolution of exaggerated sexual traits within the genus *Tyrannus*

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Abstract

Variational properties hold a fundamental role in shaping biological evolution, exerting control over the magnitude and direction of evolutionary change elicited by micro-evolutionary processes that sort variation, such as selection or drift. We studied the genus *Tyrannus* as a model for examining the conditions and drivers that facilitate the repeated evolution of exaggerated, secondary sexual traits in the face of significant functional limitations. In particular, we explore the role of allometry, sexual selection and their interaction, on the diversification of tail morphology in the genus, assessing whether and how they promoted or constrained phenotypic evolution. Non-deep-forked species tend to show reduced sexual dimorphism and moderate allometric variation in tail shape. The exaggerated and functionally constrained long feathers of deep-forked species, *T. savana* and *T. forficatus*, which show both marked sexual dimorphism and allometric tail shape variation, independently diverged from the rest of the genus following the same direction of main interspecific variation accrued during the evolution of non-deep-forked species. Moreover, the latter direction is also aligned with axes summarising sexual dimorphism and allometric variation on deep-forked species, a feature lacking in the rest of the species. Thus, exaggerated tail morphologies are interpreted as the result of amplified divergence through reorientation and co-option of allometric variation by sexual selection, repeatedly driving morphology along a historically favoured direction of cladogenetic evolution.

KEYWORDS

birds, constraints, diversification, morphology, tails

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1 | INTRODUCTION

The direction and magnitude of evolutionary change are not only largely controlled by microevolutionary processes that sort variation such as natural selection and drift (Gould, 2002; Jablonski, 2017), but also by the processes generating that variation, such as the genetic architecture underlying the affected phenotypes (Lande, 1979). The latter can enhance or impede response to selection by modulating the amount of raw material available for phenotypic changes elicited by other processes (Etterson & Shaw, 2001; Schluter, 1996) and thus are a major evolutionary factor. Over short timescales, selective responses may be biased by strong genetic correlations or simply by the absence of genetic variation, thus precluding or deviating evolutionary change towards certain phenotypes (Arnold, 1992; Blows & Hoffmann, 2005; Walsh & Blows, 2009). This includes the early stages of between-species divergence, where evolution is predicted to be biased along 'genetic lines of least resistance' defined by 'G', the additive genetic variance-covariance matrix (McGuigan, 2006; Schluter, 1996).

However, natural selection has its agency at the organismal level, acting upon available phenotypic variation (Gould, 2002). As the organismal phenotype is the result of developmental processes unfolding during ontogeny, the latter can favour the emergence of particular phenotypes (e.g. Gould, 1966) and thus has the potential to establish preferred directions for long-term evolution (Gould, 1977). In this sense, they constitute 'phenotypic lines of least resistance' defined by 'P', the phenotypic variance-covariance matrix (see Marroig & Cheverud, 2005). The influence of these constraints is well documented for relatively short evolutionary timescales (i.e. <2 million years; Bégin & Roff, 2004; Bolstad et al., 2014; Chenoweth et al., 2010; Hansen & Houle, 2008; McGuigan et al., 2005; Schluter, 1996; Walter et al., 2018; see McGlothlin et al., 2018 for a discussion).

Nonetheless, the influence of genetic and developmental constraints over greater evolutionary timescales is yet to be gauged (Gould, 2002; Schluter, 2000) as empirical studies are scarce (but see Houle et al., 2017; McGlothlin et al., 2018). Genetic constraints are frequently disregarded when studying species diversification or other long-term evolutionary phenomena under the argument that the genetic architecture of trait covariation may evolve as well (Arnold et al., 2008; Steppan et al., 2002; Turelli et al., 1988), thus altering potential genetic lines of least resistance (Arnold et al., 2001). Indeed, selection and drift can alter the G matrix (Björklund et al., 2013; Careau et al., 2015; Roff & Fairbairn, 2012; Steppan et al., 2002), but the signature of genetic constraint may persist over large timescales even in the presence of an evolving genetic architecture (McGlothlin et al., 2018). The study of phenotypic lines of least resistance can greatly improve the study of the role of developmental constraints, as they are both easier to estimate than and highly correlated with their genetic counterpart, as well as rich in information regarding evolutionary dynamics (e.g. Marroig & Cheverud, 2005; Renaud & Auffray, 2013).

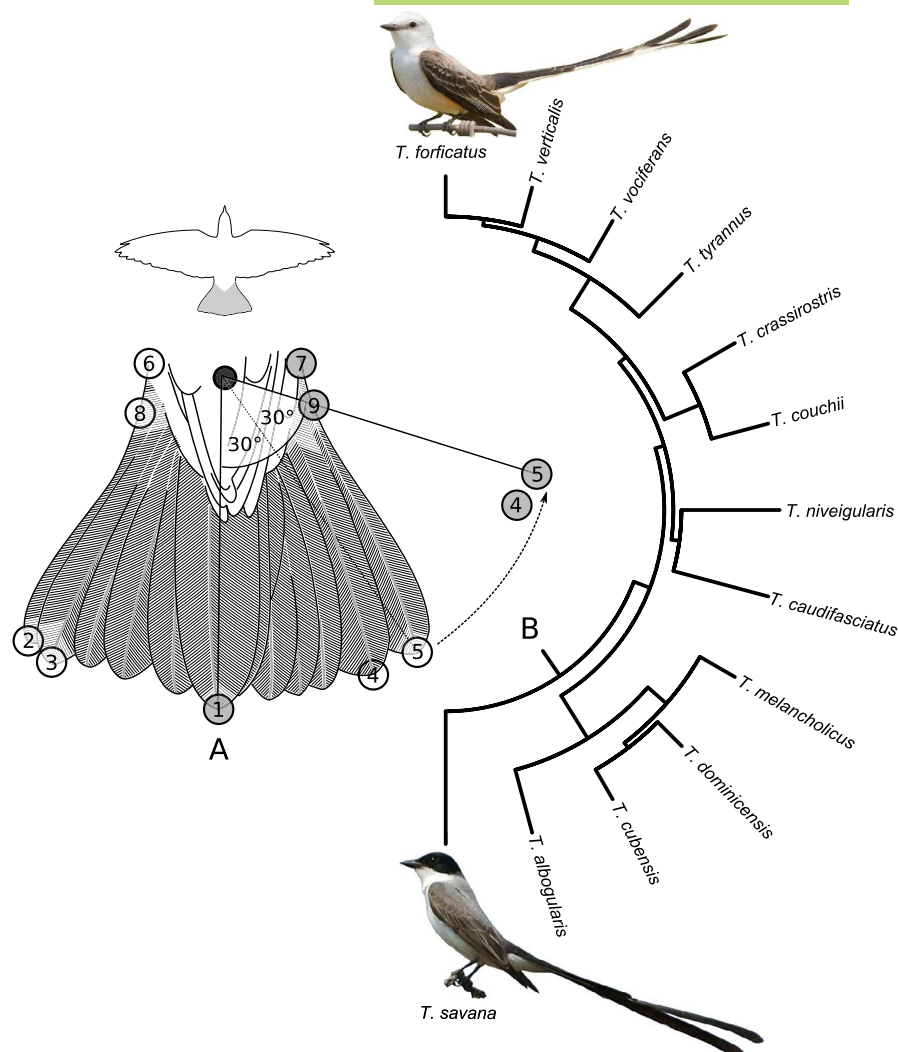
Allometry is a classic example of trait covariation and a central issue in the literature addressing developmental integration, as

changes in many morphological, physiological and life-history traits are highly correlated with changes in organ or body size (Brown & West, 2000; Schmidt-Nielsen, 1984; Zelditch et al., 2012). Because ontogenetic and evolutionary allometric relationships are often evident over large size ranges, and since allometric slopes (both static and ontogenetic) are usually rather conserved among closely related species, allometry has been considered as a constraint for morphological evolution (Björklund, 1996; Gould, 1966; Voje et al., 2014). In this view, the existence of allometric patterns is often interpreted as evidencing strong ontogenetic, physiological or other biological mechanisms restraining the rate and direction of evolution and diversification (Chernoff & Magwene, 1999; Murren, 2012). An alternative view is to consider the processes underlying the observed allometric patterns as facilitators of evolution or an adaptation on itself (Bonduriansky, 2007; Bonduriansky & Day, 2003; Eberhard, 2009; Emlen & Nijhout, 2000; Schmidt-Nielsen, 1984). Under this perspective, which is often discussed in the context of classic studies (Schmidt-Nielsen, 1984; see a discussion in Pélabon et al., 2014), the effect of selective processes that shape trait relationships or phenotypic responses are amplified by the existent covariance structure.

This latter view is widespread in ornithological studies, as allometric patterns are considered a major factor contributing to patterns of phenotypic variation across a range of avian clades (Cuervo & Møller, 2009; Kulemeyer et al., 2009). Previous studies focussed on avian traits (beaks, tails and wings) showed how ecological factors can drive the evolution of those structures with the aid of allometry (Fitzpatrick, 1985; Norberg, 1995; Pigot et al., 2016). For example, Bright et al. (2016) found a strong covariation between skull shape and size, showing that exploitation of allometric relationships is an effective mechanism by which raptor birds may modify their feeding ecology.

Tyrannus (de Lacépède, 1799) is a New World genus of passerines comprising thirteen species with a common ancestor dating back to approximately 5 MY before present and with a widespread American distribution, from Canada to Argentina (Fitzpatrick, 1985; del Hoyo et al., 2010). Those species inhabit a wide range of environments, such as savannahs, woods and even urban areas (Fitzpatrick et al., 2004; Ridgely & Tudor, 2009). Some species are seasonal migrants, although migratory behaviours within the genus are variable (e.g. partial, short-distance and long-distance migration; del Hoyo et al., 2010; MacPherson, 2017). They prey primarily on flying insects and forage almost exclusively during flight, although they also feed from high perches or on the ground (Fitzpatrick, 1980; Murphy, 1983; Traylor & Fitzpatrick, 1982). Notably, the group includes two independently evolved species with strikingly elongated, deep-forked tail feathers (hereafter, DF species): the North American scissor-tailed (*T. forficatus*) and the South American fork-tailed (*T. savana*) flycatchers (Figure 1; Jetz et al., 2014; Regosin, 2020; Tuero et al., 2019). These species have disjunct geographical distributions (Regosin, 2020) and are characterised as socially monogamous, with both male and female involved in parental care (Jahn & Tuero, 2020; Regosin & Pruett-Jones, 1995). Both species show a marked sexual dimorphism in

FIGURE 1 (a) Schematic representation of a bird tail, showing the original and postrotated position of the nine landmarks (white circles), and the centroid of the tail base (smaller black circle) used as pivot; only right-sided landmarks (grey circles) were retained for further analysis. (b) Phylogenetic tree of the *Tyrannus* species (Harvey et al., 2020), with the two deep fork-tailed species depicted (photographs by P Smith—FPAVE1304PH—and PA Guris—PhID19511—respectively)



tail length, although both females and males exhibit extremely elongated tails when compared to the other, non-deep, fork-tailed *Tyrannus* species (hereafter, NDF species) (Regosin & Pruett-Jones, 2001; Roeder et al., 2019; Tuero et al., 2019). Due to their aerodynamic cost, these long tails increase drag in relation to the lift (Evans & Thomas, 1997; Thomas, 1993), making a good example of a structure evolving under a sexual selection mechanism (Balmford et al., 1993). Also, in social monogamous species such as these, extra-pair copulations generate an opportunity to intensify a sexual selection process (Webster et al., 2007). Supporting this, high extra-pair copulation was observed in scissor-tailed flycatchers (Roeder et al., 2019).

Here, we address the genus *Tyrannus* as a model for examining conditions and drivers that facilitate the repeated evolution of exaggerated, secondary sexual traits. In particular, we explore the relationship between two major sources of intraspecific variation (sexual dimorphism and allometric variation) and the main directions of macroevolutionary change that accrued during the evolution of the clade, assessing whether they promoted or otherwise constrained the evolution of tail morphology by establishing phenotypic lines of least resistance.

2 | MATERIALS AND METHODS

2.1 | Data collection

The thirteen species of *Tyrannus* were represented in a sample of 281 museum specimens (range: 12–39 specimens per species, average: 21.6 specimens per species; American Museum of Natural History, AMNH, USA, and Museo Argentino de Ciencias Naturales, MACN, Argentina). Only adult skins of both sexes with rectrices in good condition were included.

Tails were photographed in dorsal view from a standardised vertical plane. Tail morphology was captured by placing nine landmarks on the image of the open tail of each specimen: (1) the tips of the central rectrix, (2–5) the two outermost rectrices, (6–7) the pygostyle insertion point and (8–9) the inflection point formed by the opened outer rectrix at the base of the tail of each side (Figure 1a).

Due to the fragile feathers of museum material, tails were only opened at an angle of 60°. Since an opening of 120° is considered the aerodynamic optimum (Thomas, 1993; Thomas & Balmford, 1995) and therefore a standard in studies of bird tail morphology,

the two landmarks marking the tip of the outermost rectrices of each side were further rotated 30°, using the centroid of landmarks 6–9 (defining the 'base' of the tail) as pivot (Figure 1a). In order to avoid problems reported elsewhere for supervised versions of multivariate analyses (e.g. between-group PCA and multivariate regression; e.g. Bookstein, 2019; Cardini, 2020), the symmetric component of shape variation was computed, and the four landmarks corresponding to the left side of the tail were discarded. All subsequent analyses were carried out using the five landmarks representing the right side of the tail (Figure 1a; note that these landmarks were mirrored to represent symmetric tails in all figures).

The centroid size (Bookstein, 1986) of each landmark configuration was calculated to be used as a proxy for tail size, after which the sample of landmark configurations was subjected to Generalised Procrustes Analysis and projected into tangent space (Claude, 2008; Rohlf & Slice, 1990), thus separating size from shape variation to be analysed independently.

2.2 | Interspecific shape variation

Raw shape variation within each species was processed to remove intraspecific variation by computing the shape residuals resulting from a Multivariate Linear Model (MLM) of tail shape on tail size and sex. This 'corrected' data set was further refined by means of between-group PCA (bgPCA; see Mitteroecker & Bookstein, 2011 and references therein), performed using all *Tyrannus* species as *a priori* groups, with the exception of *T. savana* and *T. forficatus*. This procedure was applied to avoid the heavy influence that deep-forked shapes (and to a lesser extent, the directions of intraspecific shape variation) exert over the orientation of the axes resulting from a regular PCA. Instead, a series of synthetic shape variables, rotated as to maximise the interspecific variation among NDF species, were constructed. Samples and mean shapes belonging to *T. savana* and *T. forficatus* were then projected into the resulting bgPCs. By using the interspecific variation displayed by NDF *Tyrannus* species as the basis for constructing our shape variables, we sought to enhance interpretability of our results by establishing the main directions of evolutionary variation resulting from 'normal' within-clade dynamics as reference.

We used the ultraconserved elements phylogeny from Harvey et al. (2020) in order to provide a phylogenetic structure for the analyses (Figure 1b). Tail shapes were reconstructed for hypothetical ancestors by optimising the species' mean shape configurations within a maximum parsimony framework (Catalano et al., 2010). This methodology reconstructs ancestral shapes maximising similarity accounted for common ancestry. The phylogenetic structure was infused into morphospace by the projection of shape configurations corresponding to the tips and nodes of the phylogeny, along with their genealogical relationships, to create a phylomorphospace (Sidlauskas, 2008).

2.3 | Intraspecific shape variation

In order to explore the relationship between interspecific and intraspecific patterns of variation, two types of intraspecific shape variation were isolated within each species (starting again from the raw shape variables). In particular, two axes representing allometric shape variation and sexual dimorphism were constructed through separate MLM of shape on log-transformed centroid size and sex respectively. In each case, the shapes expected under the corresponding relationship were estimated. The allometric and between-sex axes of each species were characterised using their slope coefficients and depicted by projecting their expected shapes into phylomorphospace.

Statistical significance of shape differences attributable to between-sex and allometric variation was assessed for each species separately through Procrustes distance-based linear models (using sex and log-transformed centroid size as independent variables respectively). The magnitude of this difference was measured using the partial Procrustes distance implied in each shape transformation. Whether the interspecific maximum variation axis and the allometric and between-sex axes were more aligned than expected by chance was tested separately for each species by comparing the Pearson correlation between the corresponding eigenvector coefficients to the distribution of the correlation between randomly permuted eigenvector coefficients, generated through 9999 iterations (Zelditch et al., 2012).

All analyses were conducted in the R environment (R Core Team, 2020) using the packages Morpho (Schlager, 2017), geomorph (Adams et al., 2019), shapes (Dryden, 2021), abind (Plate et al., 2016), retistruct (Sterratt et al., 2013), spdep (Bivand & Wong, 2018), ape (Paradis & Schliep, 2019) and phytools (Revell, 2012), and some additional functions written by PMC. The only exceptions were the digitisation of tail landmarks, carried out using tpsDig (Rohlf, 2016) and the ancestral node reconstruction, implemented in Tree Analysis using New Technology (TNT; Goloboff et al., 2008). Supporting information and files are now available at: <https://doi.org/10.5061/dryad.4mw6m90cj>

3 | RESULTS

The first three principal components resulting from bgPCA accounted for 98.21% of the corresponding variance (Figure 2). Variation along the first bgPC (the axis of maximum interspecific variation, capturing 69.56% of the original shape variance) describes differences in the degree of forking of the tail and relative base width, with negative values representing forked tails with outermost rectrices slightly more elongated than inner outer rectrices and positive values representing rounded tail fans. The second bgPC (25.16% of total variance explained) on the other hand captures differences in relative tail elongation, base width and positions of the tips of outermost rectrices relative to the sagittal

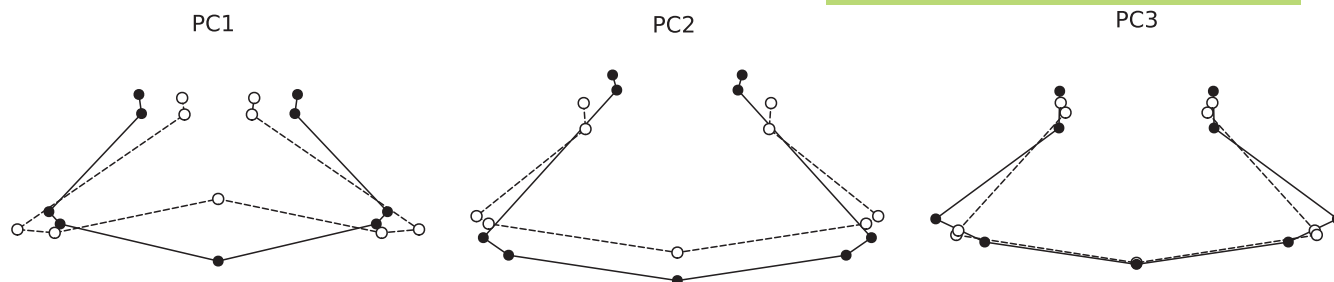


FIGURE 2 Shape transformations represented by the first three bgPCs resulting from bgPCA of Procrustes shape coordinates of NDF *Tyrannus* species. Open circles and dashed lines are used for landmarks of the configuration representing negative extremes, whereas closed circles and solid lines are used for positive extremes

plane. Finally, bgPC3 (3.48% of the original shape variance) represents differences in tail base length and separation of outermost rectrices' tips. Most *Tyrannus* species display an overlapped distribution in the resulting phylomorphospace. Unsurprisingly, *T. savana* and *T. forficatus* are the exception, diverging markedly from the rest along bgPC1 and from each other along bgPC3 (Figure 3a,b).

3.1 | Interspecific and intraspecific shape variation

In general, NDF species displayed reduced sexual dimorphism, whereas the presence of relatively substantial allometric variation is a more common phenomenon (as evidenced by both the magnitude and statistical significance of the implied shape transformations; Table 1). These axes are significantly aligned with each other in eight NDF species (Table 2). However, although their alignment with the axis of maximum interspecific variation differs (Figure 3c,d), none of these species display a significant correlation between the latter and allometric or between-sex axes (the sole exception being the allometric axis of *T. crassirostris*; Table 2, Figure 3c,d). The situation changes dramatically for the DF species, as both *T. savana* and *T. forficatus* exhibit significant allometric and between-sex variation (Table 1). However, the most remarkable aspect of these species is the alignment of both allometric and between-sex axes of variation not only with each other, but also with the axis of maximum interspecific variation computed using the rest of the species (i.e. they are approximately parallel to the main axis of NDF interspecific variation; Table 2, Figure 3c,d). Although not meeting the standard 0.05 threshold, the allometric axis of *T. savana* will be regarded as aligned with the axis of maximum interspecific variation during the discussion by virtue of its marginal nonsignificance.

4 | DISCUSSION

Allometric patterns are important aspects contributing to diversification of avian morphology (Cuervo & Møller, 2009; Kulemeyer et al., 2009), in concert with ecological pressures on phenotypes (Bright et al., 2016; Fitzpatrick, 1985; Norberg, 1995; Pigot et al.,

2016). Sexual selection is also an important evolutionary force in the context of avian evolution, affecting behaviour, colouration and morphology of birds (Barraclough et al., 1995; Payne, 1984).

In the context of bird tail morphology and sexual selection, this topic has received considerable attention (Bonduriansky, 2007; Bonduriansky & Day, 2003; Cuervo & Møller, 2009) being generally addressed from the 'classic' Huxley-Jolicoeur school of allometry, i.e. by studying the relation between tail and body size (Klingenberg, 1998). The general consensus emerging from these studies is that secondary sexual traits with exaggerated morphologies will tend to show positive allometry (i.e. larger tails will be associated with larger bodies) as the result of the balance between metabolic costs and reproductive advantage.

However, these studies address only the first of two very different allometric phenomena. The second, and the one that is the focus of this work, is the relation between trait size and shape (framed within the 'modern' Mosimann-Gould approach to allometry; Klingenberg, 1998). A very straightforward takeaway from our results is that this kind of allometric variation and sexual dimorphism are both amplified and evolutionarily coupled in the two independently evolved *Tyrannus* species with exaggerated tail morphologies (Figure 3). Evidence on ongoing sexual selection has been reported in both *T. savana* and *T. forficatus* (Regosin & Pruett-Jones, 2001; Tuero et al., 2019). Still, the coupling of sexual dimorphism, a natural byproduct of sexual selection (Andersson, 1994; Møller et al., 1998), with allometric shape variation suggests that this powerful agent of evolutionary change is being fed with a pervasive and ecologically significant source of morphological variation. This is in line with the notion that sexual selection has not only played a central role in the evolution of exaggerated tail morphologies in birds (Balmford et al., 1993; Clark, 2010; Møller, 1988; Winquist & Lemon, 1994), but also shines light on why such disparate shapes have been able to be realised in the first place.

However, neither substantial allometric variation nor alignment of between-sex and allometric variation axes are sufficient to produce DF tails, as attested by the numerous NDF species displaying both features (Tables 1 and 2). The missing piece lies in another result: the marked morphological differences between *T. savana* and *T. forficatus* and the rest of the genus can be summarised as a monotonic divergence along the same direction of main interspecific variation

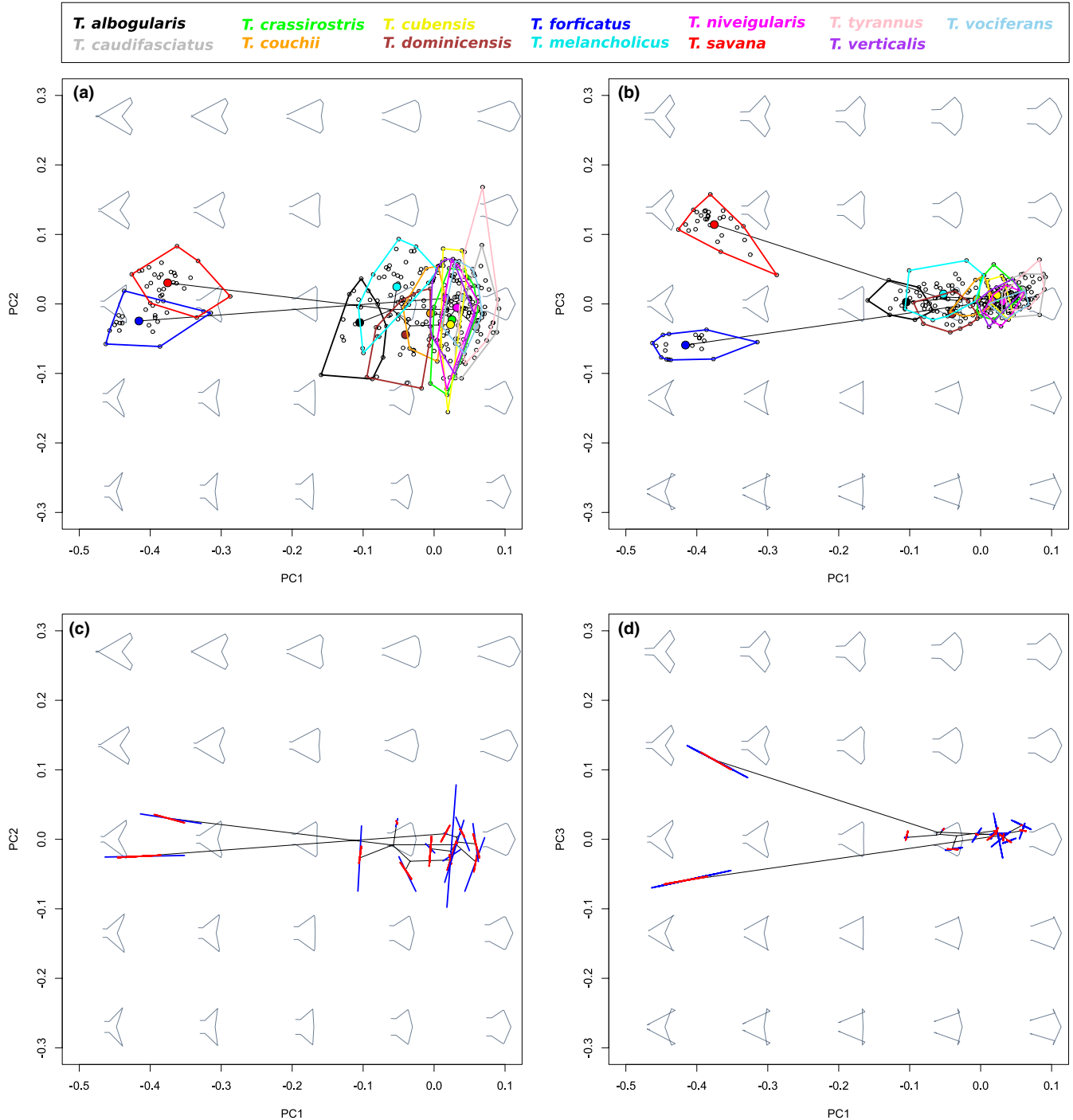


FIGURE 3 (a, b) Phylomorphospaces (bgPC1–3) displaying the distribution of the full sample of specimens (open circles) and species' mean shapes (coloured closed circles). (c, d) Intraspecific axes of variation (allometric: solid blue lines; between-sex: solid red lines)

extracted from the cluster of species with NDF tails (i.e. the axis of maximum interspecific variation, represented by bgPC1). Furthermore, axes summarising both sexual dimorphism and allometric variation of DF species are significantly aligned with the latter, which can be considered as representing the accumulation of cladogenetic change (under the reasonable assumption of the prevalence of nondirectional anagenetic patterns of change; Hunt et al., 2015). Thus, the axis of maximum interspecific variation will reflect the direction of

phenotypic evolution favoured during between-species divergence occurring during 'regular' within-clade dynamics in *Tyrannus*.

Putting all this together, we suggest that two conditions are necessary for the evolution of exaggeratedly elongated tails in *Tyrannus*: (1) the co-option of allometric variation as the primary source of raw material for sexual selection and (2) the alignment of the latter process with a macroevolutionary line of least resistance, resulting in fast divergence through an open lane of evolutionary change.

TABLE 1 Procrustes distances implied in shape transformations for intraspecific allometric and between-sex variation, along with the residual degrees of freedom, *F* values and *p*-values from Procrustes linear models

Tail type	Species	Allometric variation	Sexual dimorphism
NDF species	<i>T. albogularis</i>	0.095 (<i>df</i> = 14; <i>F</i> = 4.137; <i>p</i> = 0.024)	0.031 (<i>df</i> = 14; <i>F</i> = 1.100; <i>p</i> = 0.312)
	<i>T. caudifasciatus</i>	0.083 (<i>df</i> = 19; <i>F</i> = 3.809; <i>p</i> = 0.044)	0.034 (<i>df</i> = 19; <i>F</i> = 1.910; <i>p</i> = 0.160)
	<i>T. couchii</i>	0.029 (<i>df</i> = 15; <i>F</i> = 0.369; <i>p</i> = 0.709)	0.043 (<i>df</i> = 15; <i>F</i> = 3.666; <i>p</i> = 0.035)
	<i>T. crassirostris</i>	0.030 (<i>df</i> = 18; <i>F</i> = 0.281; <i>p</i> = 0.711)	0.046 (<i>df</i> = 18; <i>F</i> = 2.861; <i>p</i> = 0.088)
	<i>T. cubensis</i>	0.186 (<i>df</i> = 10; <i>F</i> = 5.822; <i>p</i> = 0.020)	0.021 (<i>df</i> = 10; <i>F</i> = 0.185; <i>p</i> = 0.797)
	<i>T. dominicensis</i>	0.057 (<i>df</i> = 19; <i>F</i> = 2.409; <i>p</i> = 0.100)	0.032 (<i>df</i> = 19; <i>F</i> = 1.658; <i>p</i> = 0.180)
	<i>T. melancholicus</i>	0.015 (<i>df</i> = 37; <i>F</i> = 0.142; <i>p</i> = 0.955)	0.011 (<i>df</i> = 37; <i>F</i> = 0.403; <i>p</i> = 0.745)
	<i>T. niveigularis</i>	0.096 (<i>df</i> = 17; <i>F</i> = 5.861; <i>p</i> = 0.013)	0.011 (<i>df</i> = 17; <i>F</i> = 0.182; <i>p</i> = 0.868)
	<i>T. tyrannus</i>	0.059 (<i>df</i> = 24; <i>F</i> = 2.015; <i>p</i> = 0.149)	0.035 (<i>df</i> = 24; <i>F</i> = 2.492; <i>p</i> = 0.102)
	<i>T. verticalis</i>	0.018 (<i>df</i> = 19; <i>F</i> = 0.136; <i>p</i> = 0.907)	0.030 (<i>df</i> = 19; <i>F</i> = 1.699; <i>p</i> = 0.179)
	<i>T. vociferans</i>	0.052 (<i>df</i> = 18; <i>F</i> = 1.814; <i>p</i> = 0.159)	0.016 (<i>df</i> = 18; <i>F</i> = 0.680; <i>p</i> = 0.459)
DF species	<i>T. forficatus</i>	0.102 (<i>df</i> = 18; <i>F</i> = 19.583; <i>p</i> > 0.001)	0.055 (<i>df</i> = 18; <i>F</i> = 15.825; <i>p</i> > 0.001)
	<i>T. savana</i>	0.117 (<i>df</i> = 27; <i>F</i> = 20.952; <i>p</i> > 0.001)	0.056 (<i>df</i> = 27; <i>F</i> = 13.196; <i>p</i> > 0.001)

Note: Significant allometric patterns or sexual dimorphism are highlighted in bold.

TABLE 2 Pearson correlations between the allometric and between-sex axes of each species and the axis of maximum interspecific variation, along with *p*-values from permutation tests

Tail type	Species	Allometric – Sexual	Allometric – Interspecific	Sexual – Interspecific
NDF species	<i>T. albogularis</i>	0.843 (<i>p</i> = 0.003)	0.053 (<i>p</i> = 0.883)	0.104 (<i>p</i> = 0.750)
	<i>T. caudifasciatus</i>	0.940 (<i>p</i> > 0.001)	0.330 (<i>p</i> = 0.346)	0.158 (<i>p</i> = 0.633)
	<i>T. couchii</i>	0.444 (<i>p</i> = 0.201)	0.443 (<i>p</i> = 0.189)	0.076 (<i>p</i> = 0.813)
	<i>T. crassirostris</i>	0.715 (<i>p</i> = 0.020)	0.818 (<i>p</i> = 0.007)	0.283 (<i>p</i> = 0.395)
	<i>T. cubensis</i>	0.759 (<i>p</i> = 0.031)	0.069 (<i>p</i> = 0.848)	0.121 (<i>p</i> = 0.715)
	<i>T. dominicensis</i>	0.957 (<i>p</i> > 0.001)	0.415 (<i>p</i> = 0.234)	0.497 (<i>p</i> = 0.151)
	<i>T. melancholicus</i>	0.680 (<i>p</i> = 0.032)	0.193 (<i>p</i> = 0.558)	0.150 (<i>p</i> = 0.652)
	<i>T. niveigularis</i>	0.139 (<i>p</i> = 0.675)	0.278 (<i>p</i> = 0.438)	0.066 (<i>p</i> = 0.845)
	<i>T. tyrannus</i>	0.900 (<i>p</i> = 0.003)	0.127 (<i>p</i> = 0.704)	0.245 (<i>p</i> = 0.467)
	<i>T. verticalis</i>	0.366 (<i>p</i> = 0.295)	0.229 (<i>p</i> = 0.493)	0.410 (<i>p</i> = 0.236)
	<i>T. vociferans</i>	0.747 (<i>p</i> = 0.026)	0.362 (<i>p</i> = 0.301)	0.393 (<i>p</i> = 0.252)
DF species	<i>T. forficatus</i>	0.997 (<i>p</i> > 0.001)	0.975 (<i>p</i> > 0.001)	0.980 (<i>p</i> > 0.001)
	<i>T. savana</i>	0.993 (<i>p</i> > 0.001)	0.635 (<i>p</i> = 0.052)	0.657 (<i>p</i> = 0.048)

Note: Statistically significant results are highlighted in bold.

If these lessons can be generalised, we should expect other cases of sexually related exaggerated or highly elaborated traits to represent an amplification of ‘regular’ within-clade dynamics, catalysed by a process of sexual selection and fueled by allometric—or perhaps other substantial intraspecific source of—morphological variation. In particular, we predict that (1) species with exaggerated or elaborated morphologies will diverge along the main axis of interspecific variation already present in the cluster of related species with regular morphology, and (2) the latter axis will be aligned with the axes describing intraspecific differences between sexes and allometric (or other kinds of) morphological variation.

Ornithological literature has openly understood the bird tail as a flight device, not only from the historically vast observational registers, but also most probably through the widely used theoretical models of bird flight. A ‘functionalist’ approach has been heavily supported when addressing the evolution of the many bird species showing marked sexual dimorphism and elaborated tail morphologies (e.g. Andersson, 1994; Clark, 2010; Møller et al., 1998), with most of the literature revolving around the relative contribution and putative antagonism of natural and sexual selection. In this context, net selection on tail morphology is conceived as the compromise between its role as a secondary sexual trait—i.e. its effects on mating success (Andersson, 1982; Pryke

et al., 2001)—and as a structure involved in flight—i.e. its effects on aerodynamic performance—(Balmford et al., 1993; Evans & Thomas, 1997), invoking both biomechanical conflicts (Evans, 2004) and physiological trade-offs (Cuervo & Møller, 2001; Saino & Møller, 1996).

In contrast, the other side of the functionalist coin, namely the 'structuralist' aspects (i.e. general biases in the production of variation that introduce not only limits, but also channels, for evolution; see Gould, 2002) of this study case, has received much less attention. The existence of variation, long recognised as the water to selection's mill, has been generally treated as something that is given (or not) for tail form without further consideration. Even allometry, a topic subject to recent debate, is treated as an expression of the tension between natural and sexual selection (see above). Yet, the present study hints that the existence of some highly elaborated morphologies (a feature strongly associated with selection) crucially depends on the interaction of different types, levels and specific properties of variation. Our intention is not to argue against the importance of selection (a process our results are consistent with), but to vindicate the creative role that evolutionary changes in direction, magnitude and coupling of different sources of variation (whatever their particular mechanistic base might be) plays into reaching a satisfactory explanation. In this particular case, the co-option (and potential reorientation) of allometric shape variation as a source of raw material for processes of sexual selection driving mean morphology along a historically favoured direction of cladogenetic evolution resulted in amplified divergence. Evolutionary changes in the properties of variation, and their feedback with selection and other processes, need not follow the same evolutionary dynamics as the current selective regimes identified and discussed so far in the literature, and represent an open avenue for future research.

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CONFLICT OF INTERESTS

The authors declare no competing interests.

AUTHORS CONTRIBUTIONS

MNF collected the primary data, performed the morphometric quantification, participated in data analysis and in the design of the study, and critically revised the original draft. PMC conceived and participated in the conceptualization and design of the study, carried out the data analysis and visualisation, and drafted the manuscript

along with IMS. IMS conceived the study and contributed to the study conceptualization and design, coordinated the study, provided funding, contributed to the data analysis and statistics, and drafted the manuscript along with PMC. DTT conceived and coordinated the study, participated in the design of the study, provided funding and critically revised the original draft. All authors performed revisions and editing of the final draft, gave final approval for publication and agreed to be held accountable for the work performed therein.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/jeb.14000>.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study can be accessed at <https://doi.org/10.5061/dryad.4mw6m90cj>.

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