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Allometry, sexual dimorphism, and sexual trait elaboration in the birds-of-paradise

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Abstract

Rensch's rule (RR) is a widespread macroevolutionary pattern describing a positive association between male-biased dimorphism and species size. Applied to sexual size dimorphism, RR is often associated with sexual selection, as larger body sizes may benefit males in competition and courtship. Moreover, the presence of RR in sexual traits further indicates that males reap relative performance benefits beyond large body size alone. Here we describe patterns of elaboration, variation, and sexual dimorphism in tail length in the birds-of-paradise (Aves: Paradisaeidae), which exhibit an extreme diversity in tail lengths, ranging from short-tailed species to the longest-tailed passeriform birds. We found that body size followed RR in polygynous, but not monogamous species, in accordance with the sexual selection hypothesis. However, we found no evidence of RR in tail length, indicating similar evolutionary allometries between males and females. Evolutionary allometries of male and female traits were both strongly positive among long-tailed species, suggesting that the lack of RR results from phenotypic correlations between the sexes, rather than constraints on ornament exaggeration. Our study represents the first integrative test of RR in an ornamental morphological trait and evidences how different aspects of dimorphism interact in a group with a hyperdiverse courtship trait.

Keywords: allometry, diversification, Rensch's rule, sexual dimorphism, sexual selection, trait evolution

Introduction

The origins and elaboration of sexually selected traits have consistently attracted the attention of evolutionary biologists (Darwin, 1871). Not only do sexually selected traits include some of the most extreme phenotypes in nature, but also some of the most diverse and sexually dimorphic. Previous research has examined the processes driving the evolution of sexually selected traits through patterns of allometry (i.e., the scaling relationship between the size of a body part and the size of the organism), especially through the study of static allometries (i.e., allometric patterns observed among conspecific individuals found at the same developmental stage) (Bonduriansky and Day, 2003; Eberhard et al., 2018; Rodríguez and Eberhard, 2019). However, patterns of static allometry are often not equivalent to allometric patterns observed among species (i.e., evolutionary allometry) (Pélabon et al., 2014; Voje et al., 2022), limiting the application of intraspecific patterns of allometry to macroevolutionary studies. Thus, investigating these patterns in a comparative context can provide important insight into the processes shaping the diversity of elaborate courtship phenotypes.

One of the most widely known macroevolutionary allometric patterns is Rensch's rule, in which the degree of male-biased sexual size dimorphism (male-biased SSD) increases with body size among related species (Fairbairn, 1997, p. 199; Meiri & Liang, 2021). Evidence provided by several studies suggests that the emergence of Rensch's rule is often associated with the presence of intense sexual selection in species that exhibit male–male competition for mating opportunities (e.g., Andersson, 1994; Dale et al., 2007; Gaulin & Sailer, 1984; Emlen, 2008, p. 200; Rico-Guevara & Hurme, 2019). Under sexual selection hypotheses, large body size is selected in males due to a positive relationship between size and competitive performance or female preference (Clutton-Brock, 1985; Fairbairn, 1997; Lailvaux et al., 2004; Lindenfors et al., 2002; Shine, 1978; Fairbairn et al., 2007, p. 200; Summers & Ord, 2022). Following selection on male body size, Rensch's rule could then evolve due to different alternative but not mutually exclusive processes, such as correlated selection on female body size (De Lisle & Rowe, 2013; Zeng, 1988a), lower genetic variance in females (Leutenegger & Cheverud, 1982, 1985), or ecological and energetic constraints on body size evolution (Clutton-Brock et al., 1977; Webster, 1992).

It is often assumed that competitive ability scales isometrically with body size (e.g., biomechanical models predict that both the strength of physical attacks and running speed during locomotion scale isometrically with body mass; Gaulin & Sailer, 1984; Schmidt-Nielsen, 1984), meaning that the allometry of SSD illustrated by Rensch's rule should accurately reflect the allometry of dimorphism in a given measure

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of competitive ability. However, the actual allometric relationships between body size and the traits directly involved in sexual competition, such as ornaments or weapons, are seldom examined, meaning this correspondence often goes untested (but see Machado et al., 2021; Toyama et al., 2025)

One way to deal with this disconnection is by testing Rensch's rule in both body size and the secondary sexual traits involved in sexual competition. In fact, Rensch's original "rule of sexual differences" was not only concerned with the allometry of SSD, but also with the allometry of any relative sexual difference, including sexual dimorphism in particular body parts (Adams et al., 2020; Rensch, 1950, 1959; Toyama, 2025). This implies that Rensch's rule patterns might differ across traits within the same group of related taxa. Indeed, recent empirical evidence shows that allometric patterns of SSD often do not match allometric patterns of relative dimorphism in secondary sexual traits among related species (Toyama, 2025). For example, even if Rensch's rule is not true for body size in a given group of species, it could emerge in a secondary sexual trait in this same group, such that larger species are ultimately more dimorphic in competitive or display performance than smaller species (e.g., Machado et al., 2021; Santos & Machado, 2016) due to the more positive evolutionary allometry of the focal trait in males (Rensch, 1950; Toyama, 2025). Exploring whether Rensch's rule has emerged in body size, a secondary sexual trait, both, or none can inform our knowledge of how competition-associated performance is optimized, and the possible constraints its evolution might have faced.

The tails of birds are some of the most well studied traits across animals and represent a classic example of the interplay between biomechanics and the evolution of sexual ornamentation (Andersson, 1982; Andersson and Andersson, 1994; Balmford et al., 1993, 1994). Across the diversity of birds, some species stand out in having unusually elongated or structurally modified tails, which may serve a diversity of functions, including, but not limited to, sexual signaling, enhanced aerodynamic performance, and predator avoidance (Zhou et al., 2023). In some bird clades, elongated tails exhibit clear sexual signaling functions, since signalers incorporate their tails in precise ways in display.

For instance, video documentation of nearly all known bird-of-paradise species (Aves: Paradisaeidae) has revealed exaggerated male tail phenotypes are clearly incorporated in both static poses and dynamic "dance" and flight displays (Scholes & Laman, 2012; Scholes et al., 2017b). In contrast, species lacking exaggerated tail phenotypes are not known to incorporate their tails in elaborate sexual displays (but see Frith & Cooper, 1996). Moreover, tail lengths have evolved to remarkable extremes in some species, such as the ribbon-tailed astrapia *Astrapia mayeri*, in which tails longer than one meter have been recorded at a mean body size of just ∼150 g, putatively representing the longest tail length—both in absolute and relative terms—of any known perching bird (Passeriformes) (Figure 1A) (Frith & Beehler, 1998). In contrast, males of other species, such as the short-tailed paradigalla *Paradigalla brevicauda*, as its name suggests, exhibit relatively short tails of ∼5 cm at a body weight of ∼170 g (Frith & Frith, 1997), creating a difference of 1.5 orders of magnitude in tail lengths among similarly sized species.

In addition to both the extreme elaboration and the diversity of tail lengths, birds-of-paradise also exhibit disparate patterns of sexual dimorphism in tail length (Frith & Frith, 1997). For instance, both sexes are notably long-tailed in the astrapias and sicklebills (Figure 1A and B), while, in the genera *Paradisaea* and *Cicinnurus*, only males possess elongated, wire-like central tail feathers in which the barbs are either greatly reduced in length (e.g., *Paradisaea rudolphi*) or visibly absent from one (*Cicinnuru magnificus*) or both (*P. rubra*) margins (Figure 1C) (Stonor, 1938). Overall, the tails of both sexes, but especially in males, are exceptionally variable compared to a sample of ∼6,000 passeriform species (Figure 2). This immense variation in both absolute trait size and sexual dimorphism renders the birds-of-paradise an intriguing model in which to investigate patterns of allometry in size and ornament dimorphism.

In this study, we combined classic and modern approaches to the study of Rensch's rule, the examination of sex-specific evolutionary allometries, and the estimation of phenotypic evolutionary rates and correlations to explore the macroevolutionary patterns of size and tail length dimorphism in the birds-of-paradise, taking advantage of the diversity and extravagance of ornaments that have evolved in this group.

We first hypothesized that, under a sexual selection hypothesis, Rensch's rule in body size would be followed only by the polygynous core birds-of-paradise, but not by the basal species, which form socially monogamous pairs and perform much less elaborate display behaviors (Frith & Beehler, 1998; Gilliard, 1969; Scholes & Laman, 2012). This sexual selection hypothesis is based on the expectation that, when unconstrained, male size evolves to be larger in order to maximize signaling performance (e.g., through the absolute size increase of the tail).

We then hypothesized that tail length would follow Rensch's rule in the birds-of-paradise as a way to enhance any benefits already provided to males by large body size itself. In other words, we expected the degree of dimorphism in the relative (i.e., size-corrected) length of the tail to be higher in larger species. Consequently, we expected the evolutionary allometry of male tail length to be steeper than that of females. Alternatively, Rensch's rule might not emerge if the evolution of exaggerated tail lengths in males is constrained in large species due to biomechanical or energetic limits, if tail length is not under sexual selection in such species, or if male and female phenotypes are genetically or ecologically correlated such that relative differences between sexes are not detectable (Knell et al., 2004; Tidière et al., 2017). In this case, we would expect male and female tail lengths to exhibit similar evolutionary allometries.

Finally, we compared the sex-specific allometric patterns of tail length in species where males are relatively long-tailed against those of species where males are relatively short-tailed and fitted a set of hierarchical models to test for heterogeneity in the rates of relative tail length evolution between sexes and between long- and short-tailed species. In line with a sexual selection hypothesis, we expected a steeper evolutionary allometric slope and/or a higher intercept, as well as higher rates of trait evolution, in male tail length of long-tailed species compared to short-tailed species.

Figure 1. Elaborate tail phenotypes in representative bird-of-paradise species. Among bird-of-paradise species, male Ribbon-tailed astrapia (*Astrapia mayeri*) are known to possess the longest tails among perching birds in both absolute and relative size, reaching up to ∼1.2 m ($\bar{x} = 893$ mm) in length, and which are swished about conspicuously during display (A). Other species, such as the Black Sicklebill *Epimachus fastuosus* (B), also exhibit exceptionally long tails despite displaying them rather differently with slow, rhythmic body movements. Some long-tailed bird-of-paradise species, such as the magnificent bird-of-paradise (*Cicinnurus magnificus*), have evolved unusual, wire-like central rectrices that are vibrated rapidly in display (C). Photo credits and Macaulay Library accession numbers: Dustin Chen (ML623463636), JJ Harrison (ML625188174), and Angus Pritchard (ML608778519).

Materials and methods

Quantification and statistical analysis

All statistical analyses were conducted in the R v 4.4.0 (R Core Team, 2020) coding environment. For all comparative analyses, we used the bird-of-paradise tree topology available in Ligon et al. (2018), which was modified from Irestedt et al. (2009) based on more recent phylogenetic analyses (Irestedt et al., 2017). Since *Lophorina* was initially nested in *Ptiloris* and subsequently moved to be an outgroup, the resulting tree was no longer ultrametric (tips were not equidistant from the root). To ultrametricize this updated tree topology, we used the "*force.ultrametric*" function available in the *phytools* package (Revell, 2012, 2024).

Morphological data

All morphological measurements of bird-of-paradise species were obtained from Frith and Frith (1997) (Table S1). Data for other Passeriform bird species were obtained from the AVONET database (Tobias et al., 2022), for which we calculated mean tail length values for each sex, where possible. For descriptive comparisons of bird-of-paradise tail lengths to those of other perching birds, our total sample represented values for 5945 species for males and 5613 species for females. We used this full dataset to visualize the diversity of tail length values in the birds-of-paradise compared to other perching birds shown in Figure 2. Since the AVONET database lacked body mass data for both males and females individually, we instead plotted male and female tail lengths against species mean body mass values for visualization. For bird-of-paradise data taken from Frith and Frith (1997), we calculated the average species body size as the average of male and female mass.

Since the growling riflebird *Ptiloris intercedens* is classified as a subspecies in the Frith and Frith (1997) dataset, but as a true species in the Ligon et al. (2018) phylogeny, we use measurements of *Ptiloris magnificus magnificus* as representative of *P. magnificus* in our dataset and use measurements reported for *P. magnificus intercedens* in the Frith and Frith (1997) dataset to represent the growling riflebird *P. intercedens*. While other subspecies have since been elevated to species status (e.g., Irestedt et al., 2017; Scholes & Laman, 2018; Scholes et al., 2017a), these are not included in the Ligon et al. (2018) tree. While the Eastern parotia *Parotia lawesii helenae* is included in the Irestedt et al. (2009) phylogeny, we follow Frith and Frith (1997) in considering it as a subspecies of Lawes' parotia *P. lawesii* in our analyses.

Calculation of sexual size dimorphism and relative tail length dimorphism

Since males were always larger than females across all species, we calculated SSD as (male body mass/female body

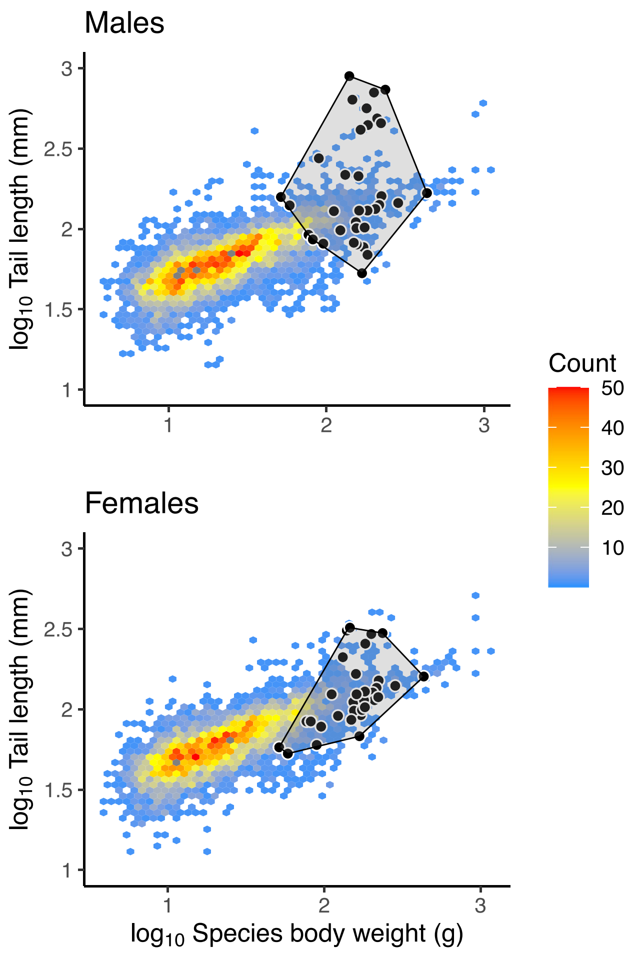

Figure 2. Exceptional elaboration and diversity in bird-of-paradise tail lengths. Tail length values are plotted for both males and females in comparison to ~6,000 other passeriform bird species represented in the AVONET database (Tobias et al., 2022). Black points show bird-of-paradise species, and hexagon heat maps show counts of all other sampled passeriform birds. Data for males includes 5,945 species and 5,613 for females. Plots indicate that both sexes, but especially males, exhibit dramatic variation in both body size and tail length. In both plots, species mean mass for non-Paradisaeidae species is plotted, as sex-specific mass measurements were not available. Tail length values represent mean measurements within each sex.

mass) − 1 (Lovich & Gibbons, 1992). In order to calculate relative tail length dimorphism, we first size-corrected tail length. Body proportions are thought to, on average, scale isometrically in birds (Schmidt-Nielsen, 1984). For this reason, we size-corrected tail length assuming an isometric scaling exponent of 0.33 describes the relationship between tail length and mass (i.e., *relative tail length* = $\log_{10}$(tail length)–0.33 5 $\log_{10}$(body mass)) (e.g., Adams et al., 2020; Toyama et al., 2025). Tail length and body mass are measurements with different dimensionality. In isometric (i.e., geometrically equivalent) structures, length, a one-dimensional variable, increases in value three times slower than mass, a three-dimensional variable. Thus, under isometry, the proportionality between length and mass can be kept by raising mass to the power of 0.33 (Houle et al., 2011; Schmidt-Nielsen, 1984). We then calculated relative tail length dimorphism as *male relative tail length—female relative tail length* (following Adams et al., 2020). Ancestral reconstructions of relative tail length values for each sex and sexual dimorphism in relative tail length were then conducted using the "*fastAnc*" function in the R package *phytools* (Revell, 2012, 2024), and the results were plotted with the *ggtree* package (Yu et al., 2017).

Categorization of species by mating system and tail phenotype

Species were categorized as either socially monogamous or polygynous in accordance with published literature and field guides (Frith & Beehler, 1998; Ligon et al., 2018; Scholes & Laman, 2012). All polygynous species exhibit traditional male display sites, female-only parental care, and, with the exception of the genus *Paradigalla*, extreme sexual dimorphism and dichromatism, as well as elaborate courtship display behavior. Monogamous species belong to the genera *Lycocorax*, *Manucodia*, and *Phonygammus*. They are mostly sexually monomorphic, and exhibit typical characteristics of socially monogamous birds, forming breeding pairs and not engaging in lek-mating or elaborate courtship displays (Frith & Beehler, 1998; Frith & Frith, 2010; Gregory, 2020; Scholes & Laman, 2012).

Species were also categorized in two phenotype groups based on the relative tail lengths of males. Upon visual inspection, the relative tail lengths of males seemed to follow a bimodal distribution (Figure S1). In order to estimate the modes and standard deviations of the two peaks observed in the distribution, we fitted normal mixture densities using the "*normalmixEM*" function from the R package *mixtools* (Benaglia et al., 2009, Figure S1). With the estimated means and standard deviations, we assigned species to one of two groups ("long-tailed" or "short-tailed") depending on 95% confidence intervals. Two species near the limits of both distributions, *Cicinnurus respublica* and *Parotia wahnesi*, were added to the "long-tailed" group given their behavioral affinity with long-tailed species (i.e., tails are likely a main trait used in courtship). Male *C. respublica* possess a wire-like tail absent in females, which they present and shake during display, while male *P. wahnesi* are unusually long-tailed among the parotias and conspicuously erect the tail during a bow display (Frith & Beehler, 1998; Scholes, 2008).

Tests of Rensch's rule

To examine whether birds-of-paradise follow Rensch's rule in body size, and how this relationship might relate to polygyny, we performed a phylogenetic generalized least squares (PGLS) regression to test for a relationship between SSD and species body size (Adams et al., 2020), with mating system ("polygyny" or "monogamy") as a covariate (i.e., SSD ~ species size × mating system). Then, to test whether tail length follows Rensch's rule, we performed a PGLS regression to test for an association between relative (i.e., size-corrected) tail length dimorphism and species size (Toyama et al., 2025). We added relative male tail length as a factor in this model to test whether species with different relative male tail elongations show different patterns. Since no interaction was found between relative male tail length and species size, we tested for an additive model (i.e., relative tail length dimorphism ~ species size + relative male tail length). We performed these phylogenetic regressions using the "*gls*" function from the *nlme* R package (Pinheiro et al., 2023), assuming that residuals were distributed following Pagel's lambda model of evolution, which allows for additional flexibility in computing phylogenetic signal λ using maximum-likelihood (ML). We thus ran PGLS models with ML estimations of λ.

Allometric comparisons between sexes and phenotypic categories

We performed nonphylogenetic linear models of the form [tail length ~ size × sex] to test for sexual differences in the evolutionary allometry of tail length for each of the two phenotypic categories: short tail and long tail. Whenever the interaction term was not significant, we modified the model to include only additive terms (e.g., tail length ~ size + sex). To test whether a hypothetical similarity between sex-specific allometries could arise due to correlation between the sexes, we obtained the residuals from a tail length ~ body mass PGLS model for each sex and then regressed male residuals on female residuals. A positive association between residuals would indicate the evolution of relatively longer tails in one sex might be driving the evolution of longer tails in the other. Additionally, using phylogenetic regressions we tested for sex-specific allometric differences between tail length categories (e.g., for each sex: tail length ~ size × tail length category). As before, whenever the interaction term was not significant, we modified the model to include only additive terms.

Hierarchical models for evolutionary rates and correlations between male and female traits

In order to test whether the evolutionary rates and correlations of male and female relative tail length differ between different evolutionary regimes, we fitted a set of hierarchical models using the function "*evolvcv.lite*" from the R package *phytools* (Revell, 2012, 2024; Revell et al., 2022). We considered phenotypic groups (i.e., "short tail" and "long tail") as indicators of the selection regimes likely experienced by different species in this analysis (e.g., we expected males from "long tail" species to be under stronger sexual selection for longer tails compared to males from "short tail" species). Eight different models were tested, which differed in how the evolutionary rates and correlations behaved for two traits (here male and female relative tail length) between the two different regimes (here represented by phenotypic groups) across the phylogeny (Table S2, Revell et al., 2022). We expected the rate of evolution of relative tail length to be higher in males than in females, at least in the "long tail" regime, and evolutionary correlation to be weaker in the "long tail" regime given the higher levels of dimorphism expected in that category. Thus, we expected models 3b and 4, both allowing the rates of male traits and correlations between sexes to vary between regimes, to have the higher support (see numeration and description of models in Table S2). In order to fit these models, we used the function "*simmap*" from *phytools* to map the estimated evolutionary history of the "long tail" and "short tail" regimes in the phylogeny. Due to the inherent uncertainty of character state reconstruction, we repeated this process 100 times, fitting the eight models on a different character mapping iteration performed on the phylogeny each time. On each iteration, we calculated Akaike weights (AICw) corresponding to each model. Finally, we calculated the average AICw, as well as average evolutionary rates and correlations estimated by each model, based on the 100 iterations.

Results

Patterns of elaboration and sexual dimorphism in bird-of-paradise tails

Plots showing the distribution of absolute tail lengths in the birds-of-paradise compared to other passeriform bird species reveal an extreme degree of variation in tail length in both males and females (Figure 2). Ancestral reconstructions of relative tail length values in both males and females further reveal diverse patterns of tail length elaboration and sexual dimorphism within the bird-of-paradise family. Both males (Figure 3A) and females (Figure 3B) exhibit marked increases in relative tail length in the core bird-of-paradise radiation. While several genera exhibit clearly elongated tails, our phylogenetic analyses suggest that long-tailedness represents a more derived trait in the birds-of-paradise, potentially originating in the common ancestor of the genera *Paradisaea*, *Cicinnurus*, *Epimachus*, *Astrapia*, and *Paradigalla*, with a potential secondary reduction in tail length in *Paradigalla* (Figure 3A).

Interestingly, females belonging to species in the genera *Paradisaea* and *Cicinnurus* remained relatively short-tailed (Figure 3B). Males in these species also exhibit modified, wire-like tail morphologies, suggesting that the increase in sexual dimorphism in this group (Figure 3C) co-occurred with stark morphological changes in the central tail feathers (Stonor, 1938) (Figure 1C). Patterns of relative tail length evolution and our estimates of evolutionary correlations between male and female traits (see below) are consistent with the hypothesis that wire-tails represent a phenotypic innovation in which there are little to no genetic correlations between the sexes influencing female trait values (Clark & Rankin, 2020; Lande, 1980). This may explain why this group exhibited a considerably greater degree of sexual dimorphism in relative tail length compared to short-tailed and other long-tailed species with more typical tail morphologies.

Rensch's rule in body size and tail length

A PGLS model indicated that the association between SSD and species body size is positive and strong in polygynous birds-of-paradise ($\beta = 0.67$, $SE = 0.14$, $t = 4.90$, $p < .001$, Figure 4A). This pattern, however, is not followed by monogamous species, which can reach large sizes but only show low or moderate levels of SSD (Figure 4A), as evidenced by the significant and negative effect of the "monogamous" category on the slope of SSD allometry ($\beta = -0.85$, $SE = 0.38$, $t = -0.85$, $p = .034$, Figure 4A). A subsequent PGLS model showed no significant interaction between species body size and relative male tail length when acting as predictors of relative tail length dimorphism ($t = -1.97$, $p = .059$); thus, the interaction term was removed from the model. The updated model showed no evidence of a relationship between relative tail length dimorphism and species body size ($t = -1.13$, $p = .266$, Figure 4B), indicating

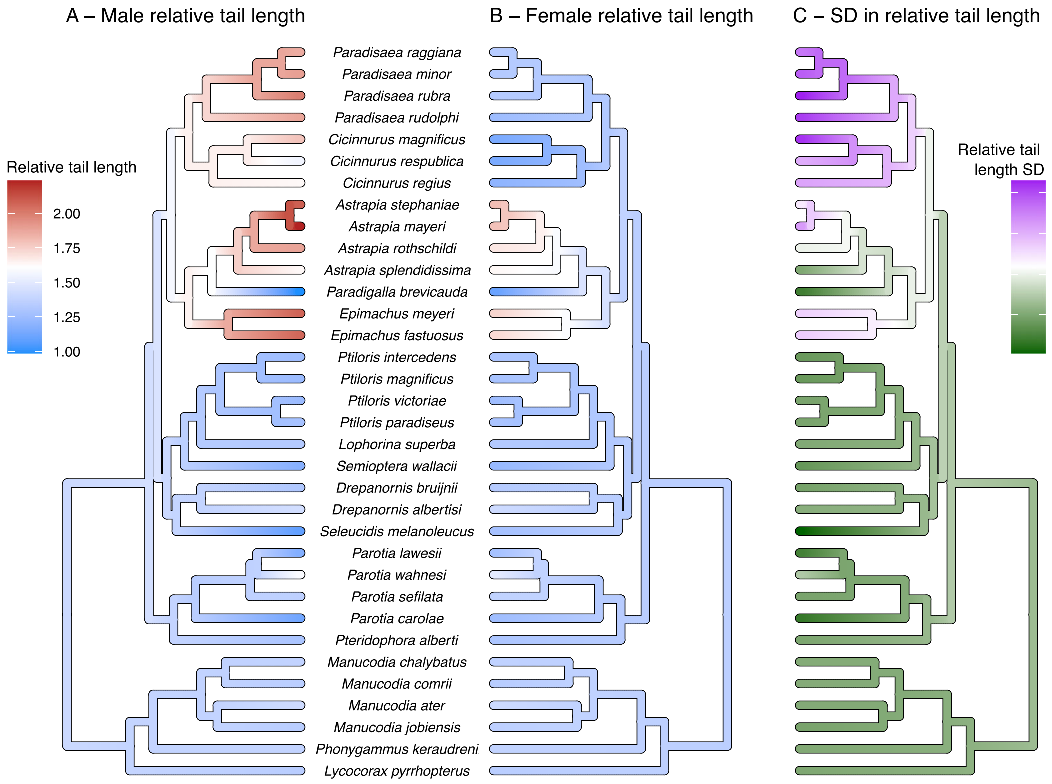

Figure 3. A complex pattern of relative tail length among male and female birds-of-paradise. Ancestral reconstructions suggest that both relative tail length (A, B) and relative tail length dimorphism (C) represent a more derived state in the bird-of-paradise radiation. Interestingly, species in the genera *Paradisaea* and *Cicinnurus* show high male, but not female relative tail lengths, resulting in extreme sexual dimorphism in this subclade (C). Trees show species for which both tail length and body mass data were available for both sexes in our dataset ($n = 34$ species). The genera *Manucodia*, *Phonygammus*, and *Lycocorax* represent the basal, socially monogamous bird-of-paradise clade, while all other species form the polygynous core bird-of-paradise radiation (Irestedt et al., 2009).

that tail length does not follow Rensch's rule. However, relative tail length dimorphism was positively associated with relative male tail length ($\beta = 0.60$, $SE = 0.06$, $t = 9.43$, $p < .001$).

Allometric comparisons between sexes and tail length categories in birds-of-paradise

Linear models performed separately on species of the two phenotypic categories (i.e., "short-tailed" and "long-tailed") showed that, among short-tailed species, tail length increased significantly with body mass ($t = 4.42$, $p < .001$), with an estimated slope of 0.39 ($SE = 0.09$). No intercept difference was found between sexes ($t = -1.29$, $p = .204$, Figure 5A). Among long-tailed species, tail length increased significantly with body mass ($t = 5.14$, $p < .001$), with an estimated slope of 0.95 ($SE = 0.19$), and the intercept was significantly higher in males ($\beta = 0.34$, $SE = 0.08$, $t = 4.46$, $p < .001$, Figure 5B). Male and female residuals obtained from tail length ~ body mass phylogenetic regressions were positively associated ($\beta = 1.39$, $SE = 0.21$, $t = 6.61$, $p < .001$, Figure S2), suggesting a possible evolutionary correlation between male and female tail lengths. Sex-specific allometric comparisons between phenotypic categories showed that both males and females from long-tailed species exhibited steeper allometric slopes than males and females from short-tailed species, respectively (interaction term for male values: $t = -2.20$, $p = .035$; interaction term for female values: $t = -3.21$, $p = .003$).

Heterogeneity of evolutionary rates and correlations between tail elongation regimes

Finally, we tested for heterogeneity in the evolutionary rates and correlations in male and female relative tail lengths between two evolutionary regimes across the phylogeny. Species were assigned to these regimes based on male relative tail lengths (i.e., "long tail" and "short tail" categories). For the first regime we assumed a strong effect of sexual selection on male tail lengths, while we assumed weak or no sexual selection for the second one. The weight of the evidence overwhelmingly supported models two (male and female relative tail lengths can have different evolutionary rates, but only a common correlation, between regimes; average AIC weight = 0.598) and four (male and female relative tail lengths can have different evolutionary rates and correlations between regimes; average AIC weight = 0.400) over the rest (Figure 6A, Table S2). The evolutionary rates of relative tail length differed between sexes and between regimes similarly under both models, following this order: rate of long-tailed males > rate of long-tailed females > rate of short-tailed males > rate of short-tailed females (Figure 6B and C, Table S2). Model 2 estimated a single evolutionary correlation of 0.87 between male and female relative tail

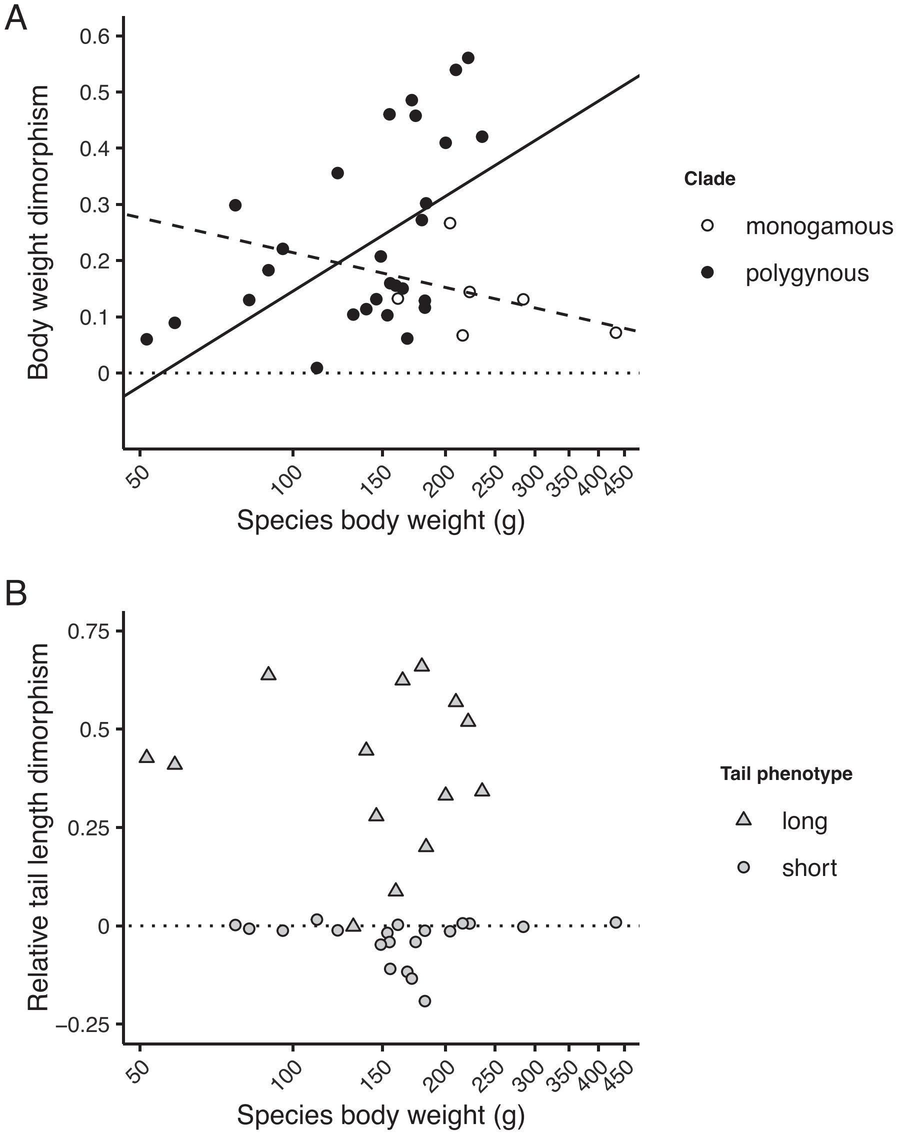

Figure 4. Rensch's rule and the evolution of tail length in the birds-of-paradise. (A) Rensch's rule was supported for body size in polygynous species (black points, solid line) but not in monogamous species (white points, dashed line; regression lines based on a PGLS model) (B). However, Rensch's rule was not met for tail length, though long-tailed species (triangles) exhibited an extreme degree of sexual dimorphism in relative tail length overall compared to short-tailed species (circles). Horizontal dotted lines in both panels indicate the absence of sexual dimorphism.

lengths for both regimes, while under model 4 the evolutionary correlation between sexes was stronger in the short-tail regime (0.90) than in the long-tail regime (0.80) (Figure 6D and E, Table S2).

Discussion

Birds-of-paradise, which are emblematic for their diverse, sexually selected plumage ornaments, exhibit some of the most diverse tail morphologies of any known bird clade. The elongate tails of some species have previously been examined intraspecifically and discussed in reference to display behavior (e.g., Frith, 1976; Scholes et al., 2017b), but macroevolutionary patterns of allometry in this trait have never been explicitly studied. Through phylogenetic comparative analyses, we estimated the evolutionary history of relative tail length in the birds-of-paradise, explored allometric patterns of sexual dimorphism in size and tail length, and estimated evolutionary rates and correlations between male and female traits.

Body size follows Rensch's rule in polygynous birds-of-paradise

In line with our predictions, body size in the core birds-of-paradise, all of which are considered to be polygynous, followed Rensch's rule. In contrast, we find no evidence of this pattern in the basal, monogamous species. However, since there are few extant socially monogamous bird-of-paradise species, this result remains suggestive (Figure 4A). Nonetheless, our findings align with a well-established pattern where Rensch's rule emerges in taxa experiencing strong sexual selection, but not in, for instance, socially monogamous species where sexual competition is comparably weak (Gaulin &

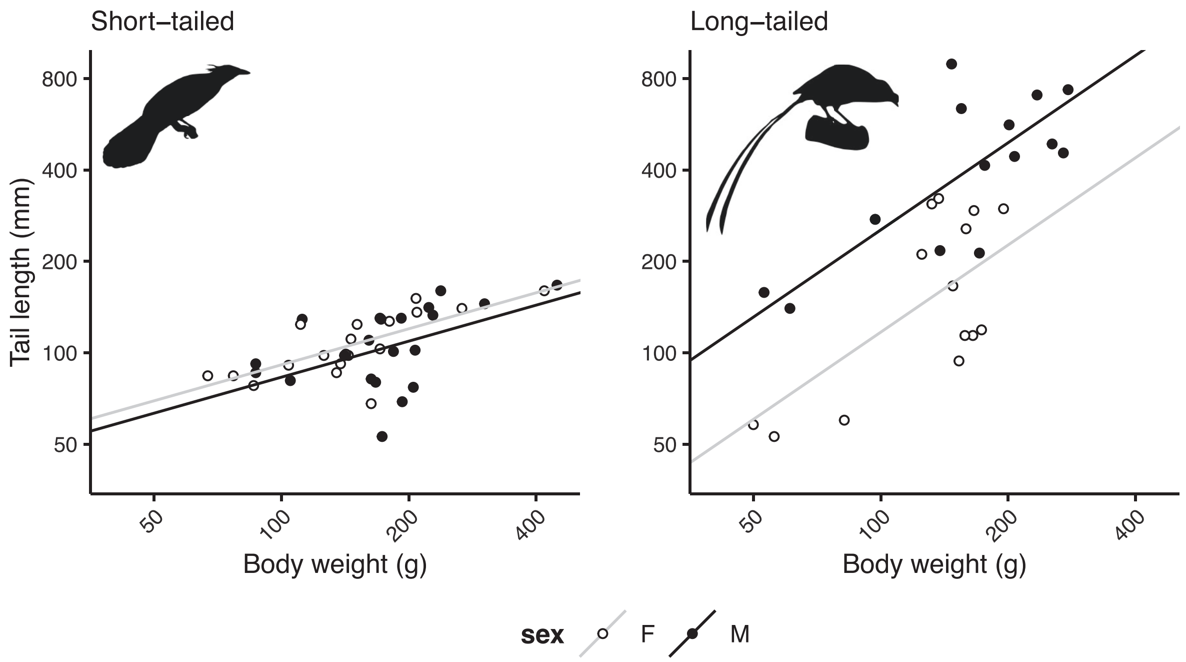

Figure 5. Evolutionary allometries of male and female tail length among birds-of-paradise with different relative tail lengths. Left and right panels show data for species with relatively short male tails and relatively long male tails, respectively. Axes are plotted on a $\log_{10}$ scale. Black and gray lines represent linear models relating tail length and body mass for males and females, respectively. Silhouettes were obtained from phylopic.org under a Creative Commons license.

Sailer, 1984; Székely et al., 2004). It is not clear why higher levels of SSD are more likely to be observed among larger species in so many taxa, although several hypotheses have been suggested. One explanation is that direct selection on male body size followed by indirect correlated selection on female size (e.g., due to shared developmental mechanisms or shared ecology) can drive patterns of interspecific allometry (De Lisle & Rowe, 2013; Zeng, 1988b), including Rensch's rule.

On the other hand, other models suggest that sexual differences in selection are not necessary for the evolution of Rensch's rule if the genetic variance in female body size is lower than in males (Leutenegger & Cheverud, 1982, 1985). Nonetheless, different studies have demonstrated a common association between the emergence of Rensch's rule in body size and the intensity and form of sexual selection (Dale et al., 2007; Serrano-Meneses et al., 2008; Székely et al., 2004), possibly due to the positive relationship between body size and competitive performance (e.g., Charlton et al., 2007; Turner, 1994). Male birds-of-paradise are well known for their elaborate sexual ornaments and courtship "dances," which evolved under intense female choice and intrasexual competition (Frith & Beehler, 1998; Pruett-Jones & Pruett-Jones, 1990). Given the importance of tail length for courtship displays in numerous bird-of-paradise species, larger sizes might enhance the efficacy of sexual signaling through the absolute elongation of tails in males, driving a Rensch's rule pattern in body size.

Tail length does not follow Rensch's rule in birds-of-paradise

Our test of Rensch's rule for tail length—a male-biased secondary sexual trait in birds-of-paradise—indicated that males from larger species do not show relatively longer tails than females given their size differences (Figure 4B). Since the emergence of Rensch's rule in a particular body part relies on a steeper evolutionary allometry of the male phenotype compared to that of females, this result seems to suggest that the evolutionary elaboration of the tail in males is constrained by some upper limit (e.g., ecological or energetic constraints). This scenario would indicate that the evolution of an overall large body size is the main way in which the absolute length of the ornamental tail can be increased (i.e., as male body size and SSD increase, the length of the tail becomes absolutely longer in males when compared to females, but not relatively longer) (Toyama, 2025; Toyama et al., 2025). However, our examination of the evolutionary allometries of males and females suggests a different explanation.

Among short-tailed species, on whose tails sexual selection likely does not act as intensely, both male and female tail length scale with body mass with an average exponent of 0.39 (Figure 5A), close to the isometric expectation of 0.33, which is often shown in different body parts in birds (Schmidt-Nielsen, 1984). In contrast, both males and females of long-tailed species showed an average allometric exponent of 0.95 (Figure 5B). This suggests that the absence of Rensch's rule in tail length is not an indicator of constraints in the evolution of exaggerated tail lengths in males of large species. Instead, these findings provide evidence that evolutionary correlations between sexes can result in the evolution of similar evolutionary allometric patterns between male and female traits, even if sexual selection acts primarily on males.

Despite the absence of Rensch's rule in tail length, relative tail length dimorphism was much higher in long-tailed species than in short-tailed ones (Figure 4B). This relative dimorphism arises due to differences in the allo-

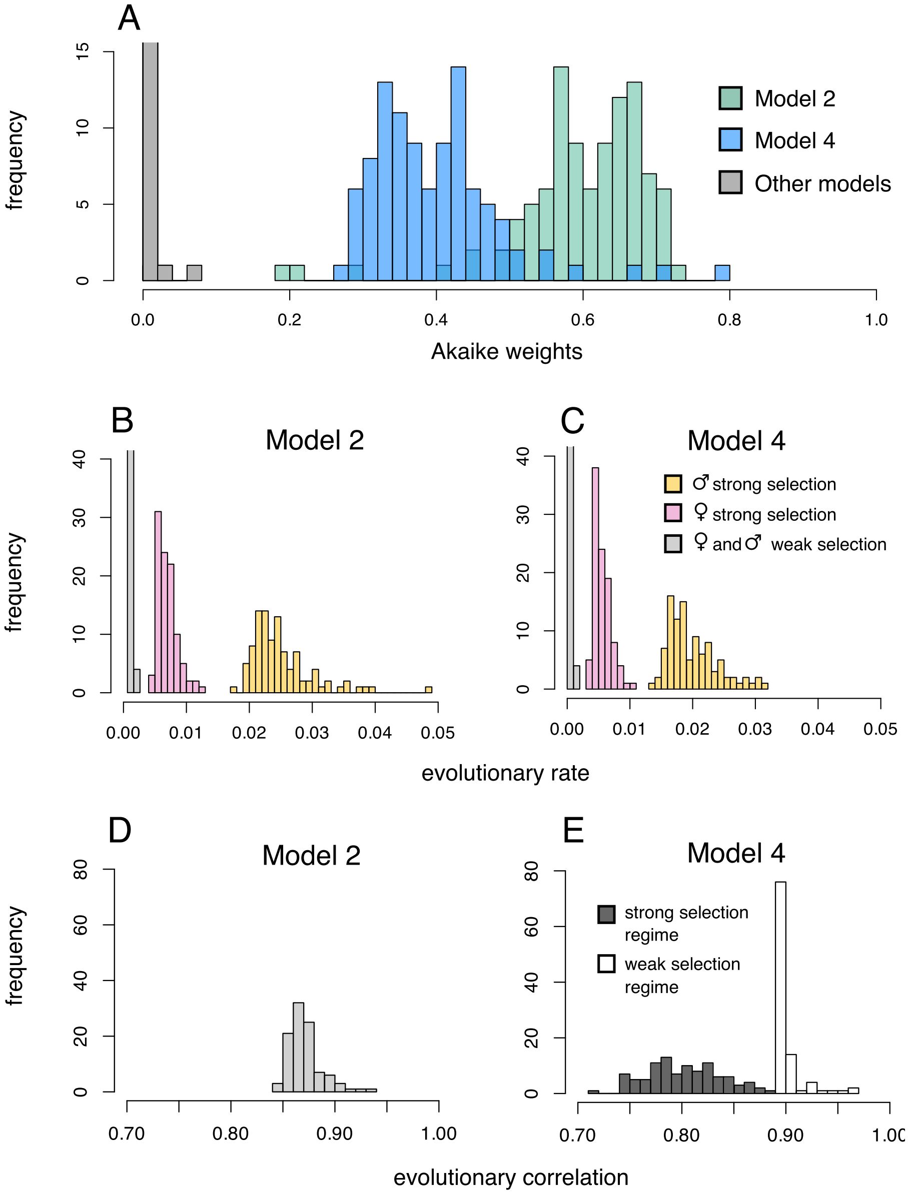

Figure 6. Best supported hierarchical models for evolutionary rates and correlations between male and female relative tail lengths for "long-tailed" and "short-tailed" evolutionary regimes. (A) Models 2 (male and female relative tail length can show different evolutionary rates in each regime, but evolutionary correlation between both traits is the same between regimes) and 4 (similar to 2, but evolutionary correlation between male and female traits can differ between regimes) were the best supported hierarchical models after 100 iterations, with ~60 and ~40% support each, respectively, based on Akaike weights. Other models had negligible support (full bin height is not shown). (B) and (C) show the distribution of evolutionary rate values after 100 iterations for male and female relative tail length under each evolutionary regime following models 2 and 4, respectively. In both cases evolutionary rates are higher in the "long-tailed" (strong sexual selection) regime, with male rates being higher than female rates. Male and female rates from the "short-tailed" (weak sexual selection) regime were comparatively low and were merged together in these panels (full bin height not shown). (D) and (E) show the distribution of evolutionary correlations between male and female relative tail lengths following models 2 and 4, respectively. Model 2 assumes there is a single correlation for both evolutionary regimes. The mean correlation for this model was found to be 0.87. Model 4 assumes different correlations for different regimes. The mean correlation values for the strong and weak selection regimes were 0.80 and 0.90, respectively.

metric intercepts of males and females from long-tailed species (Figure 5B). Positive allometry in males relative to females is often invoked to explain patterns of sexual dimorphism (Rensch, 1950; Vitt & Cooper, 1985; Voje, 2016). Nonetheless, sexual dimorphism can also emerge through evolutionary shifts in the allometric intercept (Bonduriansky, 2007), which our results suggest to be the case for birds-of-paradise.

Evolutionary rates and correlations in the tail length of birds-of-paradise

Hierarchical models shed additional light on the possible processes shaping the evolution of the tail phenotypes among birds-of-paradise. First, the two models with the highest support indicated that both male and female relative tail lengths have been evolutionarily labile across time, evolving at different rates depending on the sexual selection regime (here represented by the relative length of male tails) experienced by different clades. Second, as expected under a sexual selection hypothesis, the evolutionary rates of relative tail length in males were higher than that of females in each evolutionary regime (Figure 6B and C; Table S2). Interestingly, however, the evolutionary rates of females in the "long-tail" regime were higher than the rates of both males and females in the "short-tail" regime, indicative of rapid evolution of female tail length (Figure 6B and C). This result is concordant with the absence of a Rensch's rule pattern in tail length: the high evolutionary rate found in the female trait—possibly an indirect consequence of selection acting on males in the "long-tail" regime—has hindered the evolution of different allometric slopes between sexes, preventing the emergence of Rensch's rule (Figure 4B). We cannot reach a conclusion regarding evolutionary correlations based on the best-fitting models; however, when allowed to differ among regimes, the evolutionary correlation between male and female relative tail lengths was stronger in the "short-tailed" regime, as expected (Figure 6E). In any case, the inferred evolutionary correlations were strong, supporting the similar evolutionary allometries found for male and female tail lengths.

Recent research has pointed out how the loss or conservation of secondary sexual traits in females can drive macroevolutionary patterns of dimorphism. For example, the loss of costly pigments in the dewlap of female anoles, likely initially acquired through genetic correlation from males, is thought to have a role in defining large-scale patterns of sexual dichromatism (Westeen et al., 2025). Similarly, our results further suggest that the intricacies of phenotypic correlation between sexes, resulting in indistinguishable slopes but much different intercepts between male and female traits in birds-of-paradise, highlight the importance of the evolutionary processes experienced by females in shaping macroevolutionary patterns of dimorphism even under sexual selection scenarios.

Why do relatively longer tails evolve in the largest species?

Strong positive allometry in long-tailed species suggests a link between body size and the possibility of evolving disproportionately longer tails. While larger species could be more vulnerable to predation by raptors compared to smaller, more agile ones, predation of adult male birds-of-paradise is likely to be extremely rare (Frith & Beehler, 1998; Gilliard, 1969; TM, *personal observation*). This implies that exaggerated plumage ornaments might incur little cost, in the form of reduced aerodynamic performance required to escape predators, relative to their reproductive benefits.

Aerodynamic models of bird tails suggest that elongated tails with shallow fork morphologies—such as those seen in swallows (Hirudinidae)—are optimal for flight performance when spread, show little sexual dimorphism, and therefore suggest that natural selection can explain tail elongation in certain cases (see Balmford et al., 1993). This is because tails generate lift proportionally to the square of their maximal continuous span, with any area extending behind this span contributing primarily to drag during flight. In contrast, long, graduated tails—such as those seen in some birds-of-paradise (e.g., astrapias and sicklebills)—exhibit considerably more drag relative to lift, and are therefore likely to be highly aerodynamically costly. The costs of such long tails, however, would be relatively low in male birds-of-paradise compared to the reproductive benefits they confer, in part due to a low predation pressure.

An explanation for the evolution of disproportionately long tails in birds-of-paradise might also have a physiological component. Although metabolic rates tend to scale hypometrically with body size (Somjee et al., 2021), the metabolic costs of feather production in birds have also been found to decrease with both increasing body size and decreasing basal metabolic rate (Lindström et al., 1993). Thus, the development of increasingly exaggerated tail lengths in increasingly larger species would not be as energetically expensive as expected. This may also explain why birds-of-paradise exhibit such extreme plumage ornaments among polygynous passeriformes more broadly, as the large body sizes of most birds-of-paradise may be associated with disproportionately low costs in plumage elaboration. Overall, it seems plausible that a combination of reduced metabolic costs, absence of performance constraints, and a low predation risk has allowed the evolution of exaggerated tails in the birds-of-paradise, especially in males.

Strong positive allometry among long-tailed species contrasts with patterns of intraspecific allometry in wing length in some bird-of-paradise species: riflebirds (gen. *Ptiloris*) exhibit extremely male-biased dimorphism in relative wing length, potentially because the wings have evolved a prominent sexual signaling function (MacGillavry et al., 2024). However, despite this male-biased dimorphism, the allometric slopes of males in two species are much flatter than in females, potentially resulting from biomechanical or ecological constraints. Alternatively, signal functions executed by the wings could exhibit a threshold effect (i.e., the presence rather than magnitude of large, modified wings guarantees efficacy) instead of tuning exponential scaling in sensory processing (Kelley & Endler, 2012; Kodric-Brown et al., 2006). Since costs and constraints could vary substantially between traits, drivers of both inter- and intraspecific allometry likely depend on which trait is co-opted for sexual signaling (e.g., tails or wings) and what the precise signaling functions of those traits are. Intraspecific allometry has recently been shown to be linked to evolutionary allometry in the context of Rensch's rule (Reyes-Puig et al., 2023); thus, future studies might shed light on how counterintuitive intraspecific patterns like the one observed in riflebirds relate to allometric patterns of dimorphism at the macroevolutionary scale.

Conclusion

Birds-of-paradise follow previously described patterns in which the emergence of Rensch's rule in body size is associated with sexual selection. We also showed how the lack of Rensch's rule in tail length among birds-of-paradise is a consequence of similar evolutionary allometries between males and females, although both males and females from long-tailed species clearly showed much steeper allometries than short-tailed species, possibly due to direct selection for tail elongation in long-tailed males and indirect selection in females. These results were supported by the estimation of rates of phenotypic evolution in relative tail lengths between selective regimes ("short tailed" vs. "long tailed") across the phylogeny. Together, these results suggest that both larger body sizes and relatively longer tails contribute independently to the enhancement of competitive abilities in males in birds-of-paradise. Overall, these results represent the first integrative test of Rensch's rule that includes the evaluation of the pattern in body size as well as in a sexually-selected ornament. Further studies aiming to test for allometry in sexual dimorphism might benefit from taking different perspectives, including the (i) investigation of dimorphism in overall size and (ii) individual traits, as well as (iii) the examination of sex-specific allometries.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

All code and data required to replicate this study are available on GitHub (https://github.com/ThomasMac1998/MacGillavry.Toyama.Fusani_Rensch). They have also been archived on Open Science Framework at https://doi.org/10.17605/OSF.IO/H3TF2

Author contributions

T.M. and K.S.T. designed the study. T.M. and K.S.T. performed the analyses. T.M. and K.S.T. wrote the manuscript with input from L.F. All authors reviewed, edited, and approved the manuscript.

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Conflict of interest

The authors declare no conflict of interest.

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