

**Sexual selection drives rates of skeletal morphology between sexually dimorphic
passerine lineages**

by
Madisyn T. Guza

A thesis submitted in partial fulfillment of the requirements for the degree of Master of
Science / Ecosystem Science and Management (Environment and Sustainability) in the
University of Michigan 2026

Thesis committee:

Associate Professor Dr. Brian Weeks, Chair

Associate Professor Dr. Karen Alofs

Acknowledgements

Thank you to Dr. Brian Weeks for his encouragement, positivity, and patience throughout this process. A particular thanks goes to Dr. Jacob Berv for his countless hours of support, positivity, and enthusiasm. Thanks to the Weeks Lab: Dr. Hengxing Zou, Dr. Tiffany Dias, Charlotte Probst, Isaiah Clark, and Mark Ziebell, for general support throughout.

Table of Contents

Contents

Acknowledgements	ii
Table of Contents	iii
Abstract	iv
Introduction	5
Methods	8
<i>Trait Datasets</i>	8
<i>Indices of sexual dimorphism</i>	10
<i>Phylogenetic Comparative Analyses</i>	11
Results	14
<i>Dataset filtering</i>	14
<i>Phylogenetic Comparative Analyses: Models of Character Evolution</i>	14
<i>Phylogenetic Comparative Analyses: Stochastic Character Mapping</i>	15
<i>Phylogenetic Comparative Analyses: Multivariate GLS</i>	16
<i>Phylogenetic Comparative Analyses: State-Dependent Evolutionary Rates</i>	17
<i>Relationship between SSD and Sexual Dichromatism</i>	18
Discussion	18
Conclusions	21
Figures	23
Tables	27
References	34
Appendix	44

Abstract

Sexual selection has been hypothesized to drive phenotypic divergence, speciation, and diversification in birds. However, the link between sexual selection and morphological evolution remains poorly understood. Using comparative phylogenetic methods and a multivariate dataset of 12 skeletal measurements across more than 1,000 species of passerine birds, we characterize the morphospace occupied by sexually dimorphic and monomorphic lineages, reconstruct evolutionary transitions between dimorphism and monomorphism, and quantify the relationship between sexual size dimorphism and sexual dichromatism and rates of phenotypic evolution. We find that sexually dichromatic lineages occupy a different skeletal shape and size, or morphospace, than sexually monomorphic lineages. Lineages with sexual size dimorphism based on mass occupy a different skeletal morphospace than monomorphic lineages, though lineages with sexual size dimorphism based on skeletal size share a similar skeletal morphospace with monomorphic lineages. Additionally, consistent with other studies on sexual dichromatism, we find that transitions from sexual dimorphism to monomorphism have been more frequent than vice versa throughout the history of passerines. Finally, we find broad support for an association between sexual dimorphism and elevated rates of morphological evolution, with sexually dimorphic lineages evolving at rates that are 6% - 58% faster than rates of evolution in sexually monomorphic lineages. Given a broad correlation between sexual dimorphism and sexual selection, these results suggest that sexual selection has driven rapid morphological change in passerine birds.

Introduction

Darwin postulated that natural and sexual selection are core evolutionary processes driving behavioral and morphological variation across the tree of life (Darwin, 1859/2009, 1871/1981). Natural selection optimizes traits related to survival, while sexual selection influences traits associated with increased reproductive success (Darwin, 1859/2009). The interactions between these processes may be complex, with natural selection constraining sexual selection (Chenoweth et al., 2008; Darwin, 1871/1981; Endler, 1978; Lande, 1980), natural selection driving sexual selection through honest signaling (Cooney et al., 2019; Hill, 1991; Számadó et al., 2026) (i.e., the handicap hypothesis (Andersson, 1982; Grafen, 1990; Zahavi, 1975), or runaway sexual selection leading to exaggeration of sexual traits through linked genomic bases for preference and traits (Fisher, 1930; Henshaw & Jones, 2020; Prum, 2010). Given these dynamics, sexual selection may lead to rapid morphological evolution as a result of strong directional selection on specific traits (De Lisle et al., 2025; Gordon et al., 2015; Hoekstra et al., 2001; Prum, 2017), but it might also lead to stabilizing selection (Brooks et al., 2005; De Lisle et al., 2025; Punzalan & Rowe, 2016; Singh & Price, 2024) and reduced genetic variation (Singh & Price, 2024), potentially slowing evolution over longer timescales (Irestedt et al., 2009; Punzalan & Rowe, 2016).

Sexual selection is often assessed indirectly using two forms of sexual dimorphism: sexual size dimorphism (SSD), in which there are differences in the size of a trait(s) between sexes, and sexual dichromatism, in which there is a difference in coloration between sexes. For example, *Ceratias holboelli* (Northern Giant Seadevil) is a deep-sea fish with extreme SSD, in which females are about 65 times the length of males and roughly half a million times their weight (Bertelsen, 1961; Pietsch, 1976). Sexual dimorphism can also be complex, changing over the course of an individual's lifetime. For example, the Indian rock agama (*Psammophilus dorsalis*) is always sexually dichromatic, but to different degrees depending on whether the males are in a neutral state, courting females, or in a state of heightened aggression (Batabyal et al., 2023). Further, multiple axes of sexual dimorphism may exist within a species. For example, highly modified feathers in some of the most remarkably

sexually dimorphic bird species in the world - birds of paradise - can be much longer in males than in females, while also occupying vastly different overall plumage coloration (Beehler, 1989). Thus, while sexual dimorphism is a key characteristic across the tree of life, its role in evolutionary dynamics is multifaceted.

SSD and sexual dichromatism are often studied independently, and researchers have proposed a variety of hypotheses to explain these phenomena. A recent synthesis of SSD literature (Caron & Pie, 2024) partitioned the hypotheses into those that are related to (1) sexual selection via male-to-male competition (Beltrán et al., 2022; Bravo et al., 2024; Shogren et al., 2022; Székely et al., 2007), (2) fecundity via female reproductive output (Han & Fu, 2013; Székely et al., 2007), (3) niche divergence for resource partitioning between sexes (Bravo et al., 2024; Székely et al., 2007), and (4) allometry via Rensch's rule, in which increasing body size corresponds to more extreme SSD in male-biased species, but SSD becomes less extreme in female-biased species (Caron & Pie, 2024; Székely et al., 2007). Other studies have focused on the roles of mating systems (Dunn et al., 2001) and parental care in SSD (Berv & Prum, 2014; Lislevand et al., 2009; Owens & Hartley, 1998). The mechanisms underlying sexual dichromatism also have many hypotheses. One hypothesis is that it follows Darwin's (1871/1981) idea of sexual selection through female choice, in which a female's preference for a male trait perpetuates that trait through higher reproductive success. Another hypothesis of sexual dichromatism is rooted in natural selection, which suggests that it enables females to blend into their environment while nesting (Badyaev & Hill, 2003), provides species recognition, or warns against predators (Wallace, 1889). Furthermore, the non-mating sensory system of females that is under natural selection pressure may separately drive their preference for corresponding traits in males, known as sensory bias (Fuller et al., 2005). Others found evidence for the combined forces of sexual and natural selection (Barber et al., 2026; Beltrán et al., 2022; Delhey et al., 2023; Dunn et al., 2015; Shultz & Burns, 2017), extra-pair paternity (Owens & Hartley, 1998; Valcu et al., 2023), and honest signals (Gray, 1996). Despite the potential differences between SSD and sexual dichromatism, both have been used as proxies of intraspecific sexual selection (Januario et al., 2025).

Sexual selection's role in driving phenotypic divergence, primarily due to its implications for speciation and ultimately, diversification, has received considerable attention. The same strong sexual selection that leads to sexual dimorphism is hypothesized to drive phenotypic divergence between populations, generating reproductive isolation that is also hypothesized to result in speciation and potentially higher rates of diversification. However, there has been mixed evidence at each of those steps, from sexual selection leading to phenotypic divergence (Cooney et al., 2018, 2019; Friis & Milá, 2020; Seddon et al., 2013), sexual selection directly or via divergence causing speciation (Cally et al., 2021; Cooney et al., 2017; Huang & Rabosky, 2014; Januario et al., 2025; Kraaijeveld et al., 2011; Morrow et al., 2003; Seddon et al., 2013), and increased rates of diversification (Cally et al., 2021; Cooney et al., 2017, 2018; Maia et al., 2013; Miller et al., 2021; Portik et al., 2019). While these downstream effects of sexual selection have been explored, the upstream mechanism that connects sexual dimorphism to phenotypic divergence has received little attention.

Studies that link sexual dimorphism to phenotypic evolution have primarily focused on single phenotypic traits rather than the body as a whole (Günay et al., 2025; Punzalan & Rowe, 2015; Taylor et al., 2017). In the studies that do take a multivariate approach, complexity is often reduced through principal component analysis to the first few principal components, largely due to methodological constraints that require univariate data for downstream analyses (Günay et al., 2025; Mills, 2008; Murphy, 2007; Shultz & Burns, 2017). However, this reduced dimensionality can obscure signals of important biological relationships in lower-variance traits and misrepresent high-variance signals for early rapid divergence (Uyeda et al., 2015).

Differences in traits between sexually dimorphic and monomorphic lineages have rarely been examined in the context of rates of phenotypic evolution. In one example, Price and Birch (1996) examined *transition rates* between sexual dichromatism and monochromatism across passerine bird lineages. They found that transition rates are fluid between states, with dichromatic states more likely to transition into monochromatic states (Price & Birch, 1996). However, the rates of evolution within each state remain under-

explored, though secondary sexual traits tend to have faster rates of divergence than non-sexual traits (Cuervo & Møller, 1999; Friis & Milá, 2020). Thus, despite past evaluations of critical aspects of rates of evolution tied to sexual dimorphism, there remains a gap in understanding how the rates of phenotypic evolution differ between dimorphic and monomorphic lineages.

Here, we used phylogenetic comparative methods to test whether SSD and sexual dichromatism, which we use as proxies of sexual selection, are associated with variation in the rate of skeletal evolution across Passerine birds. Passerines are among the most well-studied clades of vertebrates, with extensive trait datasets that can be used to understand dichromatism (Cooney et al., 2022) and morphological differences among species (Weeks et al., 2023, 2025). Within birds, Passeriformes comprise the most diverse avian order, with over 6,000 species and representing over 60% of extant bird species (Oliveros et al., 2019; Schmitt & Edwards, 2022). Our analyses focus on a recently published (Berv et al., in press; Weeks et al., 2023, 2025) multivariate dataset that includes measurements of 12 skeletal dimensions, as well as body mass estimates, across >1,000 species. We investigated three main hypotheses:

1. Rates of phenotypic evolution will be higher in dimorphic species than monomorphic species, as sexual selection can generate both sexual dimorphism and rapid trait evolution.
2. Sexually dimorphic species will occupy a different region of skeletal morphospace than sexually monomorphic species, represented by a shift in the mean position of the multivariate skeletal phenotype.
3. SSD and sexual dichromatism, both proxies for sexual selection, will be independent of each other, as the proposed mechanisms resulting in each are largely different.

Methods

Trait Datasets

Our study is based on a dataset of 2,057 species of passerine birds (Aves: Passeriformes) that includes length measurements for 12 skeletal elements across 14,419

voucher specimens (Weeks et al., 2023, 2025). These skeletal traits comprise linear measurements of major hindlimb (femur, tibiotarsus, tarsometatarsus), forelimb (humerus, ulna, radius, carpometacarpus, second digit first phalanx), and axial/cranial (keel, furcula, sclerotic ring diameter, skull–bill length) elements and capture overall body shape. In addition, we combined these data with body mass estimates from Berv et al. (in press), which rely on specimen-level body mass records and represent best linear unbiased predictions of species-mean body mass under a multivariate phylogenetic model of intra- and interspecific variation (Goolsby et al., 2017).

For downstream analyses, all code was carried out in R v4.3.3 (R Core Team, 2024), and we natural-log-transformed all skeletal data. We only retained specimens with sex recorded in voucher metadata obtained from VertNet (Constable et al., 2010). This reduced the dataset to 12,973 individuals. Next, we only retained species with at least 1 male and 1 female specimen; this resulted in a dataset of 1,158 species with a median of 3 males and 2 females per species. We tested the sensitivity of our results to higher intra-specific sampling thresholds by repeating all analyses using only species with at least 3 and at least 5 males and females within each species. We acknowledge that the minimum sample sizes within each sex per species are relatively small, but there is a trade-off between capturing taxonomic breadth and minimizing within-species sampling error. Notably, downstream analyses focus on sex-specific species-level mean estimates, which maintain higher accuracy at small sample sizes (e.g., ≥ 10 individuals), compared to intraspecific variance metrics in morphometric studies (Cardini et al., 2015; Cardini & Elton, 2007). While our minimum thresholds all fall below the 10 individuals tested in those studies, we use multiple thresholds, particularly at 3 and 5, to evaluate the robustness and consistency of patterns under more stringent sample sizes. It is also worth noting that later comparative analyses derive statistical power across hundreds of species, which helps reduce species-level estimation error, but does not necessarily mitigate the original bias introduced by lower sampling sizes within each sex per species.

Indices of sexual dimorphism

We quantified sexual size dimorphism separately for skeletal traits and body mass (Figure 4). For skeletal traits, we first calculated, for each individual, the arithmetic mean of the natural-log-transformed values of the 12 skeletal measurements as an index of multivariate skeletal size. Because this quantity is an arithmetic mean on the log scale, it is equivalent to the natural logarithm of the geometric mean of the original-scale measurements. This provides a simple, consistent measure of overall skeletal size across traits, while keeping male–female differences easy to interpret as proportional differences on the original scale. We then calculated a species-level skeletal sexual size dimorphism index (SSDI) as the difference between the mean male and mean female values of this individual-level multivariate log-size index.

For body mass, which is univariate, we calculated SSDI as the difference between the mean log-transformed male mass and the mean log-transformed female mass within each species. Thus, positive values of the SSDI indicate male-size bias, and negative values indicate female-size bias. Based on this metric, we excluded one extreme outlier from downstream analyses. This species, *Corvus corax*, had an SSDI value of 1.7073, indicating a 451% size difference between the males and a single female. This is likely a result of only 1 female specimen in our dataset, which had a mean skeletal log size of 2.52 (~12 mm), compared to 4.22 (~68 mm) for the males, suggesting the female was a juvenile mislabeled as an adult or that there was an error in data entry. For reference, the next highest difference between sexes had an SSDI value of 0.2384, a 27% difference in *Psaracolius viridis*. This also held for the mass dataset. *Corvus corax* had an SSDI value of 3.1365, a 2,202% difference in mass between sexes. Again, *Psaracolius viridis* had the next highest mass disparity with an SSDI value of 0.6805, a 97% difference in the sexes, which is biologically plausible.

We classified species as dimorphic when the SSDI for the species was greater than or equal to a threshold level of difference between the sexes. We explored thresholds of 5%, consistent with other studies (Cuervo & Møller, 1999; Hoglund, 1989), and 10%. To quantify dichromatism, we extracted previously published dichromatism values from Cooney et al.

(2022), considering species with dichromatism values equal to 0 to be monochromatic and all others as dichromatic. Because some species were female-biased (negative dichromatism values), we used the absolute values of the raw dichromatism dataset.

Phylogenetic Comparative Analyses

In our comparative analyses, we use the phylogenetic hypothesis of Passeriformes from Claramunt et al. (2025), with minor modifications described by Berv et al. (in press). The core of our analyses comprises alternative multivariate phylogenetic generalized least-squares (mvPGLS) models, implemented using the `mvglsl()` function in the R package `mvMORPH` v1.2.1 (Clavel et al., 2015, 2019). These form the basis of three primary analyses: (1) investigating whether dimorphism is associated with skeletal morphology, (2) evaluating the multivariate effect of dimorphism using phylogenetic MANOVA, and (3) estimating state-dependent evolutionary rates of skeletal morphology across simulated stochastic character maps. In addition to the mvPGLS models, we used discrete-character evolution models that estimate transition rates between dimorphism states, stochastic character maps that reconstruct the phylogenetic history of each state across passerine lineages, and phylogenetic linear regressions that assess the relationship between SSD and sexual dichromatism.

For each dataset and each dimorphism classification type, we first investigated whether there was evidence of an overall effect of dimorphism on body shape across the entire dataset, while accounting for phylogenetic relationships. For these initial models, we fit multivariate models of the general form $[Y] \sim \text{mass} + \text{dimorphism}$, where $[Y]$ is the full skeletal data matrix (log-mm), mass is the species-level mass estimate (log-grams), and dimorphism is a binary factor coded to reflect alternative classification schemes (above). We include log-body-mass as a covariate to account for phylogenetic variation in size, consistent with approximate isometric expectations for linear dimensions (Spence, 2009) and following the specific approach of Berv et al. (in press). We accounted for phylogenetic non-independence among species by modeling the residual covariance structure under a Brownian motion model of evolution (i.e., the ‘BM’ model in `mvglsl`, such that expected

covariance among species is proportional to shared evolutionary history). We used the standard likelihood optimization method (method = "LL"), and enabled error estimation (error = TRUE) to account for some tip-level measurement error (e.g., (Beaulieu & O'Meara, 2024; Clavel et al., 2019)).

We tested for an overall multivariate effect of dimorphism using phylogenetic MANOVA implemented with `manova.gls()` from `mvMORPH`, applied to fitted `mvGLS` models. Using Type III tests and Pillai's trace, we evaluated whether dimorphism explained significant multivariate variation in the skeletal data after accounting for log-body-mass and phylogenetic structure. In general, these models test whether the dimorphism factor term is associated with a shift in the multivariate mean skeletal phenotype. In this framework, dimorphism is modeled as a group-level effect on the multivariate mean, such that categories may differ in their position in morphospace independent of mass.

Next, to investigate whether our proxies of sexual selection may be more directly correlated with rates of phenotypic evolution, we modeled the evolution of body shape across simulated evolutionary histories for our classified states. While there is ongoing debate about the best ways to identify evolutionary correlations between categorical and continuous variables (e.g., (Boyko et al., 2023)), our approach seeks primarily to account for 1) uncertainty in the evolutionary history of our classified states, and 2) multivariate covariance structure across skeletal elements. Thus, subsequent analyses summarize `mvGLS` models fit across distributions of simulated evolutionary histories.

For each binary classification based on specimen body mass, skeletal morphology, or dichromatism, we first fit two alternative continuous-time Markov models of discrete-character evolution: an equal-rates model (ER), which constrains forward and reverse transitions to occur at the same rate, and an all-rates-different model (ARD), which estimates these transition rates independently. We fit these models using the `ace` function from the `ape` R package v5.8.1 (Paradis et al., 2004). We compared model fit using Akaike's Information Criterion (AIC), which balances fit and complexity (Akaike, 1974), and selected the preferred transition model based on the difference in AIC between the ARD and ER models.

To account for uncertainty in the evolutionary history of each discrete classification (SSDI or dichromatism), we generated stochastic character maps (SCM) that represent plausible histories of state change across the phylogeny. SCM reconstructs the probabilistic history of a discrete trait given a phylogeny, observed tip states, and a continuous-time Markov model of evolution (Huelsenbeck et al., 2003). Rather than relying on a single ancestral-state estimate, we sampled 1,800 mappings across each dataset (chosen based on maximum computing ability), drawing the number, timing, and placement of transitions along branches conditional on the fitted transition-rate matrix. We implemented this procedure using the stochastic mapping function, `make.simmap`, in the `phytools` package v2.4.4 (Revell, 2024), parameterized by the preferred ER or ARD model identified with `ace()`, and applying the root prior described by FitzJohn et al. (2009).

We then used these simulated character histories to estimate whether multivariate rates of skeletal evolution differ between states. For each stochastic character map, we fit a multivariate phylogenetic generalized least-squares model in `mvMORPH` using `mvgl`s under the ‘BMM’ model, allowing Brownian evolutionary rates to vary across discrete regimes defined by the mapped states. In this framework, lineages assigned to different states evolve under distinct multivariate rate parameters. We repeated this procedure across the full distribution of simulated maps and extracted the state-specific multivariate rate parameter from each fitted model. By summarizing these estimates across all simulated histories, we obtained distributions of state-dependent evolutionary rates that integrate both uncertainty in discrete character history and covariance among skeletal traits. To quantify the magnitude of the difference in the evolutionary rate between sexually dimorphic and monomorphic lineages, we calculated the fold change (F_c), which is the ratio of the dimorphic evolutionary rate to the monomorphic evolutionary rate. $F_c > 1$ indicates that dimorphic lineages evolve faster than monomorphic lineages, and $F_c < 1$ indicates the opposite.

Lastly, we explored whether there was any signal of a relationship between SSD and sexual dichromatism. To do this, we fit a phylogenetic linear regression model, using the `phylolm` package v2.6.5 (Ho & Ané, 2014), to predict species dichromatism as a function of

SSDI under Brownian motion ('BM'). We used 1,000 bootstrap replicates to generate 95% confidence intervals for relevant parameters.

Results

Dataset filtering

Across skeletal data and body mass, the number of sexually dimorphic and monomorphic species varied substantially (Table 1). Across the 5% and 10% SSDI thresholds, the 1, 3, and 5 males and females per species thresholds resulted in 1,158, 459, and 257 total species, respectively. Within the skeletal dataset, depending on the threshold of individuals per sex per species, the proportion of dimorphic species ranged from 1.5% to 23.5%. Specifically, within the 5% SSDI threshold models, there was a range in the proportion of dimorphic species from 13.2% to 23.5%, while the 10% SSDI threshold models ranged from 1.5% to 3.3% in the proportion of dimorphic species per model. On the other hand, when body mass was the basis of each SSDI model, the proportion of dimorphic species per model was larger overall compared to the skeletal models, ranging from 20.2% to 56.9%. Specifically, the 10% mass-based SSDI dataset contained fewer dimorphic species overall than the 5% mass-based SSDI threshold, ranging from 20.2% to 30.9%, compared to 44% to 56.9%.

By contrast, the dichromatism dataset, as mentioned in the methods section, was coded at the species-level (Cooney et al., 2022), so it ultimately had the highest overall sample sizes within monomorphic ($n = 1,098$, 60.3%) and dimorphic ($n = 724$, 39.7%) categories.

Phylogenetic Comparative Analyses: Models of Character Evolution

Our trait evolution models generally supported the ARD model over the ER model across body mass, skeletal morphology, and dichromatism datasets, with all models offering support for the ARD model (Table 2). According to the rule-of-thumb ΔAIC cutoffs established by Burnham & Anderson (2004), a $\Delta AIC \leq 2$ is considered substantial support for that model as a viable candidate, a ΔAIC between 4 and 7 offers “considerably less

support”, and a $\Delta AIC > 10$ indicates no support. Burnham and Anderson did not label the values between 2 and 4 (Burnham & Anderson, 2004). Still, they could reasonably be interpreted as an intermediate level of support, given the labels provided on either side of this range. The ARD model was well supported by the dichromatism dataset ($\Delta AIC_{ER} = 21.36$), the skeletal dataset at a 5% SSDI (ΔAIC_{ER} : 4.25 to 58.31), and the mass dataset at a 10% SSDI (ΔAIC_{ER} : 16.00 to 80.04). However, there were more mixed results in the mass dataset at a 5% SSDI and in the skeletal dataset at a 10% SSDI. The skeletal dataset at a 10% SSDI mostly supported the ARD model, in which the ΔAIC_{ER} for the 1 and 3 minimum threshold for each sex per species was greater than 4 (ΔAIC_{ER} : 41.27, 4.56, respectively), but at the 5 individual per sex per species threshold was just under 4 ($\Delta AIC_{ARD} = 3.91$), which lies in the gray area of potentially demonstrating intermediate support. However, the mass dataset at a 5% SSDI threshold generally showed stronger support for the ER model, as the ΔAIC_{ER} at the 3 and 5 minimum individuals per sex per species thresholds were both less than 2 (ΔAIC_{ARD} : 1.95, 1.62, respectively). The model with at least 1 male and 1 female per species provided substantial support for the ARD model ($\Delta AIC_{ER} = 16.22$). Critically, although the ER model was technically preferred over the ARD model in three cases, the ARD model still maintained intermediate to substantial support as well. In contrast, there were many cases where the ER model was well above the threshold of 10, which suggested no support for that model. Therefore, to maintain consistent model interpretation, all models were run on the ARD model for downstream analyses. All ancestral state reconstructions under the ARD model are provided in supplemental Figures S1-S13.

Phylogenetic Comparative Analyses: Stochastic Character Mapping

Across the ARD stochastic character maps, the likelihood of dimorphic lineages transitioning to a monomorphic state is generally higher than the likelihood of monomorphic species transitioning to a dimorphic state, consistent with other bird studies (Omland, 1997; Price & Birch, 1996) (Table 3). Additionally, the ratio of the transition rate from dimorphism to monomorphism to the reverse transition rate generally increased

across models, within each dataset, as the minimum number of individuals per sex per species became stricter. Notably, the skeletal dataset at a 10% SSDI threshold had a highly asymmetric rate compared to the other models, with transition rates from dimorphism to monomorphism ranging from 35 to 161 times higher than the rates at which monomorphic lineages become dimorphic. Furthermore, within the skeletal dataset at a 10% SSDI threshold, the highest ratio is found in the model with a minimum number of 3 individuals per sex per species. Across all other models, the asymmetry is more moderate. The skeletal dataset at a 5% SSDI threshold shows that dimorphic lineages are 3 to 5 times more likely to become monomorphic than vice versa. In the mass dataset, the only model that predicts monomorphic lineages are more likely to become dimorphic is the model based on a 5% SSDI threshold and a minimum of 1 individual per sex per species, in which the monomorphic lineages are 1.32 times more likely to become dimorphic than vice versa (transition rate of dimorphism to monomorphism/transition rate of monomorphism to dimorphism = 0.757). When the minimum is 3 and 5 individuals per sex per species in the mass dataset, the ratio is nearly 1 (Ratio = 1.029, 1.135). Within the mass dataset at a 10% SSDI threshold, the dimorphic lineages are 2 to 4 times more likely to become monomorphic than the other way around (Ratio = 2.246-4.015). The dichromatism model demonstrates that dimorphic lineages are nearly 3 times more likely to become monomorphic than monomorphic lineages transitioning to dimorphism (Ratio = 2.884; see Figures S14-S26).

Phylogenetic Comparative Analyses: Multivariate GLS

Overall, dimorphism had a weak predictive power for skeletal morphology across models (Table 4). Dimorphism never significantly predicted skeletal morphology in the skeletal dataset (Pillai < 0.069, $F < 1.53$, $p > 0.10$). In the mass dataset, dimorphism significantly predicted skeletal morphology in the 5% SSDI threshold at the 1 (Pillai = 0.023, $F = 2.23$, $p = 0.009$) and 3 (Pillai = 0.061, $F = 2.42$, $p = 0.005$) individuals per sex per species, and in the 10% SSDI threshold at the 3 individuals per sex per species (Pillai = 0.056, $F = 2.19$, $p = 0.012$). However, the effect sizes for dimorphism are small across those models:

roughly 2.3%, 6.1%, and 5.6%, respectively. Sexual dichromatism was also a significant predictor of skeletal morphology, explaining roughly 18% of skeletal variance (Pillai = 0.183, $F = 33.71$, $p < 2 \times 10^{-16}$). Mass was included as a covariate in this MANOVA, and across every model, it explained over 99% of the variance in skeletal variance (Pillai > 0.99, $F > 1.65 \times 10^5$, $p < 2 \times 10^{-16}$).

Phylogenetic Comparative Analyses: State-Dependent Evolutionary Rates

Nearly all models show a significant difference in evolutionary rates between the dimorphic and monomorphic lineages ($p < 0.0001$), and there is a general trend toward greater differences at increasingly strict thresholds (Table 5; see Table S1 in the Appendix for the mode version). Curiously, evolutionary rates within the monomorphic and dimorphic lineages tended to peak at the 3 male and 3 female minimum requirement per species, rather than at the threshold of 5. Sexually dimorphic lineages evolve between 6% ($F_c = 1.062$, log mean difference = 0.051) and 58% ($F_c = 1.576$, log mean difference = 0.341) faster than monomorphic lineages. A single model suggested that sexually dimorphic species evolve at a slower rate than monomorphic lineages in the mass dataset with a 10% SSDI threshold and a minimum threshold of 1 male and 1 female per species ($F_c = 0.949$, log mean difference = -0.06, $p < 0.0001$). There were also two models that did not demonstrate a significant difference in evolutionary rates between sexually dimorphic and monomorphic lineages in the skeletal and mass datasets at the 5% SSDI threshold when only 1 individual per sex per species was required. The skeletal dataset shows larger differences in magnitude in the evolutionary rate between dimorphic and monomorphic species than the mass dataset (Figure 1, Figure 2). The highest fold changes in the skeletal data reach up to 49% at the 5% SSDI threshold and 58% at the 10% threshold (Figure 1, Figure 2) compared to the highest fold changes in the mass dataset at 10% at the 5% SSDI threshold and 20% at the 10% SSDI threshold. Additionally, in the sexual dichromatism dataset, sexually dichromatic species evolve 30% faster ($F_c = 1.298$, log mean difference = 0.26, $p < 0.0001$) than monochromatic species (Figure 3). Notably, all significant rate differences remain

significant after Bonferroni correction for multiple testing at $\alpha = 0.05$ across 13 tests ($\alpha_{\text{corrected}} = 0.0038$).

Relationship between SSD and Sexual Dichromatism

Neither skeletal nor mass-based SSDI predicted sexual dichromatism (Table 6). All p-values were much greater than the alpha of 0.05 ($p > 0.10$), and the R^2 values were all less than 1%, ranging from 8.03×10^{-6} to 9.20×10^{-3} . This was also supported by the 95% bootstrap confidence intervals, all of which included 0, suggesting no relationship. The standard errors of the skeletal models were higher than the mass models, indicating relatively higher variance in the regression estimates.

Discussion

While sexual selection is broadly expected to influence the rates of morphological evolution, empirical assessment of this relationship has been limited. Here, we use sexual size dimorphism and sexual dichromatism as indices of sexual selection to test whether lineages that are sexually dimorphic have different rates of morphological evolution than sexually monomorphic lineages. Across most models, we find that the mean evolutionary rate of skeletal morphology was significantly higher within sexually size-dimorphic and sexually dichromatic species (Figures 1-3). Within this general trend, one model (the mass dataset at a 10% SSDI and 1 male and female threshold) showed that monomorphic lineages evolve faster than the dimorphic lineages ($F_c = 0.949$, mean diff = -0.06, $p < 0.0001$). We are cautious about interpreting this exception because the low sampling threshold (minimum 1 male and female) and the high rate of variability in mass may introduce significant sampling error. Broadly, we find that increasing sexual dimorphism is associated with higher rates of morphological evolution. This suggests that sexual selection is associated with greater rates of morphological evolution at the species level, as expected given the increased rates of intra-specific phenotypic divergence associated with sexual selection (Cooney et al., 2019; Friis & Milá, 2020; Seddon et al., 2013). This also suggests that the faster rate of evolution of secondary sexual traits (Cuervo & Møller, 1999) scales up

to the whole-phenome level, with the impact of sexual selection extending beyond the sexually selected traits into the overall rate of skeletal evolution.

While sexually dimorphic species evolve at faster rates than monomorphic species, the evidence that these lineages occupy different areas of skeletal morphospace was mixed. Dimorphism was only a significant predictor of skeletal morphology in a handful of models after controlling for mass. The sexual dichromatism dataset showed the largest statistical difference between sexually dimorphic and monomorphic lineages (Pillai = 0.183, $F = 33.71$, $p < 2 \times 10^{-16}$), while sexual size dimorphism results were less clear. The mass dataset showed a muddled signal, with half of the models finding that mass-based dimorphism detects differences in skeletal morphology between sexually dimorphic and monomorphic species. At the 5% SSDI threshold, with the minimum individuals per sex per species being 1 and 3, dimorphism significantly predicted skeletal morphology (Pillai = 0.023, $F = 2.23$, $p = 8.86 \times 10^{-3}$) (Pillai = 0.061, $F = 2.42$, $p = 4.81 \times 10^{-3}$). This was also true for the mass dataset at the 10% SSDI threshold with a minimum of 3 per sex per species (Pillai = 0.056, $F = 2.19$, $p = 1.16 \times 10^{-2}$). However, skeletal dimorphism was never a significant predictor of skeletal morphology after accounting for mass. This means that overall, skeletal-based sexually dimorphic species do not have a different skeletal body plan than their sexually monomorphic species counterparts. Additionally, there is a weak signal that sexually dimorphic species via mass occasionally have a different skeletal body plan than sexually monomorphic species. Finally, sexually dichromatic species follow a different body plan than sexually monochromatic species. This is particularly surprising since dichromatism is rooted in plumage rather than a metric of body size, suggesting that sexual dichromatism is associated with distinct skeletal morphology independent of size dimorphism. Because the phylogenetic MANOVA run in this study cannot identify which traits drive skeletal morphology differences between dichromatic and monochromatic lineages, future work should include a phylogenetic principal component analysis (pPCA) or univariate comparisons of specific skeletal traits to capture the morphological distinction between them.

There have not been many studies that directly connect SSD and sexual dichromatism. We hypothesized that SSD and sexual dichromatism are both proxies for sexual selection, but the dynamics of their relationship with sexual selection may vary. Despite our expectation that both indices reflect sexual selection, we find that there is no association between SSD and sexual dichromatism in our dataset. A study on parrots similarly found that SSD did not predict sexual dichromatism (Carballo et al., 2020). Overall, this may indicate that there is a true separation between these types of sexual dimorphism, meaning that if a species is sexually dimorphic in mass or skeletal structure, it is not necessarily sexually dichromatic as well, and vice versa. Owens and Hartley (1998) assessed the covariation between behavior and sexual dimorphism (SSD and sexual dichromatism) and discovered that SSD was associated with differences in social mating systems and parental care, while sexual dichromatism was associated with the frequency of fertilizations occurring outside of the traditionally understood bonded individuals for the respective mating system. Thus, our finding that SSD and sexual dichromatism may be influenced by different selection pressures, ultimately resulting in their morphological independence in our dataset, is not without precedent.

While transition rates between dimorphic states were not the focus of this study, it is noteworthy that stochastic character mapping across most models revealed a higher likelihood of dimorphic lineages transitioning to a monomorphic state than of monomorphic lineages transitioning to a dimorphic state. Our findings are consistent with studies of sexual dichromatism in non-passerine and passerine birds (Omland, 1997; Price & Birch, 1996). The ratio of the transition rate of dimorphism to monomorphism and the transition rate of monomorphism to dimorphism was greater than 1 for all datasets, except in the mass dataset at a 5% SSDI threshold, where only 1 individual per sex per species was required, with a ratio of 0.757. Furthermore, almost all models had ratios less than 5, yet the skeletal dataset at an SSDI threshold of 10% exhibited exceptionally large ratios across the sex thresholds of 1, 3, and 5: 35.1, 161, and 92.5. Curiously, unlike the other models, the ratio did not increase with threshold strictness; instead, it dipped back down when 5 males and females were required per sex per species. Therefore, the skeletal dataset at a 10%

SSDI clearly exhibits a particularly strong biological signal from the dimorphic species and warrants further investigation.

Our analysis has important limitations. There is a tradeoff between within-species sampling thresholds and the number of species included in each model. At the 1 minimum male and female threshold, the models included 1,158 species, but species with only a single representative of each sex introduce sampling error into the SSDI, potentially weakening downstream analyses. Additionally, increasingly strict thresholds reduced the number of species classified as dimorphic to less than 10 in two of the skeletal models. The importance of this trade-off is reflected in the increasing difference in morphological evolution rates between dimorphic and monomorphic species as the sampling threshold per species increases. Additionally, we classified species as monochromatic only when the sexes are exactly the same (i.e., they had a dichromatism value of 0, per Cooney et al. (2022)). However, values up to the absolute value of 1 could have been considered monochromatic, as Cooney et al. (2022) labeled them as weakly dichromatic. Therefore, future work should test the sensitivity of the dichromatism threshold, as with the skeletal and mass indices, and compare differences in morphospace and rates of morphological evolution across the different sexual dichromatism thresholds. Furthermore, understanding which traits in particular drive differences in skeletal morphology and rates of evolution between states of sexual dimorphism could reveal which traits, and which lineages, are under the highest selection pressure across passerines. Still, there is a clear trend: whether skeletal, mass, or dichromatism is the basis of sexual dimorphism, there is an association with morphological evolution, leading dimorphic lineages to evolve faster than monomorphic lineages in passerine birds.

Conclusions

This study provides evidence that sexual selection, as measured by SSD and sexual dichromatism, leaves a detectable signal on rates of skeletal evolution in passerine birds. While we found that SSD and sexual dichromatism operate independently in sexual selection, both are associated with skeletal morphology. Sexually dichromatic and mass-

based dimorphic lineages occupy a distinct skeletal morphospace compared with sexually monomorphic lineages. However, skeletally dimorphic lineages share a similar skeletal morphospace with monomorphic lineages. Additionally, similar to findings from other studies on sexual dichromatism, there is evidence that sexually dimorphic lineages transition to monomorphic lineages more frequently than monomorphic lineages transition to dimorphism, suggesting that dimorphism is more likely to be lost in passerine lineages. Finally, the skeletal morphology of sexually dimorphic lineages evolves faster than that of sexually monomorphic lineages, suggesting that sexual selection can drive rapid morphological change in passerine birds.

Figures

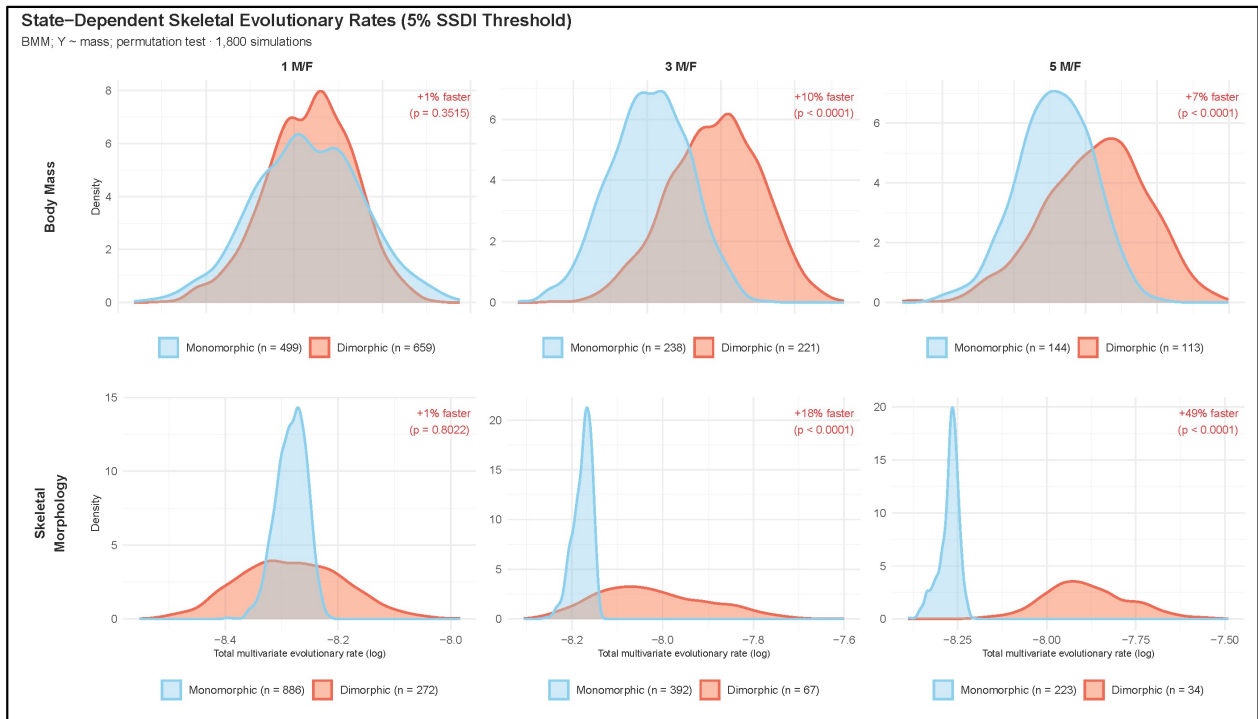


Figure 1. State-dependent skeletal evolutionary rates at a 5% SSDI threshold for sexually dimorphic and monomorphic passerine lineages. These density plots show the distribution of estimated rates of skeletal evolution across each of the 1,800 stochastic character map simulations across dimorphic and monomorphic lineages under a Brownian motion with multiple rates (BMM) model. Mass was included as a covariate. The top row shows body mass, and the bottom row shows skeletal morphology models across 1, 3, and 5 minimum numbers of individuals per sex per species. Blue indicates monomorphic lineages, and red indicates dimorphic lineages. The percent fold change (mean dimorphic rate/ mean monomorphic rate) was provided in red in the top right corners of each graph, as well as the permutation test p-value.

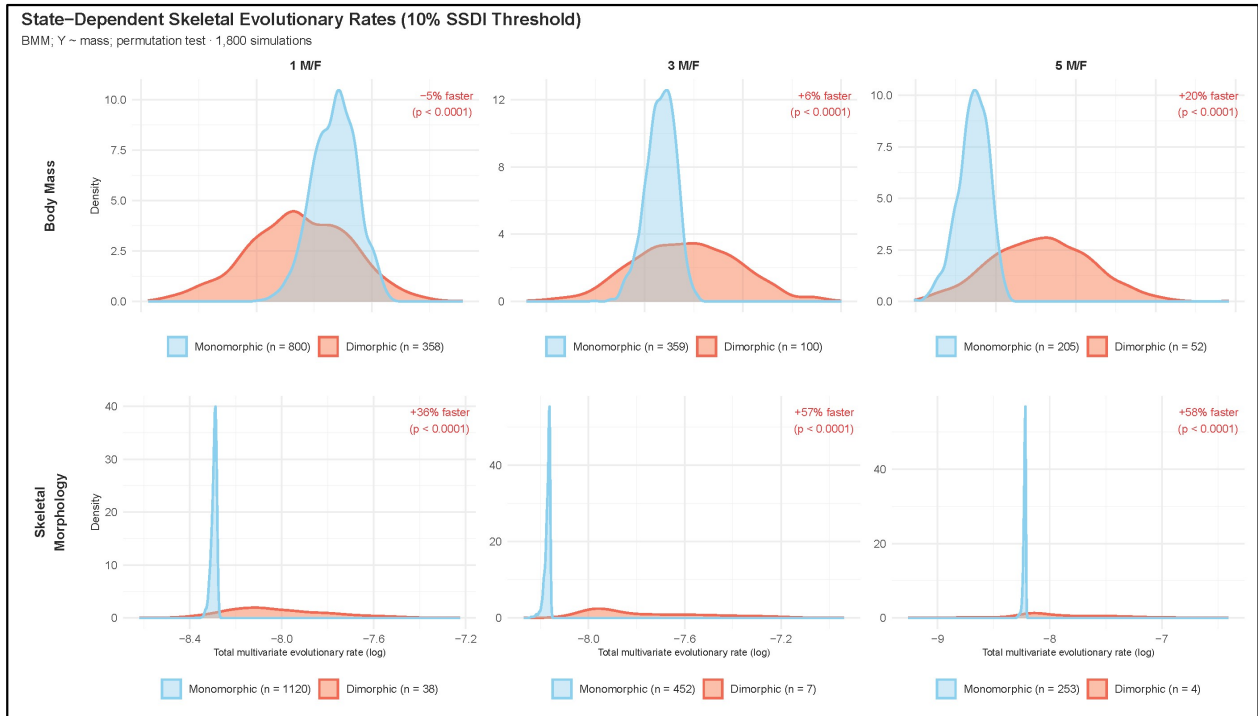


Figure 2. State-dependent skeletal evolutionary rates at a 10% SSDI threshold for sexually dimorphic and monomorphic passerine lineages. These density plots show the distribution of estimated rates of skeletal evolution across each of the 1,800 stochastic character map simulations across dimorphic and monomorphic lineages under a Brownian motion with multiple rates (BMM) model. Mass was included as a covariate. The top row shows body mass, and the bottom row shows skeletal morphology models across 1, 3, and 5 minimum numbers of individuals per sex per species. Blue indicates monomorphic lineages, and red indicates dimorphic lineages. The percent fold change (mean dimorphic rate/ mean monomorphic rate) was provided in red in the top right corners of each graph, as well as the permutation test p-value.

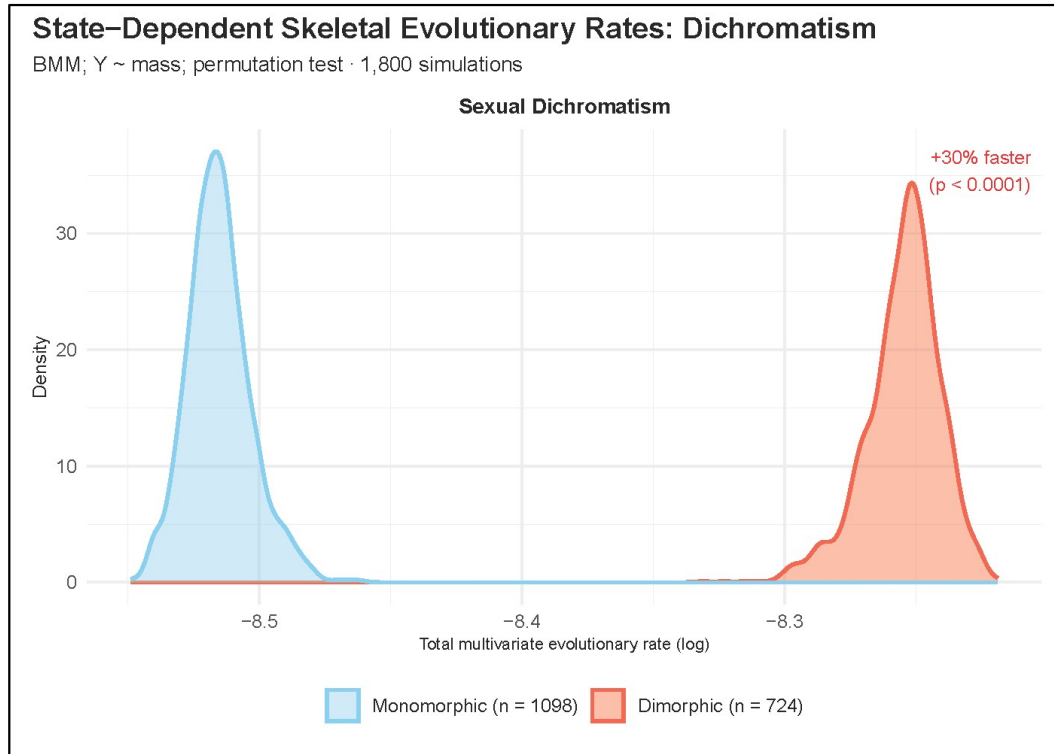


Figure 3. State-dependent skeletal evolutionary rates for sexually dichromatic and monochromatic passerine lineages. These density plots show the distribution of estimated rates of skeletal evolution across the 1,800 stochastic character map simulations across dichromatic and monochromatic lineages under a Brownian motion with multiple rates (BMM) model. Mass was included as a covariate. Blue indicates monochromatic lineages, and red indicates dichromatic lineages. The percent fold change (mean dichromatic rate/mean monochromatic rate) was provided in red in the top right corners of each graph, as well as the permutation test p-value.

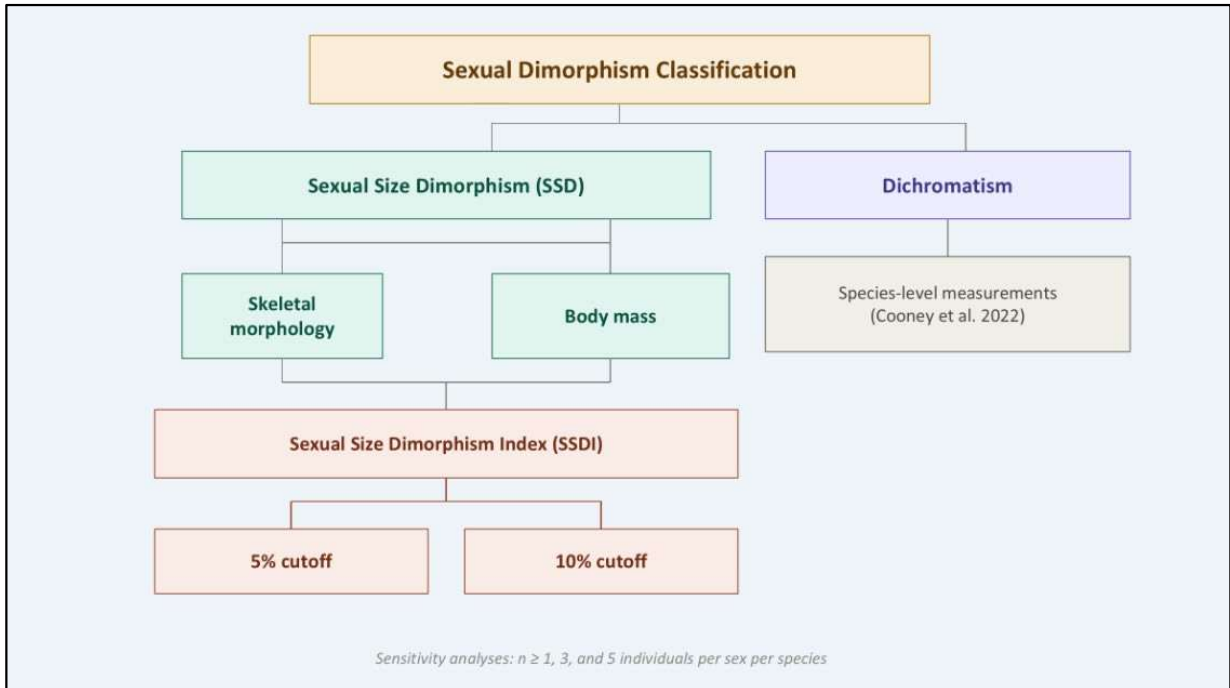


Figure 4. A schematic describing how the Sexual Size Dimorphism Index (SSDI) was created across each model to classify a species as sexually dimorphic or monomorphic. Sexual size dimorphism (SSD) and sexual dichromatism were proxies for sexual selection. Within sexual size dimorphism, skeletal morphology and body mass served as the basis for two distinct binaries at the individual-specimen level. The dichromatism data were at the species-level (Cooney et al. 2022). Under the SSD category, the SSDI was calculated across the 12 skeletal traits within each individual using the geometric mean, then averaged intrasexually within each species. The SSDI value per species was then calculated as the difference between the male and female means. Species were classified as either dimorphic or monomorphic when the SSDI value was at or greater than the 5% or 10% difference between the sexes. Sensitivity analyses were run at minimum thresholds of 1, 3, and 5 individuals per sex per species.

Tables

Species Classification by Dataset, SSDI, and Sex Thresholds					
Passerine birds across alternative dimorphism classification schemes					
Thresholds		Classification			
SSDI Threshold ¹	Sex Threshold	Total Species	Monomorphic (n)	Dimorphic (n)	% Dimorphic
Skeletal					
5%	1 M/F	1158	886	272	23.5
5%	3 M/F	459	392	67	14.6
5%	5 M/F	257	223	34	13.2
10%	1 M/F	1158	1120	38	3.3
10%	3 M/F	459	452	7	1.5
10%	5 M/F	257	253	4	1.6
Mass					
5%	1 M/F	1158	499	659	56.9
5%	3 M/F	459	238	221	48.1
5%	5 M/F	257	144	113	44.0
10%	1 M/F	1158	800	358	30.9
10%	3 M/F	459	359	100	21.8
10%	5 M/F	257	205	52	20.2
Dichromatism					
NA	NA	1822	1098	724	39.7
NA	NA	1822	1098	724	39.7
¹ Light shading = 5% SSDI threshold; dark shading = 10% SSDI threshold. Teal = Skeletal dataset; Orange = Mass dataset; Purple = Dichromatism dataset.					

Table 1. Species classification by dataset, SSDI threshold, and minimum sex thresholds per species across Passerines. The table is split between the skeletal (upper, teal) and mass (lower, orange) datasets. The SSDI Threshold is either set to 5% or 10%, corresponding to differences between sexes within species of natural-log-transformed data. Species were classified as “Dimorphic” when the SSDI value was greater than or equal to the SSDI threshold and classified as “Monomorphic” when less than the SSDI threshold. A minimum of 1, 3, or 5 individuals per sex per species was required, corresponding to decreases in the total number of available species in the datasets: 1,158, 459, and 257, respectively.

Model Selection: ARD vs. ER Ancestral State Reconstruction Across All Threshold Combinations				
Δ AIC calculated relative to best-fitting model (Δ AIC = 0 indicates preferred model)				
SSDI [†]	Sex	Δ AIC (ER)	Δ AIC (ARD)	Preferred Model
Skeletal				
5%	1 M/F	58.306	0.000	ARD
5%	3 M/F	8.001	0.000	ARD
5%	5 M/F	4.254	0.000	ARD
10%	1 M/F	41.268	0.000	ARD
10%	3 M/F	4.555	0.000	ARD
10%	5 M/F	0.000	3.913	ER
Mass				
5%	1 M/F	16.220	0.000	ARD
5%	3 M/F	0.000	1.946	ER
5%	5 M/F	0.000	1.615	ER
10%	1 M/F	80.041	0.000	ARD
10%	3 M/F	30.987	0.000	ARD
10%	5 M/F	16.004	0.000	ARD
Dichromatism				
NA	NA	21.360	0.000	ARD

[†] Teal = Skeletal; Orange = Mass; Purple = Dichromatism. Δ AIC values are calculated relative to the best-fitting model per row (Δ AIC = 0 indicates the preferred model). ARD allows separate rates for gaining and losing dimorphism; ER constrains forward and reverse rates to be equal.

Table 2. Maximum likelihood ancestral state reconstruction under an ER and ARD model.

The Δ AIC values are relative to the model; Δ AIC = 0 indicates the preferred model.

According to Burnham and Anderson (2004), a Δ AIC ≤ 2 suggests substantial support for the model, a Δ AIC between 4 and 7 suggests considerably less support, and a Δ AIC > 10 suggests no support. Δ AIC values between 2 and 4 were not provided an interpretation (Burnham and Anderson, 2004) but are interpreted as intermediate support here. SSDI refers to the sexual size dimorphism index, which has two possible thresholds: 5% and 10% differences between the sexes within a species. Within each SSDI threshold, there are also three minimum-individual thresholds per sex per species: 1, 3, and 5. Species under the skeletal and mass datasets were classified as dimorphic when the SSDI value was greater than or equal to the SSDI threshold and classified as monomorphic when less than the SSDI threshold. Under the dichromatism dataset, species were classified as monochromatic when their dichromatism value was exactly 0, and dichromatic when the absolute value of their dichromatism value was greater than 0.

Ancestral State Reconstruction Transition Rates Across All Threshold Combinations ARD model; stochastic character mapping								
SSDI [†]	Sex	Species				Transition rates (Q)		
		N	Mono	Dim	% Dim	Mono→Dim	Dim→Mono	Ratio
Skeletal								
5%	1 M/F	1158	886	272	23.5	0.04289	0.13071	3.048
5%	3 M/F	459	392	67	14.6	0.01463	0.06503	4.445
5%	5 M/F	257	223	34	13.2	0.01157	0.05569	4.813
10%	1 M/F	1158	1120	38	3.3	0.00586	0.20573	35.108
10%	3 M/F	459	452	7	1.5	0.00105	0.16900	160.952
10%	5 M/F	257	253	4	1.6	0.00196	0.18124	92.469
Mass								
5%	1 M/F	1158	499	659	56.9	0.18833	0.14264	0.757
5%	3 M/F	459	238	221	48.1	0.09914	0.10199	1.029
5%	5 M/F	257	144	113	44.0	0.06677	0.07576	1.135
10%	1 M/F	1158	800	358	30.9	0.11913	0.26752	2.246
10%	3 M/F	459	359	100	21.8	0.04468	0.16310	3.650
10%	5 M/F	257	205	52	20.2	0.03555	0.14273	4.015
Dichromatism								
NA	NA	1822	1098	724	39.7	0.01263	0.03643	2.884

[†] Teal = Skeletal; Orange = Mass; Purple = Dichromatism. Mono→Dim = rate of gaining dimorphism; Dim→Mono = rate of losing dimorphism Ratio = Dim→Mono / Mono→Dim; values > 1 indicate the state is lost faster than it is gained. Bold ratio values indicate strong asymmetry (ratio > 5). % Dim = percentage of species classified as dimorphic

Table 3. Ancestral state reconstruction transition rates across all datasets and thresholds in Passerine birds. Transition rates (Q) were estimated using a maximum-likelihood ARD stochastic character mapping model. Mono to Dim is the rate of transitioning from a monomorphic to a dimorphic state, while Dim to Mono is the reverse rate of transition. The ratio was calculated by dividing the rate of going from dimorphic to monomorphic by the rate of transitioning from monomorphic to dimorphic. A ratio greater than 1 indicates that there is a higher likelihood of a lineage transitioning from a dimorphic to monomorphic state. Values in bold in the ratio column indicate high asymmetry in the likelihood of one state transitioning to the other (Ratio > 5). SSDI refers to the sexual size dimorphism index, which has 2 possible thresholds: 5% and 10% differences between the sexes within a species. Within each SSDI threshold, there are also 3 thresholds for the minimum number of individuals per sex per species: 1, 3, and 5. Species under the skeletal and mass datasets were classified as dimorphic when the SSDI value was greater than or equal to the SSDI threshold and classified as monomorphic when less than the SSDI threshold. Under the dichromatism model, species were classified as monochromatic when their Dichro value was 0, and dichromatic when the absolute value of their Dichro value was positive.

Phylogenetic MANOVA Results Across All Threshold Combinations									
Pillai trace test; $Y \sim \text{mass} + \text{dimorphism}$; Brownian motion									
Thresholds		Species			Mass (covariate)			Dimorphism	
SSDI [†]	Sex	N	Mono	Dim	Pillai	F	p	Pillai	F p
Skeletal									
5%	1 M/F	1158	886	272	0.999965	2.75×10^6	<2e-16	0.006475	0.62 8.26e-01
5%	3 M/F	459	392	67	0.999924	4.86×10^3	<2e-16	0.019357	0.73 7.2e-01
5%	5 M/F	257	223	34	0.999878	1.65×10^5	<2e-16	0.036417	0.77 6.86e-01
10%	1 M/F	1158	1120	38	0.999965	2.76×10^6	<2e-16	0.015795	1.53 1.07e-01
10%	3 M/F	459	452	7	0.999924	4.87×10^3	<2e-16	0.020150	0.76 6.89e-01
10%	5 M/F	257	253	4	0.999878	1.65×10^5	<2e-16	0.069031	1.50 1.24e-01
Mass									
5%	1 M/F	1158	499	659	0.999966	2.76×10^6	<2e-16	0.022874	2.23 8.86e-03
5%	3 M/F	459	238	221	0.999925	4.96×10^3	<2e-16	0.061195	2.42 4.81e-03
5%	5 M/F	257	144	113	0.999879	1.68×10^5	<2e-16	0.035707	0.75 7.02e-01
10%	1 M/F	1158	800	358	0.999966	2.77×10^6	<2e-16	0.009143	0.88 5.67e-01
10%	3 M/F	459	359	100	0.999925	4.96×10^3	<2e-16	0.055664	2.19 1.16e-02
10%	5 M/F	257	205	52	0.999880	1.69×10^5	<2e-16	0.037018	0.78 6.72e-01
Dichromatism									
—	—	1822	1098	724	0.999975	6.05×10^6	<2e-16	0.182826	33.71 <2e-16

[†] Light shading = 5% SSDI threshold; dark shading = 10% SSDI threshold. Teal = Skeletal; Orange = Mass; Purple = Dichromatism. Bold p-values indicate significance at $\alpha = 0.05$.

Table 4. Phylogenetic MANOVA results across all datasets and thresholds across Passerines. The response variable (Y) is a matrix of 12 skeletal traits, and the two explanatory variables are mass and a binary metric of sexual dimorphism (mass + dimorphism), either for the skeletal or the mass dataset, or for sexual dichromatism. All models used multivariate GLS under Brownian motion. The table is split between the skeletal (upper, teal) and mass (middle, orange) datasets, and dichromatism (lower, purple). The SSDI threshold is either 5% or 10%, corresponding to differences between sexes within species of natural-log-transformed data. However, there is no SSDI threshold because it is a species-level metric. Species under the skeletal and mass models were classified as dimorphic when the SSDI value was greater than or equal to the SSDI threshold and classified as monomorphic when less than the SSDI threshold. Under the dichromatism model, species were classified as monochromatic when their Dichro value was 0, and dichromatic when the absolute value of their Dichro value was positive.

State-Dependent Evolutionary Rates Across All Threshold Combinations									
BMM; Y ~ mass; permutation test on mean log rate difference									
Species					BMM Rates (σ^2 / time)				
SSDI [†]	Sex	N	Mono	Dim	Rate (mono)	Rate (dim)	Fold change	Mean diff (log scale)	p
Skeletal									
5%	1 M/F	1158	886	272	2.53×10^{-4}	2.54×10^{-4}	1.008	0.001	0.8022
5%	3 M/F	459	392	67	2.81×10^{-4}	3.30×10^{-4}	1.179	0.154	< 0.0001
5%	5 M/F	257	223	34	2.55×10^{-4}	3.78×10^{-4}	1.486	0.386	< 0.0001
10%	1 M/F	1158	1120	38	2.50×10^{-4}	3.40×10^{-4}	1.364	0.281	< 0.0001
10%	3 M/F	459	452	7	2.83×10^{-4}	4.43×10^{-4}	1.570	0.413	< 0.0001
10%	5 M/F	257	253	4	2.68×10^{-4}	4.20×10^{-4}	1.576	0.341	< 0.0001
Mass									
5%	1 M/F	1158	499	659	2.53×10^{-4}	2.53×10^{-4}	1.008	0.002	0.3515
5%	3 M/F	459	238	221	2.76×10^{-4}	3.02×10^{-4}	1.100	0.088	< 0.0001
5%	5 M/F	257	144	113	2.64×10^{-4}	2.79×10^{-4}	1.067	0.057	< 0.0001
10%	1 M/F	1158	800	358	2.58×10^{-4}	2.43×10^{-4}	0.949	-0.060	< 0.0001
10%	3 M/F	459	359	100	2.84×10^{-4}	3.00×10^{-4}	1.062	0.051	< 0.0001
10%	5 M/F	257	205	52	2.60×10^{-4}	3.10×10^{-4}	1.202	0.171	< 0.0001
Dichromatism									
NA	NA	1822	1098	724	2.00×10^{-4}	2.60×10^{-4}	1.298	0.260	< 0.0001

[†] Teal = Skeletal; Orange = Mass; Purple = Dichromatism. Bold p-values indicate significance at $\alpha = 0.05$. Fold change = mean(dim rate / mono rate). Mean diff = mean difference in log-transformed rates (dim – mono). p = permutation test p-value (10,000 permutations); values of 0 displayed as < 0.0001. All models used 1,800 simulations.

Table 5. State-dependent multivariate evolutionary rates across all datasets and threshold combinations in Passerine birds. Evolutionary rates were estimated using Brownian motion multivariate models (BMMs) simulated with stochastic character maps. Each dataset ran 1,800 simulations each. All models ran with mass as a covariate for the 12 skeletal traits (Y ~ mass), with 2 possible underlying states: monomorphic (Mono) or dimorphic (Dim). Rate (mono) and Rate (dim) are the mean evolutionary rates, sigma squared per unit time, within each group, and Fold change is the mean of the dimorphic rate divided by the monomorphic rate. Mean diff (log scale) is the mean difference of the log-transformed evolutionary rates across all simulations. Positive values indicate faster dichromatic lineage evolution rates. The p refers to the p-value from the two-sided permutation test calculated across 10,000 permutations of the log rate differences. The table is split into 3 datasets: Skeletal (teal), Mass (orange), and Dichromatism (purple). SSDI refers to the sexual size dimorphism index, which has 2 possible thresholds: 5% and 10% differences between the sexes within a

species. Within each SSDI threshold, there are also 3 thresholds for the minimum number of individuals per sex per species: 1, 3, and 5. Species under the skeletal and mass datasets were classified as dimorphic when the SSDI value was greater than or equal to the SSDI threshold and classified as monomorphic when less than the SSDI threshold. Under the dichromatism model, species were classified as monochromatic when their Dichro value was 0, and dichromatic when the absolute value of their Dichro value was positive.

Phylogenetic Regression Between SSD and Sexual Dichromatism								
phylolm; abs(Dichro) ~ abs(SSDI_log); BM model; 1000 bootstrap replicates								
Sex Threshold [†]	N	Estimate	SE	t	Bootstrap CI		p	R ²
					Lower 95% CI	Upper 95% CI		
Skeletal								
3 M/F	432	−0.334	0.834	−0.401	−1.932	1.291	0.6888	3.73 × 10 ^{−4}
5 M/F	245	−1.759	1.171	−1.502	−4.153	0.541	0.1344	9.20 × 10 ^{−3}
Mass								
3 M/F	432	0.015	0.262	0.059	−0.541	0.554	0.9532	8.03 × 10 ^{−6}
5 M/F	245	0.047	0.400	0.117	−0.698	0.753	0.9069	5.64 × 10 ^{−5}
[†] Teal = Skeletal dataset; Orange = Mass dataset. Estimate = slope of abs(SSDI_log) predicting abs(Dichro) after controlling for phylogeny under Brownian motion. Bootstrap CIs based on 1000 replicates. Bold p-values indicate significance at α = 0.05.								

Table 6. Phylogenetic relationship between sexual size dimorphism and sexual dichromatism across Passerine birds. The response variable is the absolute value of the dichromatism (Dichro) scores from Cooney et al. 2022, and the explanatory variable is the absolute value of the log-transformed SSDI values. In the skeletal dataset, the SSDI_log was calculated as the difference in the geometric mean across skeletal traits within an individual, which was then averaged intrasexually across species. The same was done with the mass dataset, but only using the body mass. The models were fit using phylogenetic generalized least squares regression under a Brownian motion model across 1,000 bootstrap replicates. Sex threshold refers to the minimum number of individuals required per sex within a species. N is the number of species present in the skeletal, mass, and dichromatism datasets. The Estimate is the slope of the regression for the abs(SSDI_log) predicting abs(Dichro) when phylogenetic history is controlled. SE is the standard error, and t is the t-value, which is the Estimate/SE. The 1,000 bootstrap replicates have an upper and lower bound CI of 95%. All p-values are greater than an alpha of 0.05, and little variance in the abs(Dichro) values is explained by either skeletal or mass abs(SSDI_log), since the R² values are very small.

References

- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6), 716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- Andersson, M. (1982). Sexual selection, natural selection and quality advertisement. *Biological Journal of the Linnean Society*, 17(4), 375–393. <https://doi.org/10.1111/j.1095-8312.1982.tb02028.x>
- Badyaev, A. V., & Hill, G. E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 27–49. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132441>
- Barber, R., Yang, J., Marcondes, R., Brumfield, R., & Tobias, J. (2026). *Sex differences in avian plumage evolution: Stronger effects of natural selection and social competition on females*. Life Sciences. <https://doi.org/10.32942/X22Q1V>
- Batabyal, A., Zambre, A., McLaren, T., Rankin, K. J., & Stuart-Fox, D. (2023). The extent of rapid colour change in male agamid lizards is unrelated to overall sexual dichromatism. *Ecology and Evolution*, 13(7), e10293. <https://doi.org/10.1002/ece3.10293>
- Beaulieu, J. M., & O'Meara, B. C. (2024). *Navigating “tip fog”: Embracing uncertainty in tip measurements*. Evolutionary Biology. <https://doi.org/10.1101/2024.08.19.608647>
- Beehler, B. M. (1989). The birds of paradise. *Scientific American*, 261(6), 116–123. <https://www.jstor.org/stable/10.2307/24987520>
- Beltrán, D. F., Araya-Salas, M., Parra, J. L., Stiles, F. G., & Rico-Guevara, A. (2022). The evolution of sexually dimorphic traits in ecological gradients: An interplay between natural and sexual selection in hummingbirds. *Proceedings of the Royal Society B: Biological Sciences*, 289(1989), 20221783. <https://doi.org/10.1098/rspb.2022.1783>
- Bertelsen, E. (1961). *The ceratioid fishes: Ontogeny, taxonomy, distribution and biology* (Dana Reports No. 39). Brill. <https://doi.org/10.1163/9789004628465>
- Berv, J. S., & Prum, R. O. (2014). A comprehensive multilocus phylogeny of the Neotropical cotingas (Cotingidae, Aves) with a comparative evolutionary analysis of breeding system and plumage dimorphism and a revised phylogenetic classification.

- Molecular Phylogenetics and Evolution*, 81, 120–136.
<https://doi.org/10.1016/j.ympev.2014.09.001>
- Berv, J. S., Probst, C. M., Claramunt, S., Shipley, J. R., Friedman, M., Smith, S. A., Fouhey, D. F., & Weeks, B. C. (in press). Rates of passerine body plan evolution in time and space. *Nature Ecology & Evolution*.
- Boyko, J. D., O'Meara, B. C., & Beaulieu, J. M. (2023). A novel method for jointly modeling the evolution of discrete and continuous traits. *Evolution*, 77(3), 836–851.
<https://doi.org/10.1093/evolut/qpad002>
- Bravo, C., Bautista-Sopelana, L. M., & Alonso, J. C. (2024). Revisiting niche divergence hypothesis in sexually dimorphic birds: Is diet overlap correlated with sexual size dimorphism? *Journal of Animal Ecology*, 93(4), 460–474.
<https://doi.org/10.1111/1365-2656.14058>
- Brooks, R., Hunt, J., Blows, M. W., Smith, M. J., Bussière, L. F., & Jennions, M. D. (2005). Experimental evidence for multivariate stabilizing sexual selection. *Evolution*, 59(4), 871–880. <https://doi.org/10.1111/j.0014-3820.2005.tb01760.x>
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33(2), 261–304.
<https://doi.org/10.1177/0049124104268644>
- Cally, J. G., Stuart-Fox, D., Holman, L., Dale, J., & Medina, I. (2021). Male-biased sexual selection, but not sexual dichromatism, predicts speciation in birds. *Evolution*, 75(4), 931–944. <https://doi.org/10.1111/evo.14183>
- Carballo, L., Delhey, K., Valcu, M., & Kempenaers, B. (2020). Body size and climate as predictors of plumage colouration and sexual dichromatism in parrots. *Journal of Evolutionary Biology*, 33(11), 1543–1557. <https://doi.org/10.1111/jeb.13690>
- Cardini, A., & Elton, S. (2007). Sample size and sampling error in geometric morphometric studies of size and shape. *Zoomorphology*, 126(2), 121–134.
<https://doi.org/10.1007/s00435-007-0036-2>
- Cardini, A., Seetah, K., & Barker, G. (2015). How many specimens do I need? Sampling error in geometric morphometrics: testing the sensitivity of means and variances in simple

- randomized selection experiments. *Zoomorphology*, 134(2), 149–163.
<https://doi.org/10.1007/s00435-015-0253-z>
- Caron, F. S., & Pie, M. R. (2024). The macroevolution of sexual size dimorphism in birds. *Biological Journal of the Linnean Society*, blad168.
<https://doi.org/10.1093/biolinnean/blad168>
- Chenoweth, S. F., Rundle, H. D., & Blows, M. W. (2008). Genetic Constraints and the Evolution of Display Trait Sexual Dimorphism by Natural and Sexual Selection. *The American Naturalist*, 171(1), 22–34. <https://doi.org/10.1086/523946>
- Clavel, J., Aristide, L., & Morlon, H. (2019). A penalized likelihood framework for high-dimensional phylogenetic comparative methods and an application to New World monkeys brain evolution. *Systematic Biology*, 68(1), 93–116.
<https://doi.org/10.1093/sysbio/syy045>
- Clavel, J., Escarguel, G., & Merceron, G. (2015). mvMORPH: an R package for fitting multivariate evolutionary models to morphometric data. *Methods in Ecology and Evolution*, 6(11), 1311–1319. <https://doi.org/10.1111/2041-210X.12420>
- Constable, H., Guralnick, R., Wieczorek, J., Spencer, C., Peterson, A. T., & The VertNet Steering Committee. (2010). VertNet: A New Model for Biodiversity Data Sharing. *PLoS Biology*, 8(2), e1000309. <https://doi.org/10.1371/journal.pbio.1000309>
- Cooney, C. R., He, Y., Varley, Z. K., Nouri, L. O., Moody, C. J. A., Jardine, M. D., Liker, A., Székely, T., & Thomas, G. H. (2022). Latitudinal gradients in avian colourfulness. *Nature Ecology & Evolution*, 6(5), 622–629. <https://doi.org/10.1038/s41559-022-01714-1>
- Cooney, C. R., MacGregor, H. E. A., Seddon, N., & Tobias, J. A. (2018). Multi-modal signal evolution in birds: Re-examining a standard proxy for sexual selection. *Proceedings of the Royal Society B: Biological Sciences*, 285(1889), 20181557.
<https://doi.org/10.1098/rspb.2018.1557>
- Cooney, C. R., Tobias, J. A., Weir, J. T., Botero, C. A., & Seddon, N. (2017). Sexual selection, speciation and constraints on geographical range overlap in birds. *Ecology Letters*, 20(7), 863–871. <https://doi.org/10.1111/ele.12780>

- Cooney, C. R., Varley, Z. K., Nouri, L. O., Moody, C. J. A., Jardine, M. D., & Thomas, G. H. (2019). Sexual selection predicts the rate and direction of colour divergence in a large avian radiation. *Nature Communications*, 10(1), 1773. <https://doi.org/10.1038/s41467-019-09859-7>
- Cuervo, J. J., & Møller, A. P. (1999). Evolutionary rates of secondary sexual and non-sexual characters among birds. *Evolutionary Ecology*, 13(3), 283–303. <https://doi.org/10.1023/A:1006733405877>
- Darwin, C. (2009). On the origin of species: By means of natural selection (6th ed.). The Floating Press. (Original work published 1859)
- Darwin, C. (1981). The descent of man, and selection in relation to sex. Princeton University Press. <https://doi.org/10.5962/bhl.title.70891> (Original work published 1871)
- De Lisle, S. P., Brändén, A., & Pääjärvi Våg, E. (2025). Multivariate sexual selection of color and morphology in a complex trait: The *Drosophila* wing. *Evolution*, 79(7), 1361–1370. <https://doi.org/10.1093/evolut/qpaf086>
- Delhey, K., Valcu, M., Muck, C., Dale, J., & Kempenaers, B. (2023). Evolutionary predictors of the specific colors of birds. *Proceedings of the National Academy of Sciences*, 120(34), e2217692120. <https://doi.org/10.1073/pnas.2217692120>
- Dunn, P. O., Armenta, J. K., & Whittingham, L. A. (2015). Natural and sexual selection act on different axes of variation in avian plumage color. *Science Advances*, 1(2), e1400155. <https://doi.org/10.1126/sciadv.1400155>
- Dunn, P. O., Whittingham, L. A., & Pitcher, T. E. (2001). Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution*, 55(1), 161–175. <https://doi.org/10.1111/j.0014-3820.2001.tb01281.x>
- Endler, J. A. (1978). A predator's view of animal color patterns. In M. K. Hecht, W. C. Steere, & B. Wallace (Eds.), *Evolutionary Biology* (pp. 319–364). Springer US. https://doi.org/10.1007/978-1-4615-6956-5_5
- FitzJohn, R. G., Maddison, W. P., & Otto, S. P. (2009). Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic Biology*, 58(6), 595–611. <https://doi.org/10.1093/sysbio/syp067>

- Friis, G., & Milá, B. (2020). Change in sexual signalling traits outruns morphological divergence across an ecological gradient in the post-glacial radiation of the songbird genus *Junco*. *Journal of Evolutionary Biology*, 33(9), 1276–1293.
<https://doi.org/10.1111/jeb.13671>
- Fuller, R. C., Houle, D., & Travis, J. (2005). Sensory bias as an explanation for the evolution of mate preferences. *The American Naturalist*, 166(4), 437–446.
<https://doi.org/10.1086/444443>
- Goolsby, E. W., Bruggeman, J., & Ané, C. (2017). Rphylopars: Fast multivariate phylogenetic comparative methods for missing data and within-species variation. *Methods in Ecology and Evolution*, 8(1), 22–27. <https://doi.org/10.1111/2041-210X.12612>
- Gordon, S. P., Reznick, D., Arendt, J. D., Roughton, A., Ontiveros Hernandez, M. N., Bentzen, P., & López-Sepulcre, A. (2015). Selection analysis on the rapid evolution of a secondary sexual trait. *Proceedings of the Royal Society B: Biological Sciences*, 282(1813), 20151244. <https://doi.org/10.1098/rspb.2015.1244>
- Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, 144(4), 517–546. [https://doi.org/10.1016/S0022-5193\(05\)80088-8](https://doi.org/10.1016/S0022-5193(05)80088-8)
- Gray, D. A. (1996). Carotenoids and sexual dichromatism in North American passerine birds. *The American Naturalist*, 148(3), 453–480. <https://doi.org/10.1086/285935>
- Günay, E., Szara, T., Çakar, B., Deveci, E. İ., Coşkun, A. S., Gün, G., Yiğit, F., Gündemir, O., Duro, S., & Spataru, M. C. (2025). Geometric morphometric analysis of sexual dimorphism in the bill of the white stork (*Ciconia ciconia*). *Animals*, 15(9), 1312.
<https://doi.org/10.3390/ani15091312>
- Han, X., & Fu, J. (2013). Does life history shape sexual size dimorphism in anurans? A comparative analysis. *BMC Evolutionary Biology*, 13(1), 27.
<https://doi.org/10.1186/1471-2148-13-27>
- Henshaw, J. M., & Jones, A. G. (2020). Fisher's lost model of runaway sexual selection. *Evolution*, 74(2), 487–494. <https://doi.org/10.1111/evo.13910>
- Hill, G. E. (1991). Plumage coloration is a sexually selected indicator of male quality. *Nature*, 350(6316), 337–339. <https://doi.org/10.1038/350337a0>

- Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hoang, A., Hill, C. E., Beerli, P., & Kingsolver, J. G. (2001). Strength and tempo of directional selection in the wild. *Proceedings of the National Academy of Sciences*, 98(16), 9157–9160. <https://doi.org/10.1073/pnas.161281098>
- Hoglund, J. (1989). Size and plumage dimorphism in lek-breeding birds: A comparative analysis. *The American Naturalist*, 134(1), 72–87. <https://doi.org/10.1086/284966>
- Huang, H., & Rabosky, D. L. (2014). Sexual Selection and Diversification: Reexamining the Correlation between Dichromatism and Speciation Rate in Birds. *The American Naturalist*, 184(5), E101–E114. <https://doi.org/10.1086/678054>
- Huelsenbeck, J. P., Nielsen, R., & Bollback, J. P. (2003). Stochastic mapping of morphological characters. *Systematic Biology*, 52(2), 131–158. <https://doi.org/10.1080/10635150390192780>
- Irestedt, M., Jønsson, K. A., Fjeldså, J., Christidis, L., & Ericson, P. G. (2009). An unexpectedly long history of sexual selection in birds-of-paradise. *BMC Evolutionary Biology*, 9(1), 235. <https://doi.org/10.1186/1471-2148-9-235>
- Januario, M., Macedo-Rego, R. C., & Rabosky, D. L. (2025). Evolutionary lability of sexual selection and its implications for speciation and macroevolution. *The American Naturalist*, 205(4), 388–412. <https://doi.org/10.1086/734457>
- Kraaijeveld, K., Kraaijeveld-Smit, F. J. L., & Maan, M. E. (2011). Sexual selection and speciation: The comparative evidence revisited. *Biological Reviews*, 86(2), 367–377. <https://doi.org/10.1111/j.1469-185X.2010.00150.x>
- Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, 34(2), 292–305. <https://www.jstor.org/stable/2407393>
- Lislevand, T., Figuerola, J., & Székely, T. (2009). Evolution of sexual size dimorphism in grouse and allies (Aves: Phasianidae) in relation to mating competition, fecundity demands and resource division. *Journal of Evolutionary Biology*, 22(9), 1895–1905. <https://doi.org/10.1111/j.1420-9101.2009.01802.x>

- Maia, R., Rubenstein, D. R., & Shawkey, M. D. (2013). Key ornamental innovations facilitate diversification in an avian radiation. *Proceedings of the National Academy of Sciences*, 110(26), 10687–10692. <https://doi.org/10.1073/pnas.1220784110>
- Miller, E. C., Mesnick, S. L., & Wiens, J. J. (2021). Sexual dichromatism is decoupled from diversification over deep time in fishes. *The American Naturalist*, 198(2), 232–252. <https://doi.org/10.1086/715114>
- Mills, A. M. (2008). Passerines are sexually dimorphic in shape as well as size. *The Condor*, 110(2), 354–358. <https://doi.org/10.1525/cond.2008.8303>
- Morrow, E. H., Pitcher, T. E., & Arnqvist, G. (2003). No evidence that sexual selection is an ‘engine of speciation’ in birds. *Ecology Letters*, 6(3), 228–234. <https://doi.org/10.1046/j.1461-0248.2003.00418.x>
- Murphy, M. T. (2007). A cautionary tale: Cryptic sexual size dimorphism in a socially monogamous passerine. *The Auk*, 124(2), 515–525. <https://doi.org/10.1093/auk/124.2.515>
- Oliveros, C. H., Field, D. J., Ksepka, D. T., Barker, F. K., Aleixo, A., Andersen, M. J., Alström, P., Benz, B. W., Braun, E. L., Braun, M. J., Bravo, G. A., Brumfield, R. T., Chesser, R. T., Claramunt, S., Cracraft, J., Cuervo, A. M., Derryberry, E. P., Glenn, T. C., Harvey, M. G., ... Faircloth, B. C. (2019). Earth history and the passerine superradiation. *Proceedings of the National Academy of Sciences*, 116(16), 7916–7925. <https://doi.org/10.1073/pnas.1813206116>
- Omland, K. E. (1997). Examining two standard assumptions of ancestral reconstructions: Repeated loss of dichromatism in dabbling ducks (Anatini). *Evolution*, 51(5), 1636–1646. <https://doi.org/10.1111/j.1558-5646.1997.tb01486.x>
- Owens, I. P. F., & Hartley, I. R. (1998). Sexual dimorphism in birds: Why are there so many different forms of dimorphism? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 265(1394), 397–407. <https://doi.org/10.1098/rspb.1998.0308>
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20(2), 289–290. <https://doi.org/10.1093/bioinformatics/btg412>

- Pietsch, T. W. (1976). Dimorphism, Parasitism and Sex: Reproductive Strategies among Deepsea Ceratioid Anglerfishes. *Copeia*, 1976(4), 781.
<https://doi.org/10.2307/1443462>
- Portik, D. M., Bell, R. C., Blackburn, D. C., Bauer, A. M., Barratt, C. D., Branch, W. R., Burger, M., Channing, A., Colston, T. J., Conradie, W., Dehling, J. M., Drewes, R. C., Ernst, R., Greenbaum, E., Gvoždík, V., Harvey, J., Hillers, A., Hirschfeld, M., Jongsma, G. F. M., ... McGuire, J. A. (2019). Sexual dichromatism drives diversification within a major radiation of African amphibians. *Systematic Biology*, 68(6), 859–875.
<https://doi.org/10.1093/sysbio/syz023>
- Price, T., & Birch, G. (1996). Repeated evolution of sexual color dimorphism in passerine birds. *The Auk*, 113(4), 842–848. <https://doi.org/10.2307/4088862>
- Prum, R. O. (2010). The Lande-Kirkpatrick mechanism is the null model of evolution by intersexual selection: Implications for meaning, honesty, and design in intersexual signals. *Evolution*, 64(11), 3085–3100. <https://doi.org/10.1111/j.1558-5646.2010.01054.x>
- Punzalan, D., & Rowe, L. (2015). Evolution of sexual dimorphism in phenotypic covariance structure in *Phymata*. *Evolution*, 69(6), 1597–1609.
<https://doi.org/10.1111/evo.12680>
- Punzalan, D., & Rowe, L. (2016). Concordance between stabilizing sexual selection, intraspecific variation, and interspecific divergence in *Phymata*. *Ecology and Evolution*, 6(22), 7997–8009. <https://doi.org/10.1002/ece3.2537>
- R Core Team. (2024). R: A language and environment for statistical computing (Version 4.3.3). R Foundation for Statistical Computing. <https://www.R-project.org/>
- Revell, L. J. (2024). phytools 2.0: An updated R ecosystem for phylogenetic comparative methods (and other things). *PeerJ*, 12, e16505. <https://doi.org/10.7717/peerj.16505>
- Schmitt, C. J., & Edwards, S. V. (2022). Passerine birds. *Current Biology*, 32(20), R1149–R1154. <https://doi.org/10.1016/j.cub.2022.08.061>
- Seddon, N., Botero, C. A., Tobias, J. A., Dunn, P. O., MacGregor, H. E. A., Rubenstein, D. R., Uy, J. A. C., Weir, J. T., Whittingham, L. A., & Safran, R. J. (2013). Sexual selection

- accelerates signal evolution during speciation in birds. *Proceedings of the Royal Society B: Biological Sciences*, 280(1766), 20131065.
<https://doi.org/10.1098/rspb.2013.1065>
- Shogren, E. H., Anciães, M., Barske, J., Cestari, C., DuVal, E. H., Gaiotti, M. G., Johnson, E. I., Kimball, R. T., Marini, M. A., Ryder, T. B., Scholer, M. N., Ungvári, J., White, S. A., & Boyle, W. A. (2022). Dancing drives evolution of sexual size dimorphism in manakins. *Proceedings of the Royal Society B: Biological Sciences*, 289(1974), 20212540.
<https://doi.org/10.1098/rspb.2021.2540>
- Shultz, A. J., & Burns, K. J. (2017). The role of sexual and natural selection in shaping patterns of sexual dichromatism in the largest family of songbirds (Aves: Thraupidae). *Evolution*, 71(4), 1061–1074. <https://doi.org/10.1111/evo.13196>
- Singh, P., & Price, T. D. (2024). Evolution of species recognition when ecology and sexual selection favor signal stasis. *Evolution*, 78(10), 1647–1660.
<https://doi.org/10.1093/evolut/qpae099>
- Spence, A. J. (2009). Scaling in biology. *Current Biology*, 19(2), R57–R61.
<https://doi.org/10.1016/j.cub.2008.10.042>
- Számadó, S., Zachar, I., & Penn, D. J. (2026). A general signalling theory: Why honest signals are explained by trade-offs rather than costs or handicaps. *Journal of Evolutionary Biology*, 39(2), 171–189. <https://doi.org/10.1093/jeb/voaf144>
- Székely, T., Lislevand, T., & Figuerola, J. (2007). Sexual size dimorphism in birds. In D. J. Fairbairn, W. U. Blanckenhorn, & T. Székely (Eds.), *Sex, size and gender roles* (pp. 27–37). Oxford University Press.
<https://doi.org/10.1093/acprof:oso/9780199208784.003.0004>
- Taylor, G. W., Santos, J. C., Perrault, B. J., Morando, M., Vásquez Almazán, C. R., & Sites Jr, J. W. (2017). Sexual dimorphism, phenotypic integration, and the evolution of head structure in casque-headed lizards. *Ecology and Evolution*, 7(21), 8989–8998.
<https://doi.org/10.1002/ece3.3356>

- Ho, L. S. T., & Ané, C. (2014). A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology*, 63(3), 397–408.
<https://doi.org/10.1093/sysbio/syu005>
- Uyeda, J. C., Caetano, D. S., & Pennell, M. W. (2015). Comparative analysis of principal components can be misleading. *Systematic Biology*, 64(4), 677–689.
<https://doi.org/10.1093/sysbio/syv019>
- Valcu, M., Valcu, C., & Kempenaers, B. (2023). Extra-pair paternity and sexual dimorphism in birds. *Journal of Evolutionary Biology*, 36(5), 764–779.
<https://doi.org/10.1111/jeb.14172>
- Weeks, B. C., Zhou, Z., O'Brien, B. K., Darling, R., Dean, M., Dias, T., Hassena, G., Zhang, M., & Fouhey, D. F. (2023). A deep neural network for high-throughput measurement of functional traits on museum skeletal specimens. *Methods in Ecology and Evolution*, 14(2), 347–359. <https://doi.org/10.1111/2041-210X.13864>
- Weeks, B. C., Zhou, Z., Probst, C. M., Berv, J. S., O'Brien, B., Benz, B. W., Skeen, H. R., Ziebell, M., Bodt, L., & Fouhey, D. F. (2025). Skeletal trait measurements for thousands of bird species. *Scientific Data*, 12(1), 884. <https://doi.org/10.1038/s41597-025-05234-y>
- Zahavi, A. (1975). Mate selection—A selection for a handicap. *Journal of Theoretical Biology*, 53(1), 205–214. [https://doi.org/10.1016/0022-5193\(75\)90111-3](https://doi.org/10.1016/0022-5193(75)90111-3)

Appendix

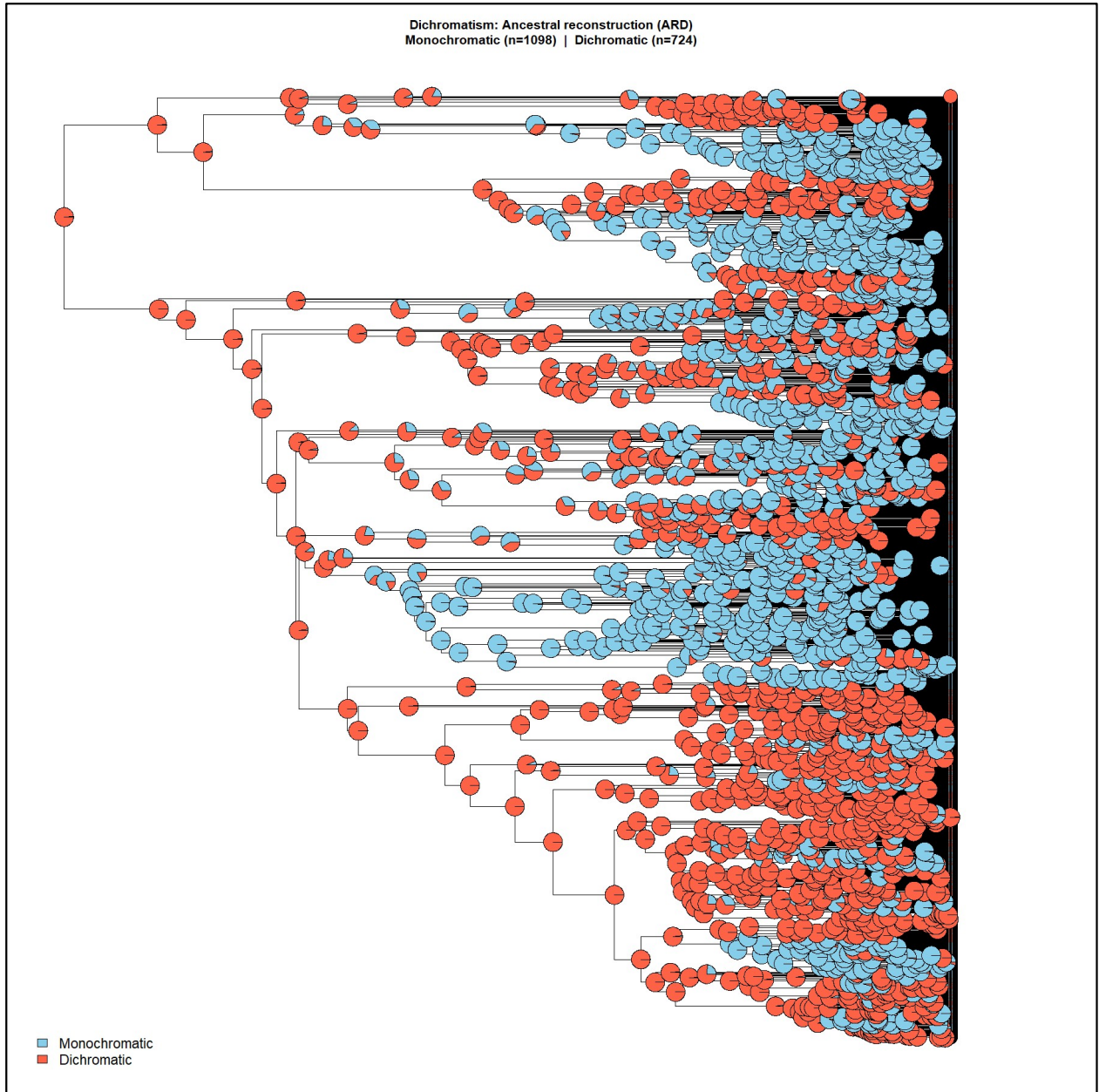


Figure S1. Ancestral state reconstruction of sexual dichromatism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monochromatic (blue, $n = 1,098$) or dichromatic (red, $n = 724$) state at that node.

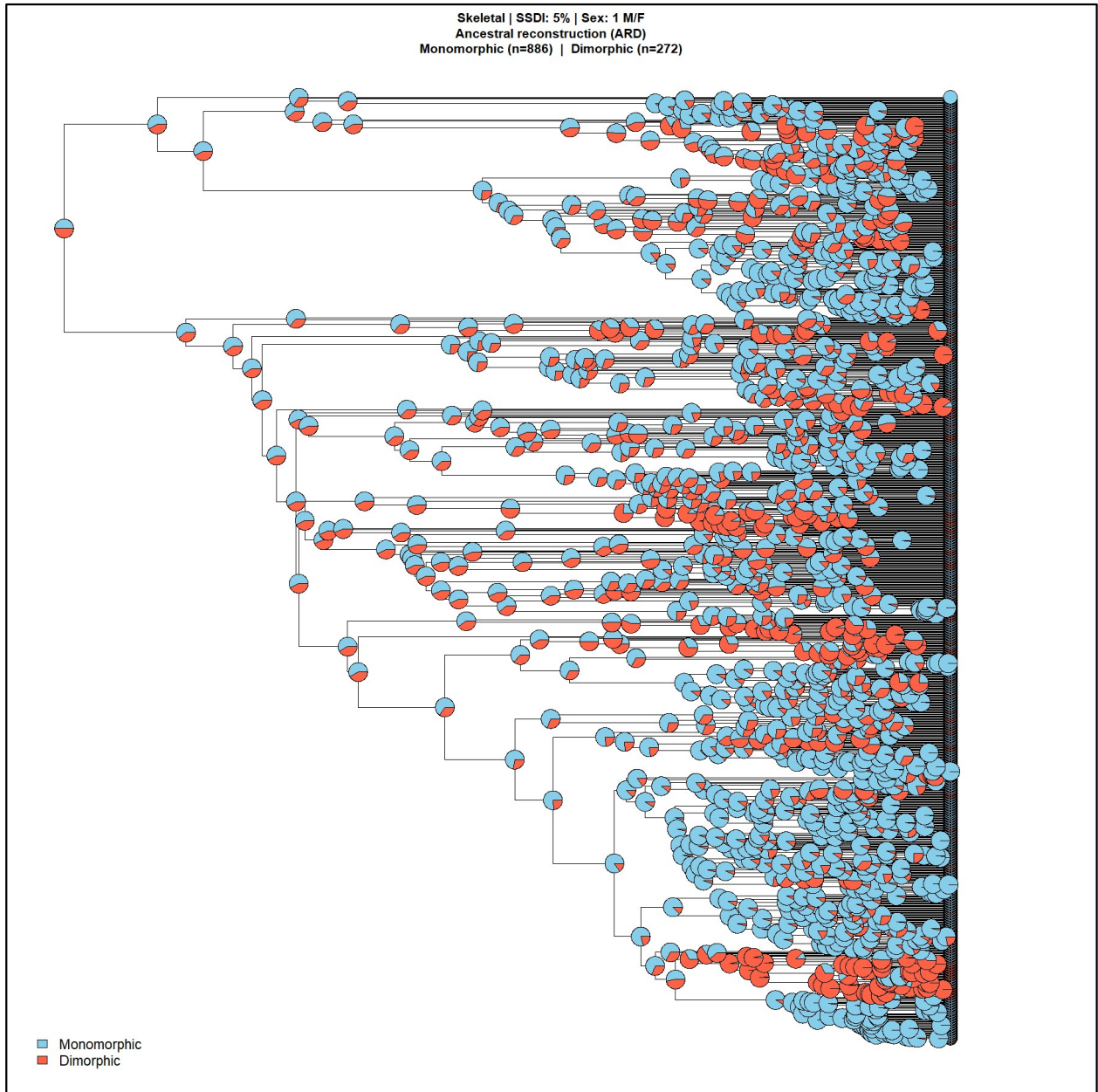


Figure S2. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, n = 886) or dimorphic (red, n = 272) state at that node.

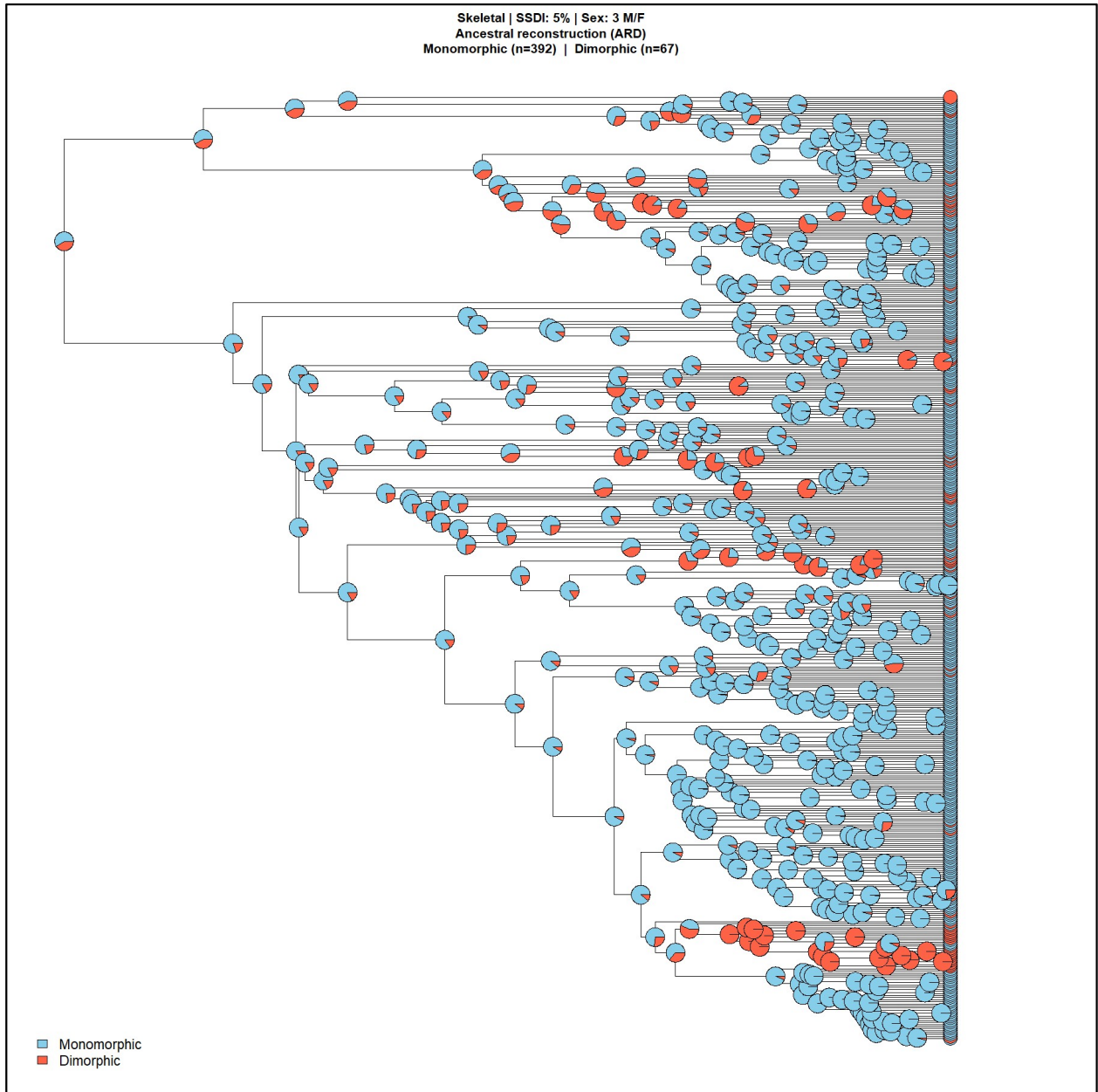


Figure S3. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, n = 392) or dimorphic (red, n = 67) state at that node.

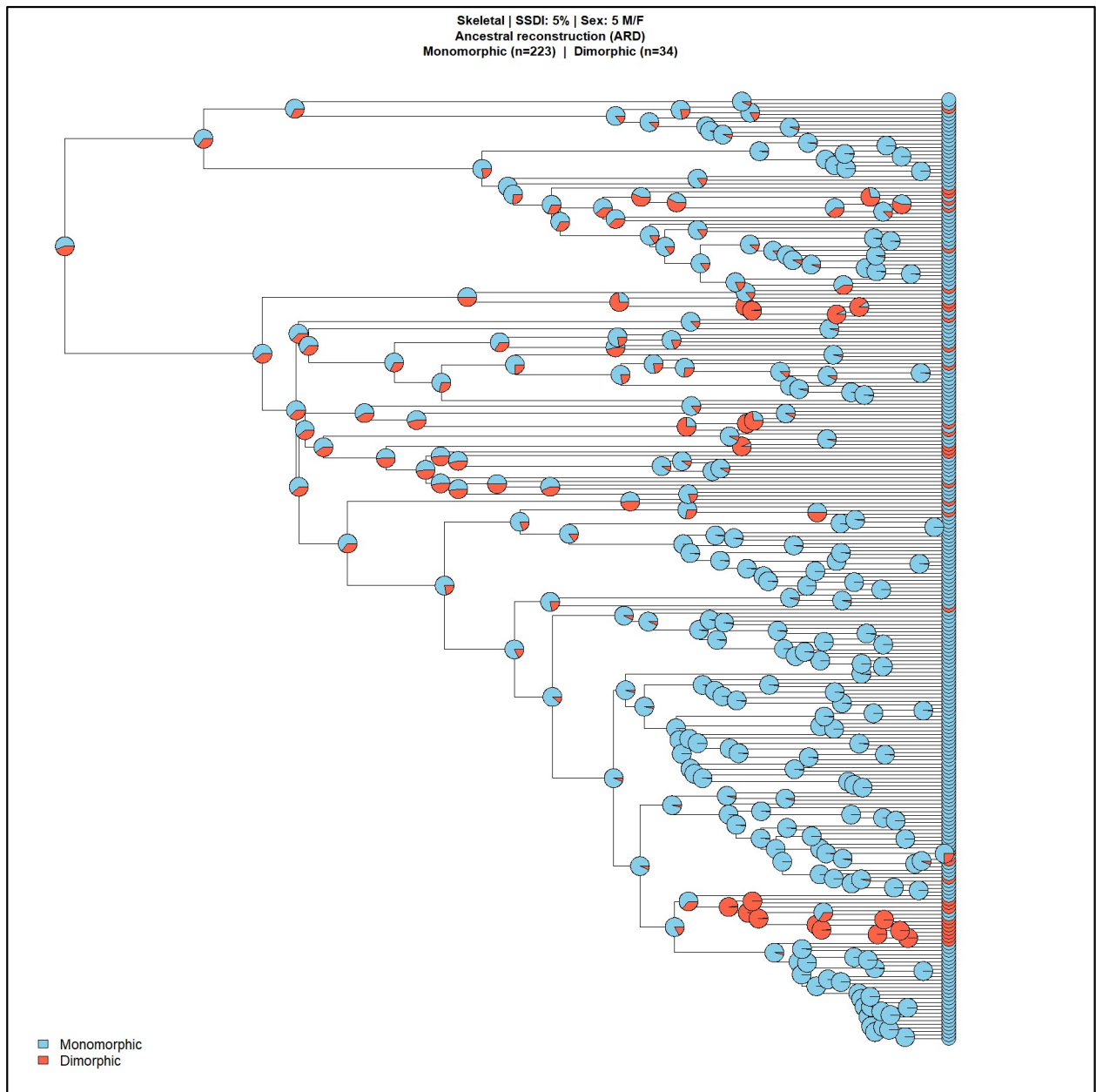


Figure S4. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, n = 223) or dimorphic (red, n = 34) state at that node.

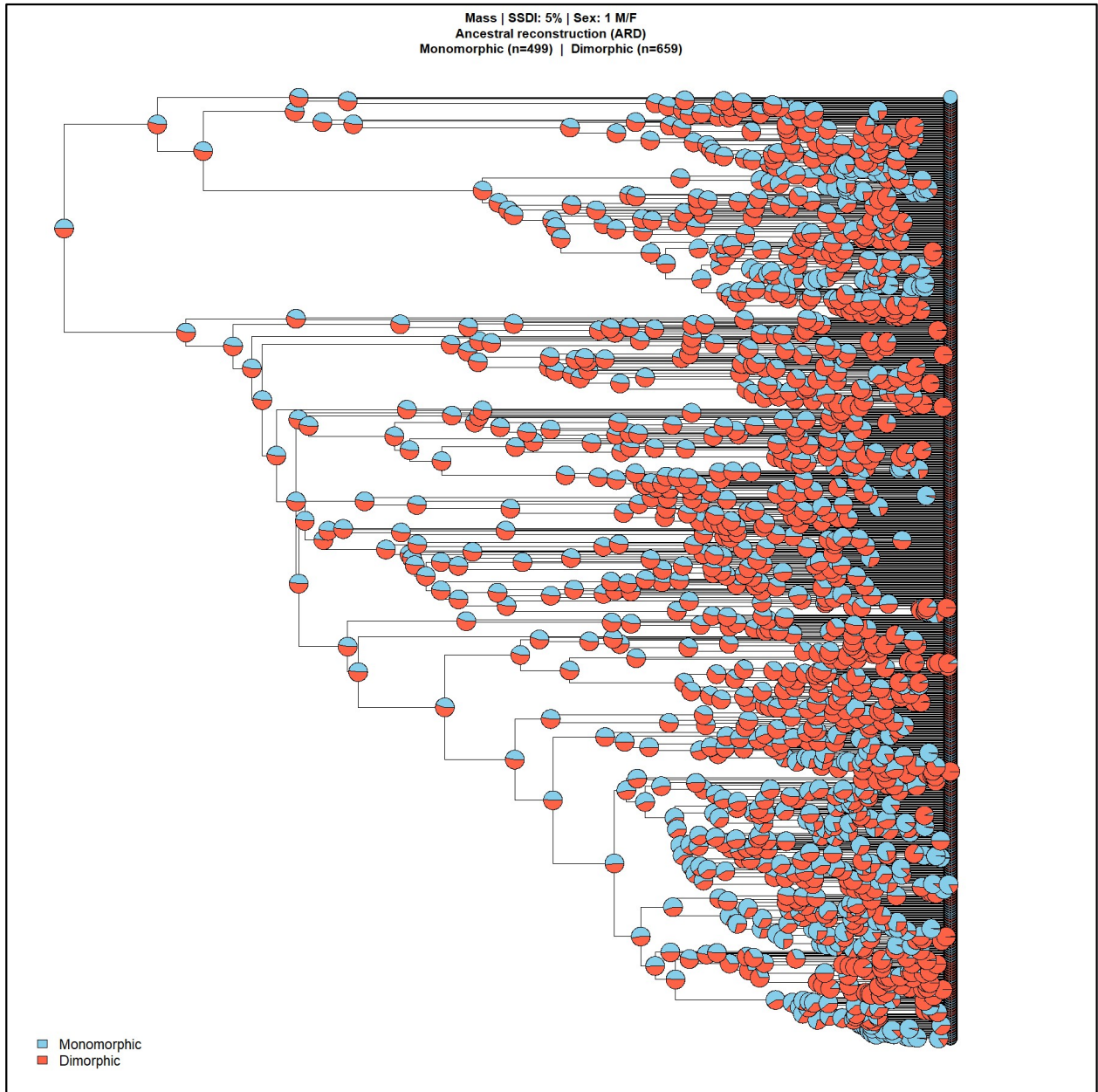


Figure S5. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, n = 499) or dimorphic (red, n = 659) state at that node.

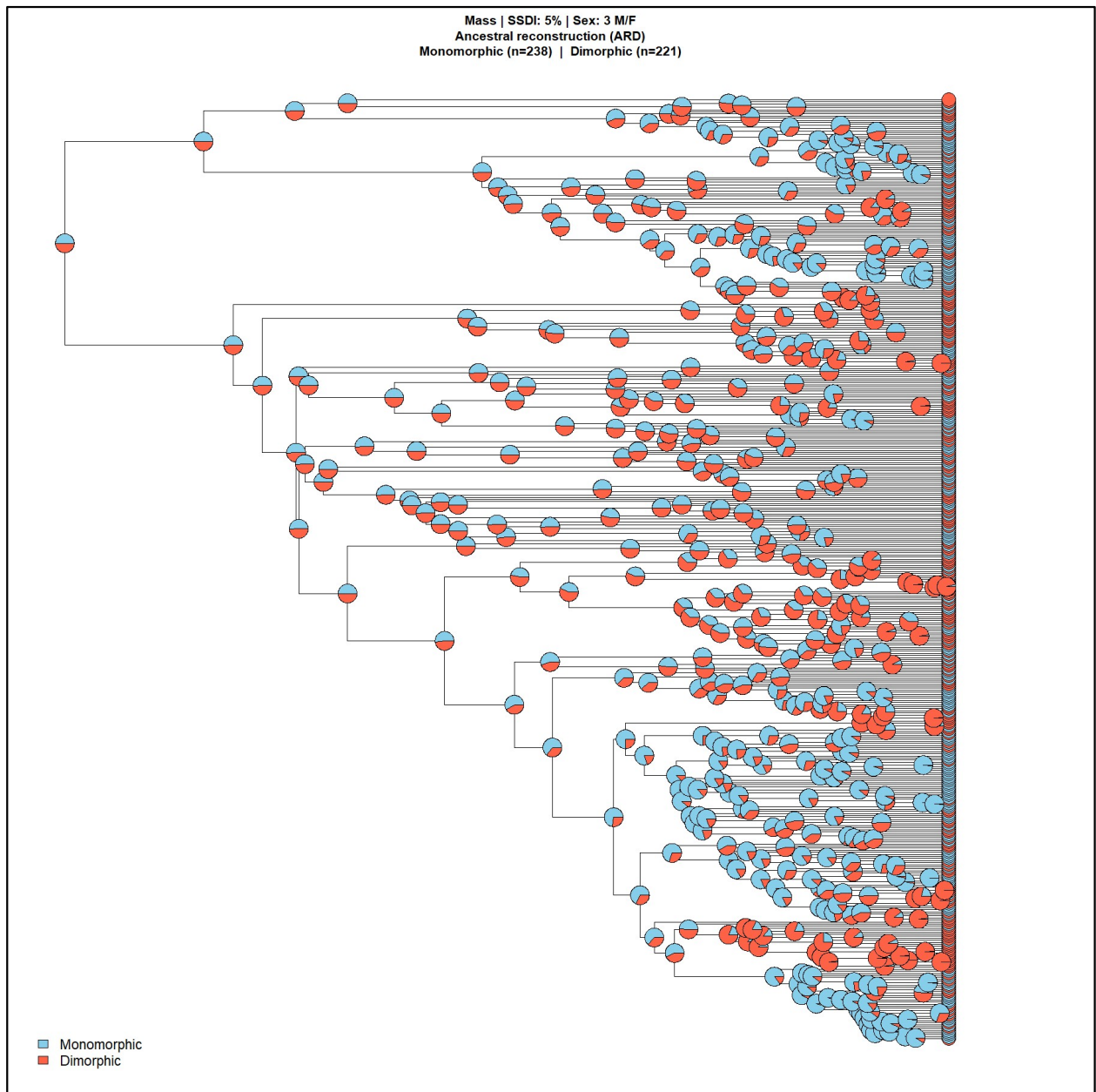


Figure S6. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, n = 238) or dimorphic (red, n = 221) state at that node.

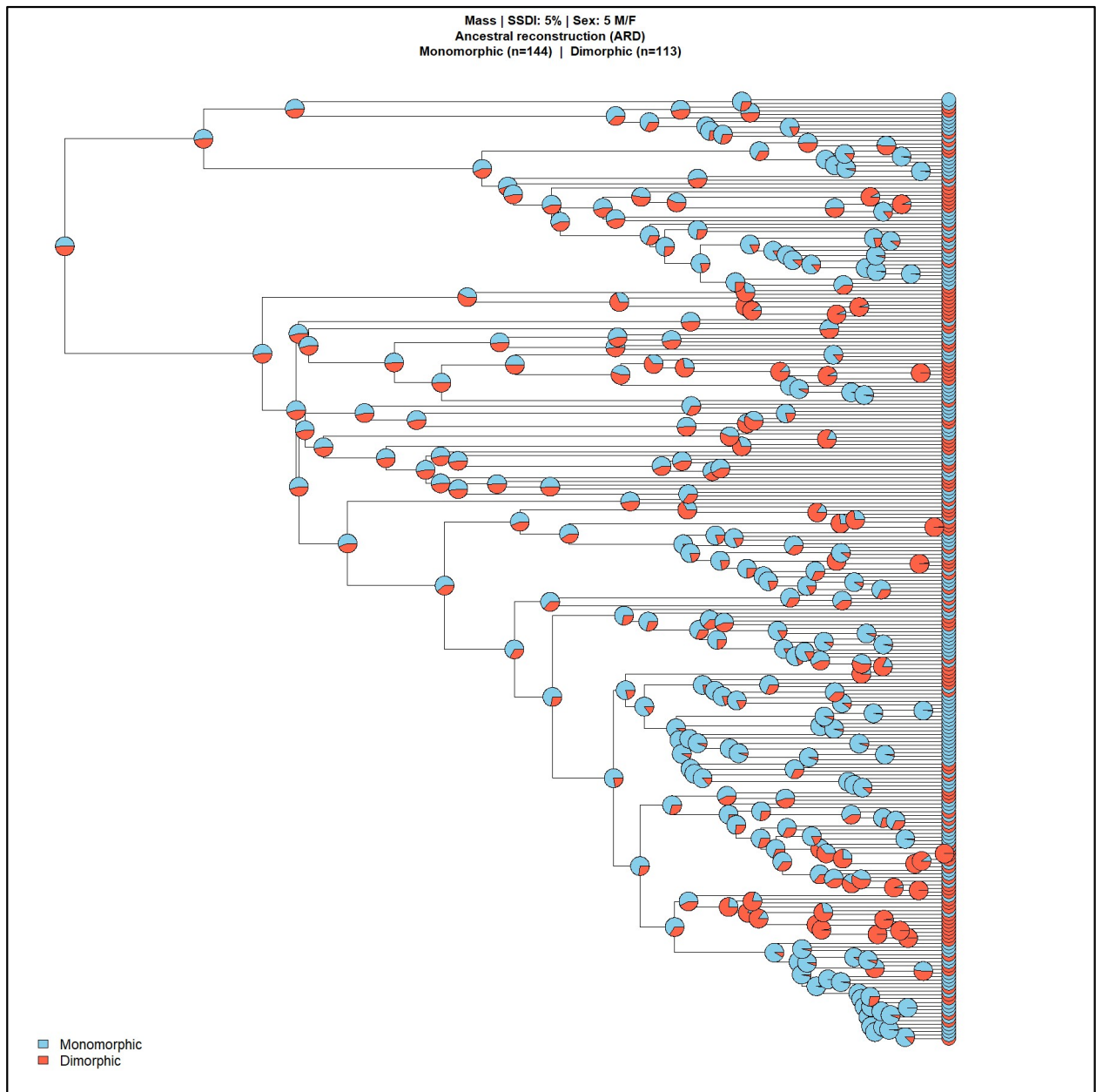


Figure S7. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, n = 144) or dimorphic (red, n = 113) state at that node.

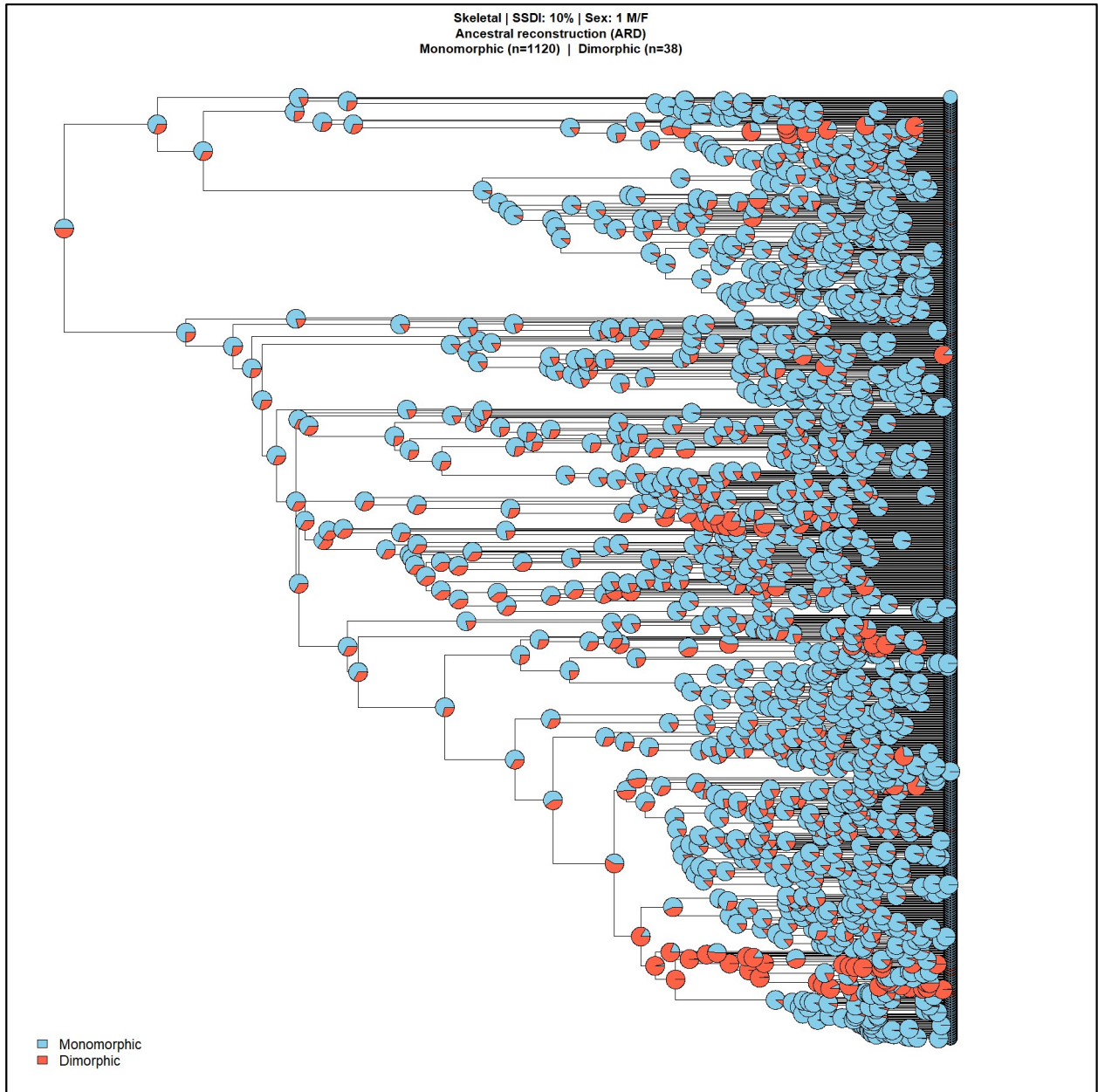


Figure S8. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, $n = 1,120$) or dimorphic (red, $n = 38$) state at that node.

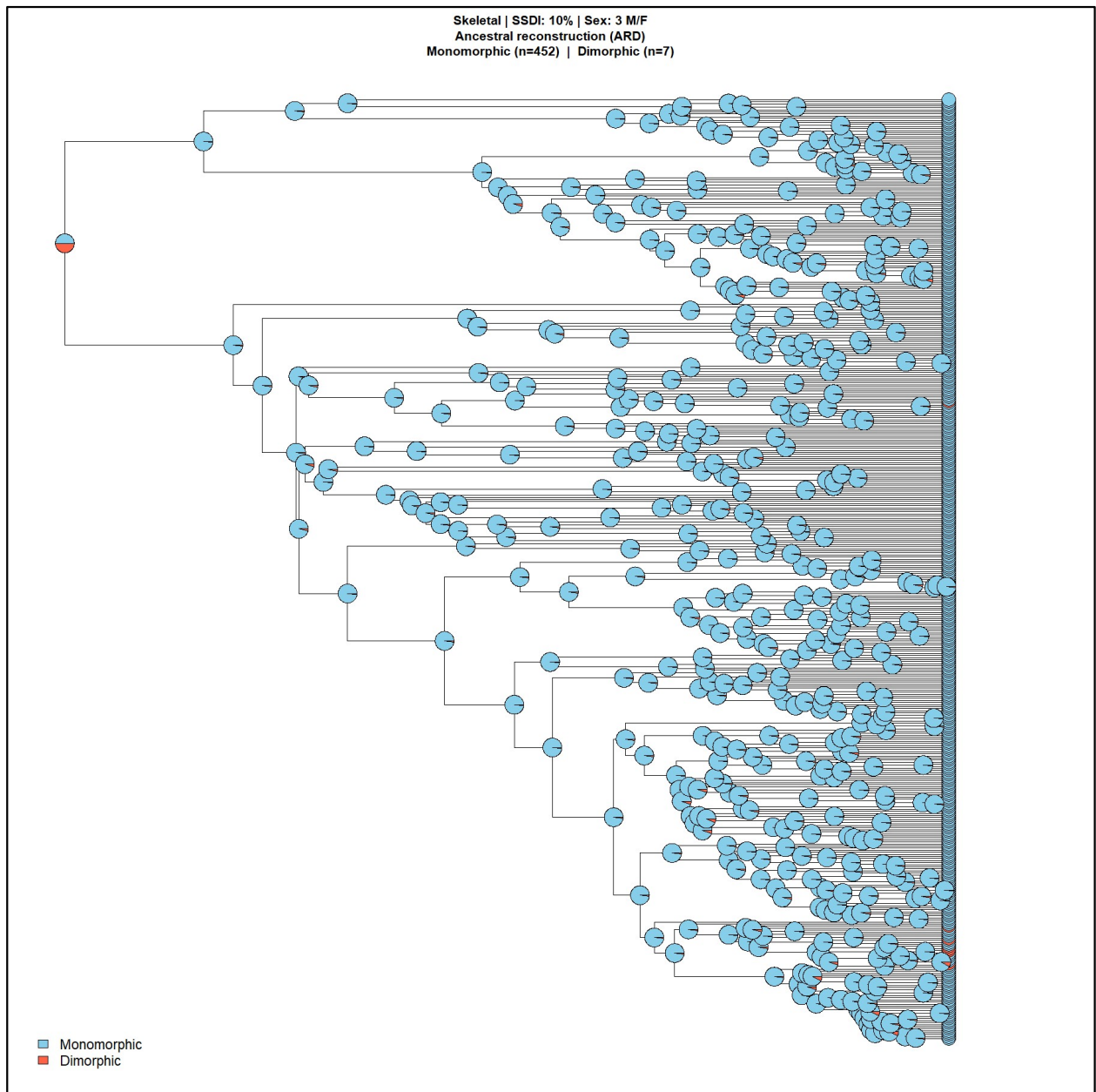


Figure S9. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, n = 452) or dimorphic (red, n = 7) state at that node.

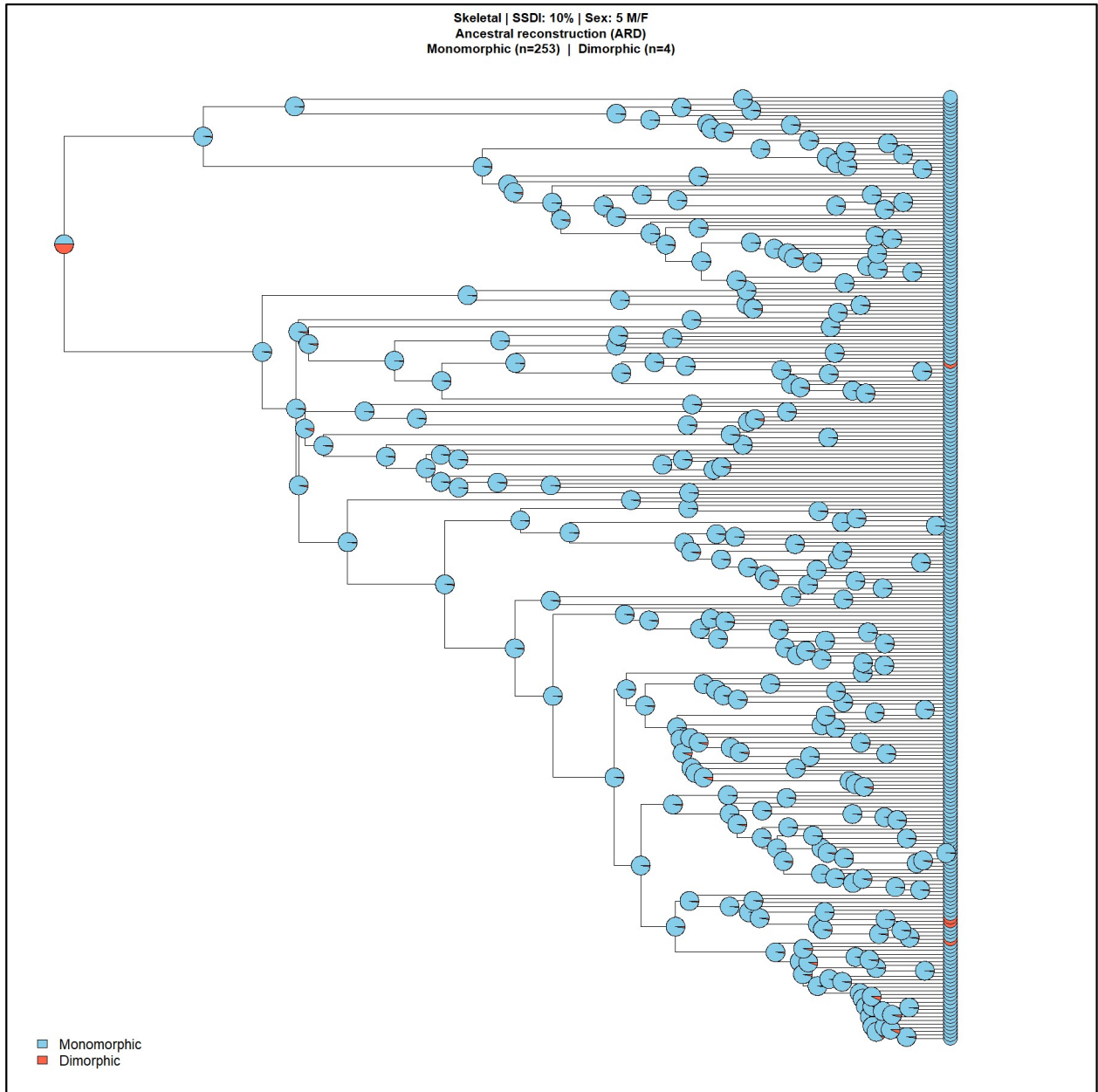


Figure S10. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, n = 253) or dimorphic (red, n = 4) state at that node.

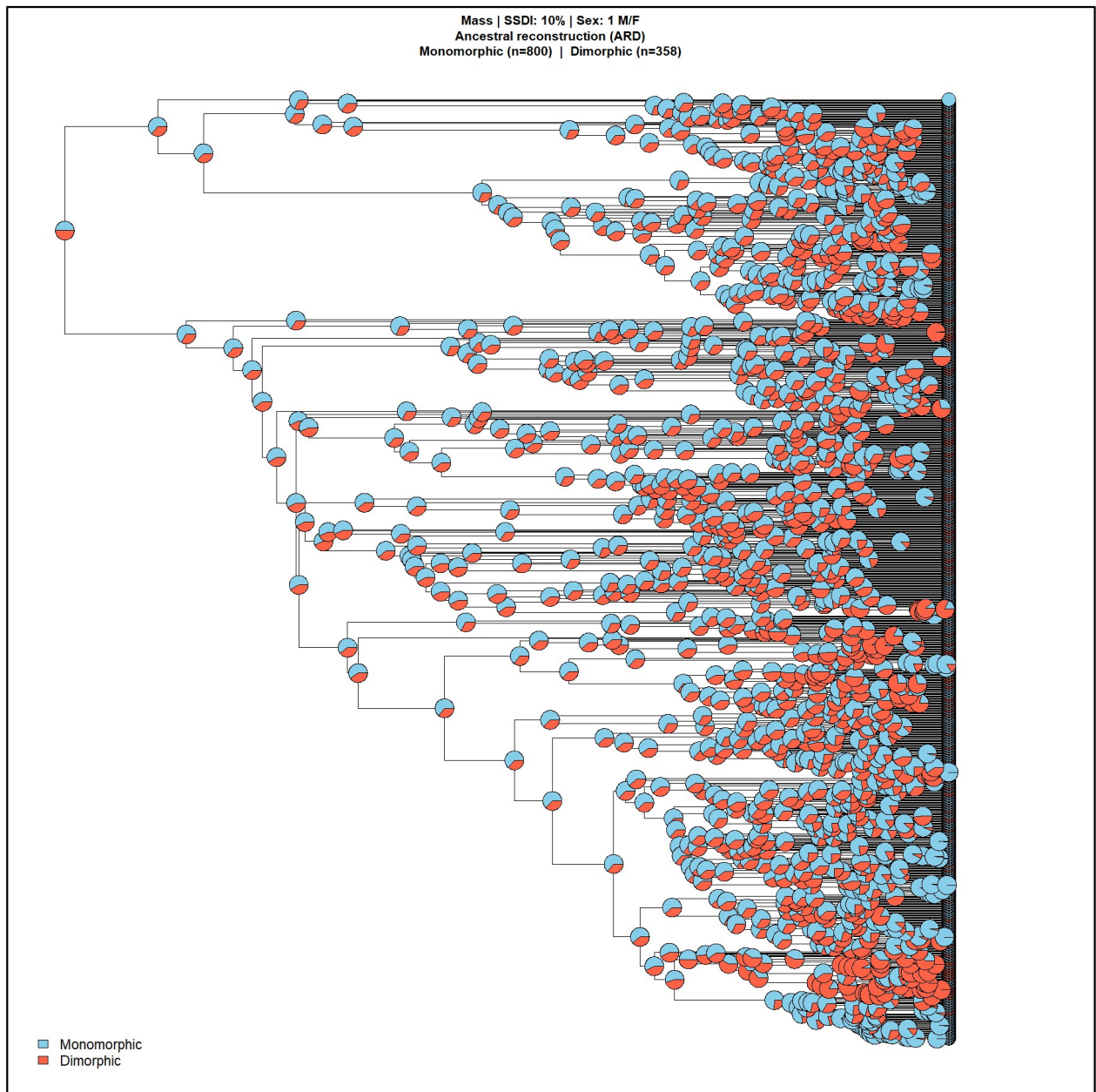


Figure S11. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, $n = 800$) or dimorphic (red, $n = 358$) state at that node.

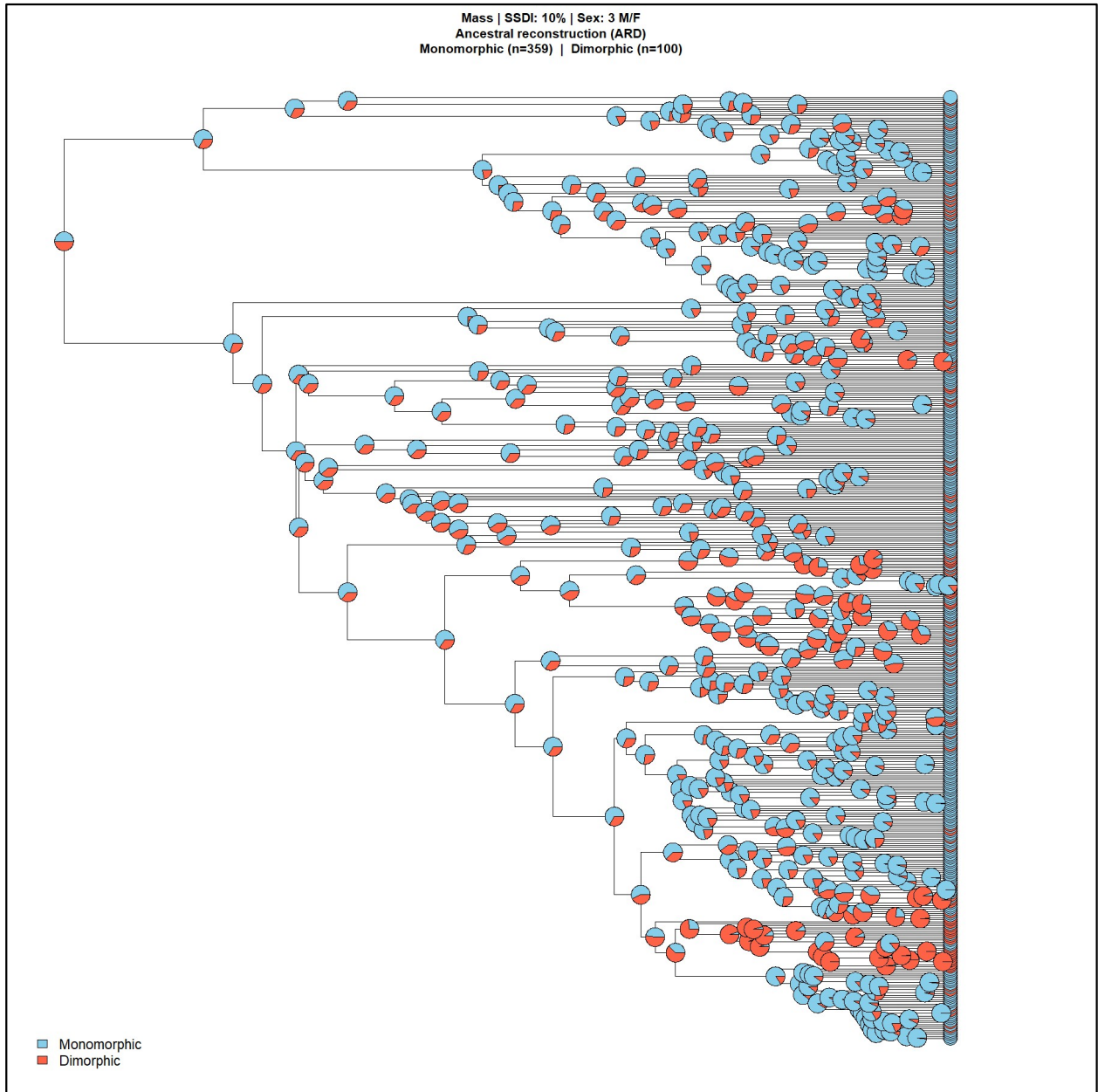


Figure S12. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, $n = 359$) or dimorphic (red, $n = 100$) state at that node.

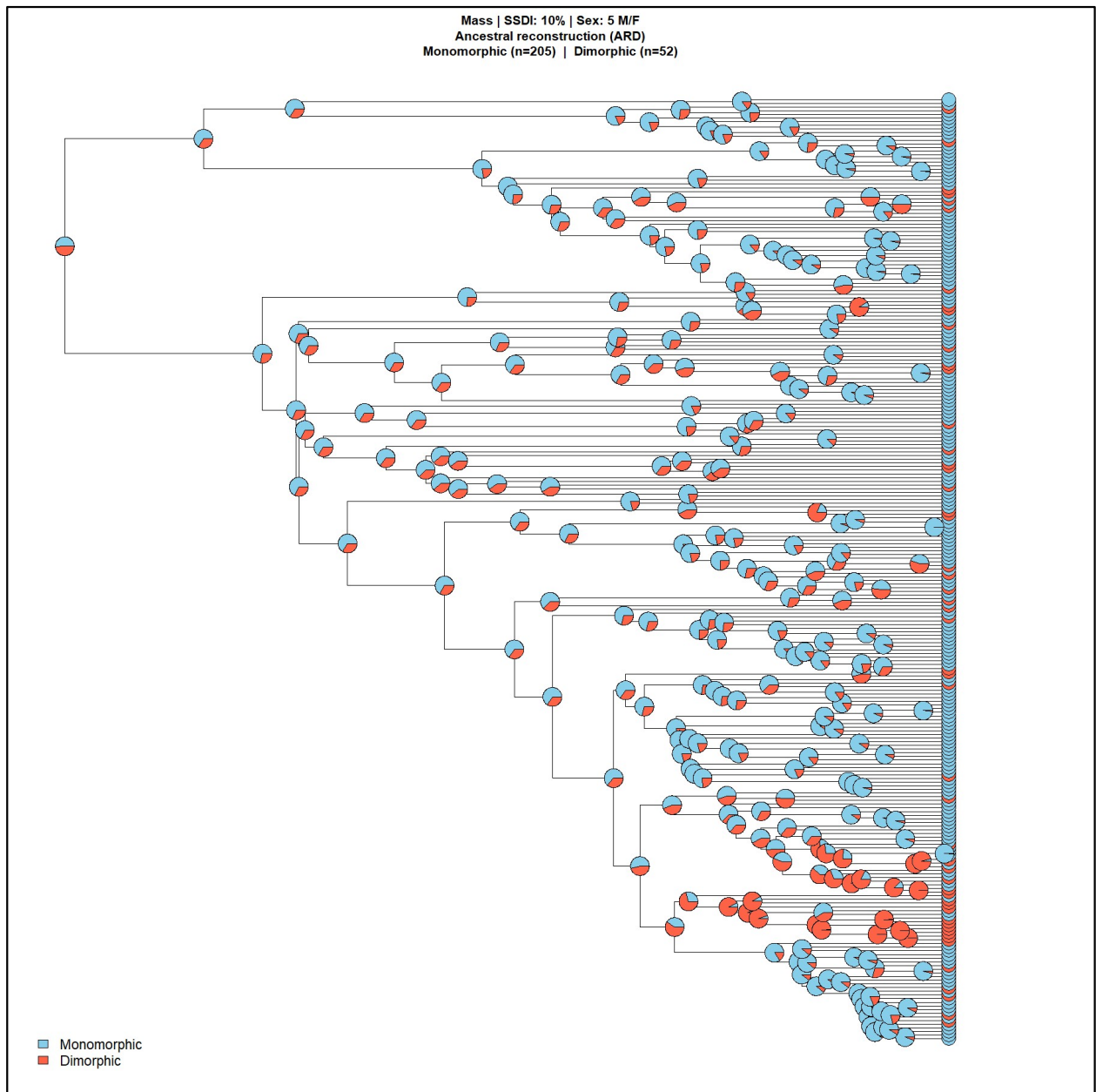


Figure S13. Ancestral state reconstruction of sexual dimorphism across passerine birds using an all-rates-different (ARD) model. Pie charts represent the likelihood of being in the monomorphic (blue, n = 205) or dimorphic (red, n = 52) state at that node.

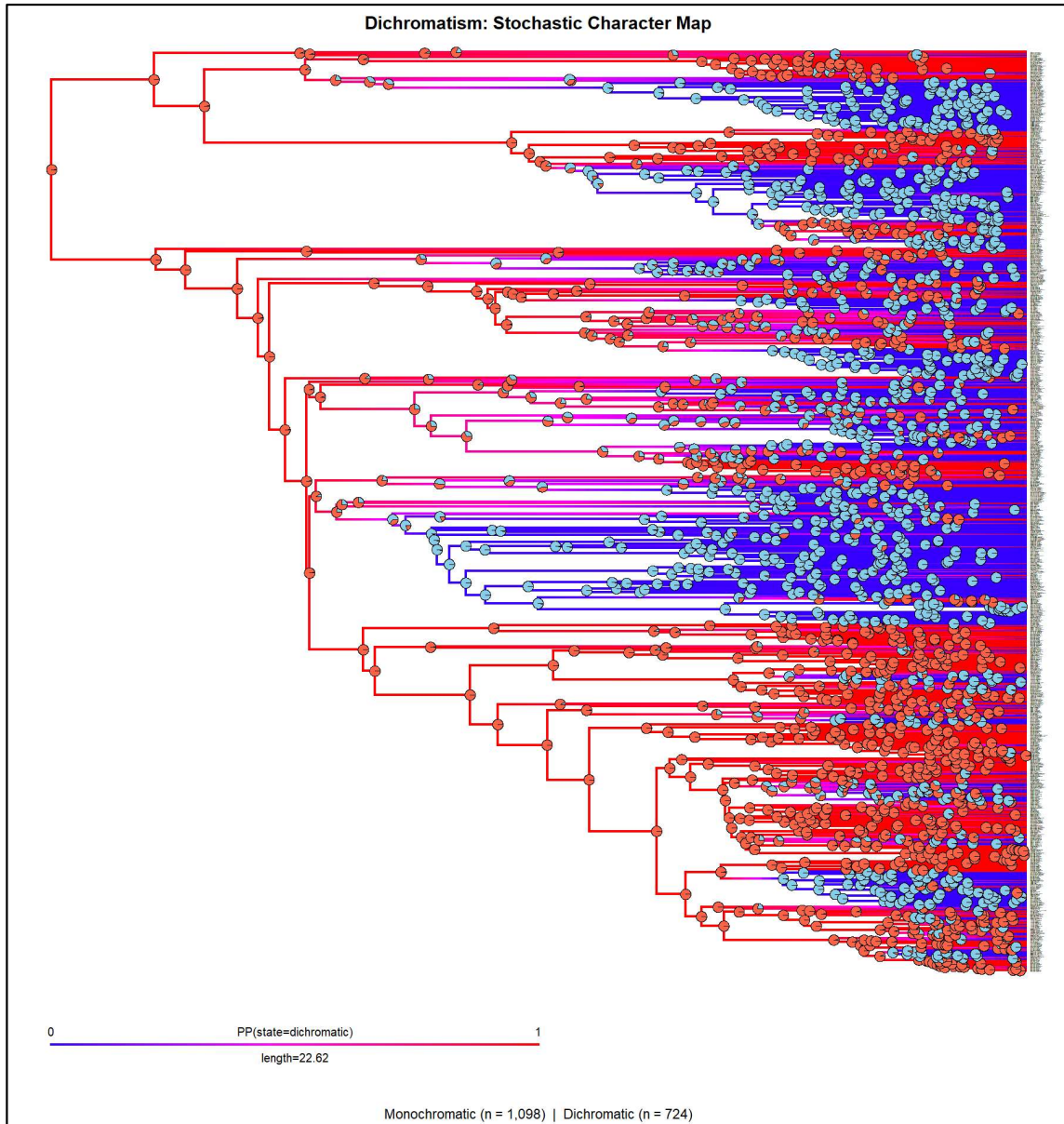


Figure S14. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dichromatism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dichromatic versus monochromatic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monochromatism, and red (1) are high certainty of dichromatism, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monochromatic (blue, n = 1,098) or dichromatic (red, n = 724) state at a given node.

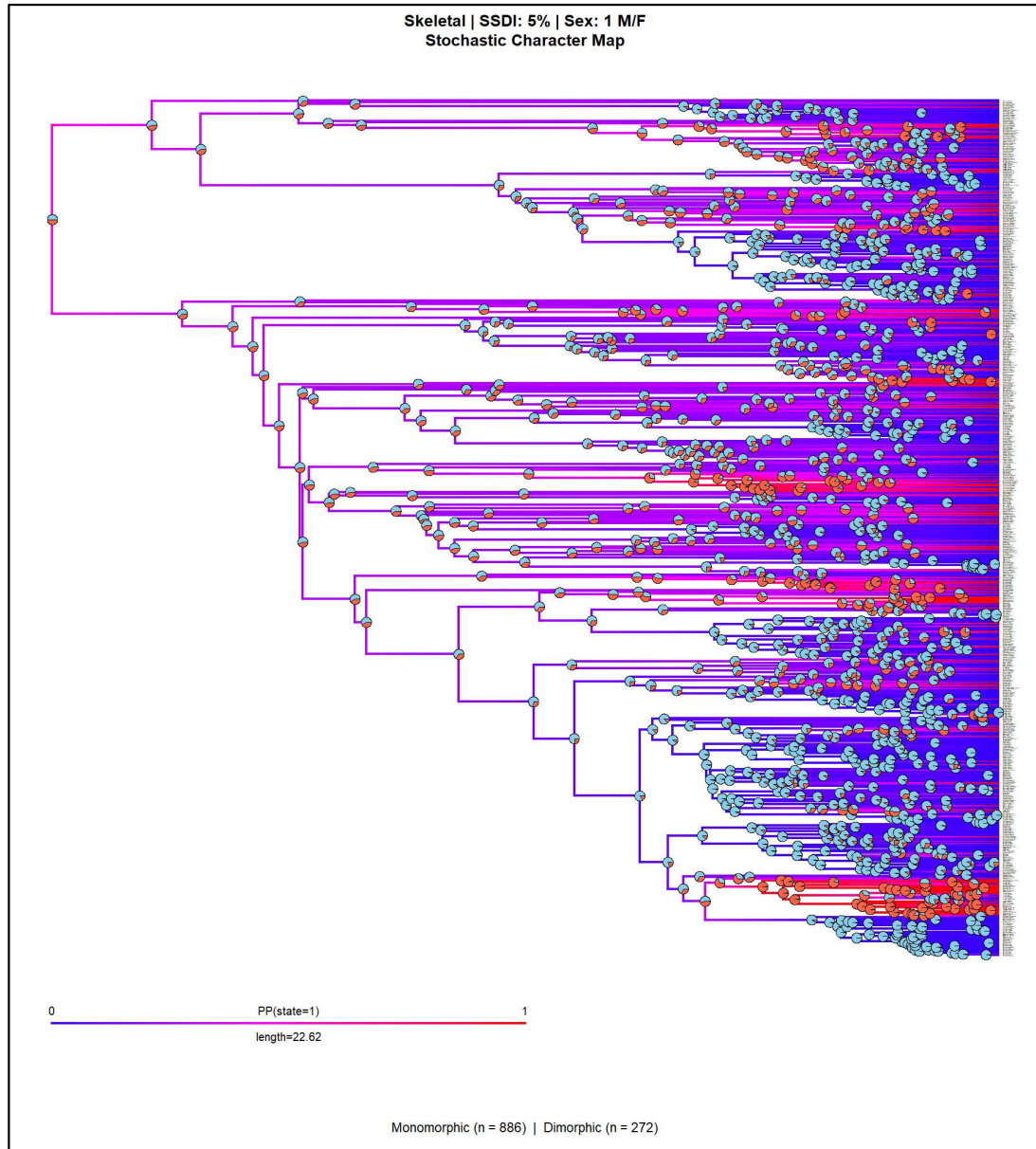


Figure S15. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 886) or dimorphic (red, n = 272) state at a given node.

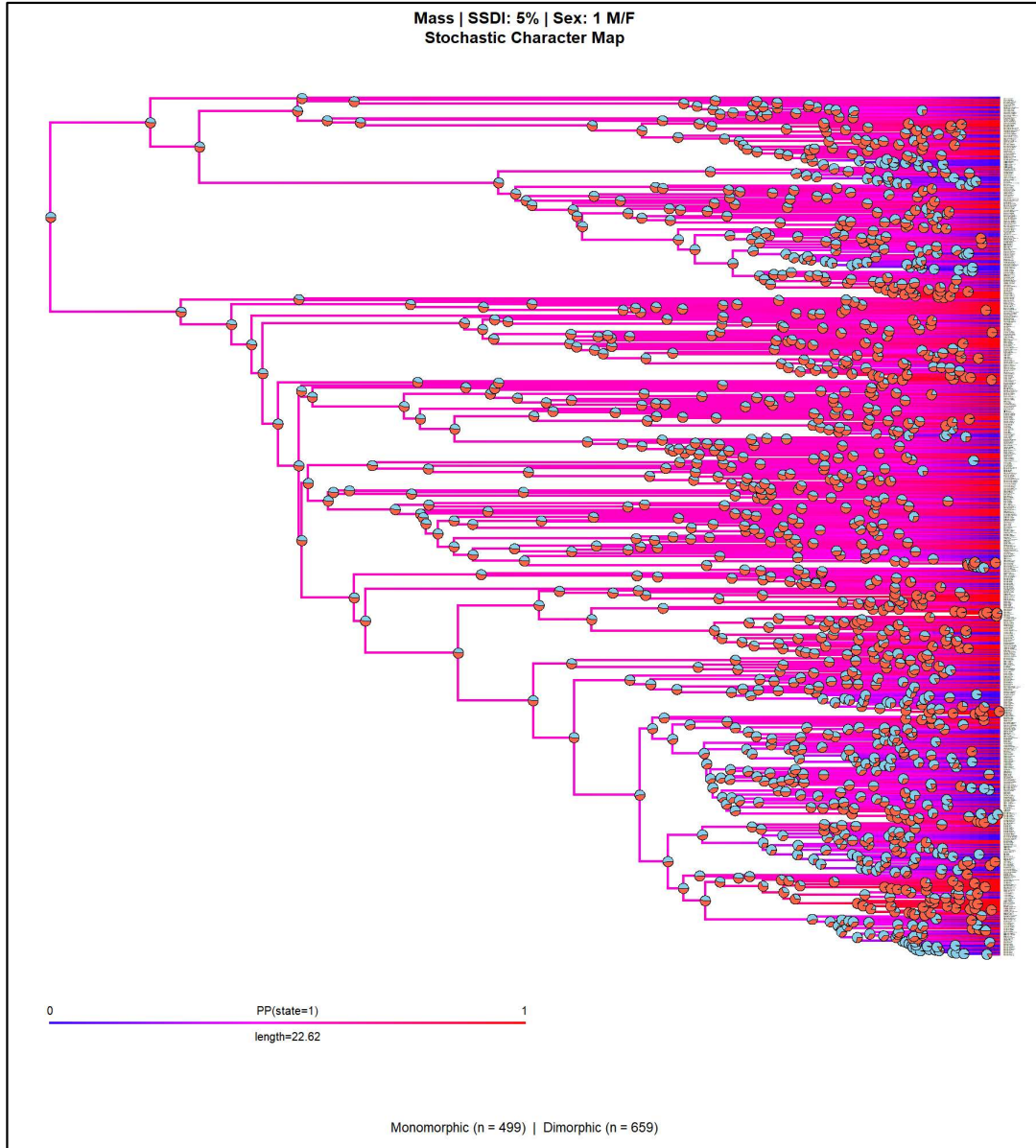


Figure S16. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 499) or dimorphic (red, n = 659) state at a given node.

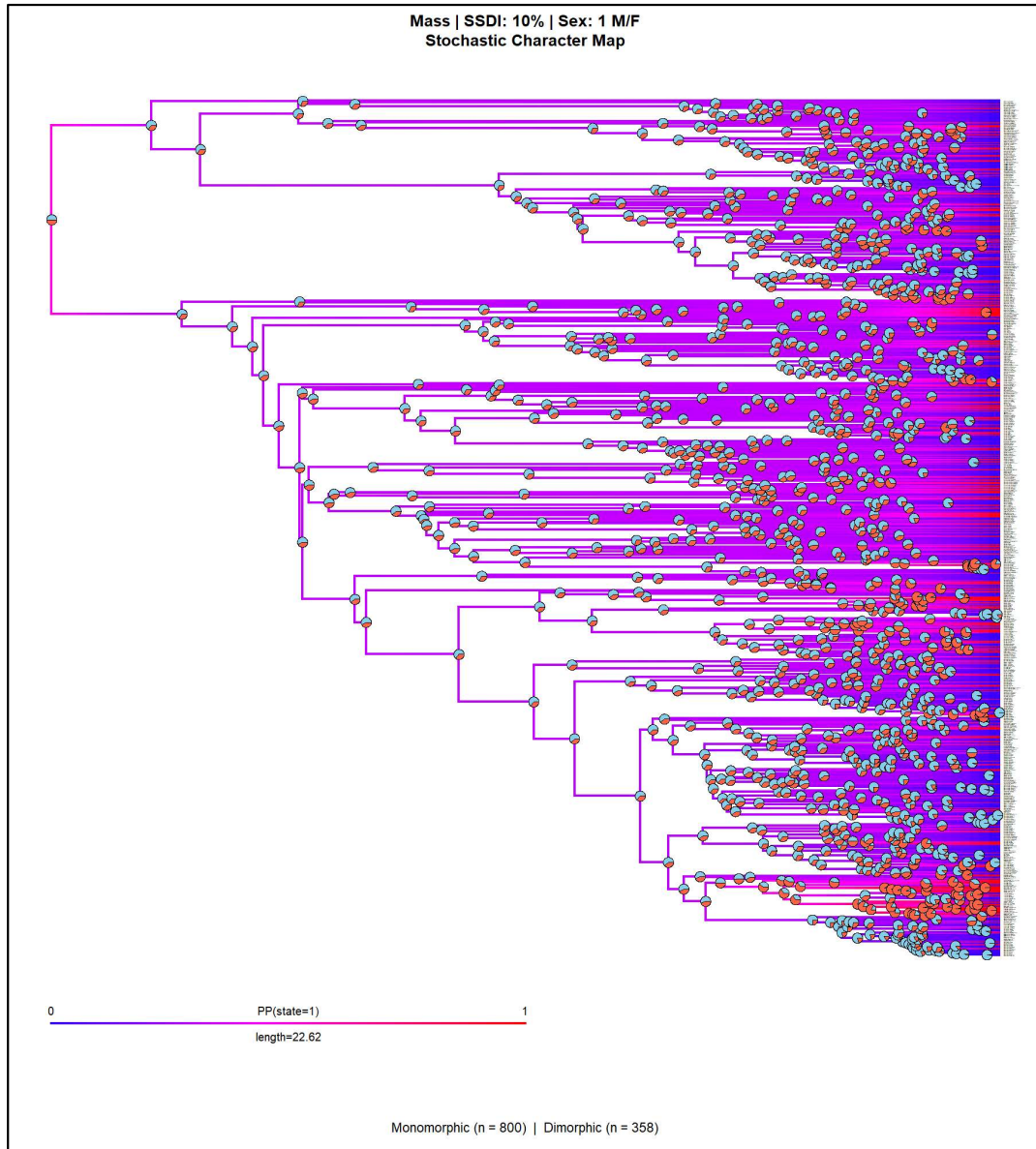


Figure S17. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 886) or dimorphic (red, n = 272) state at a given node.

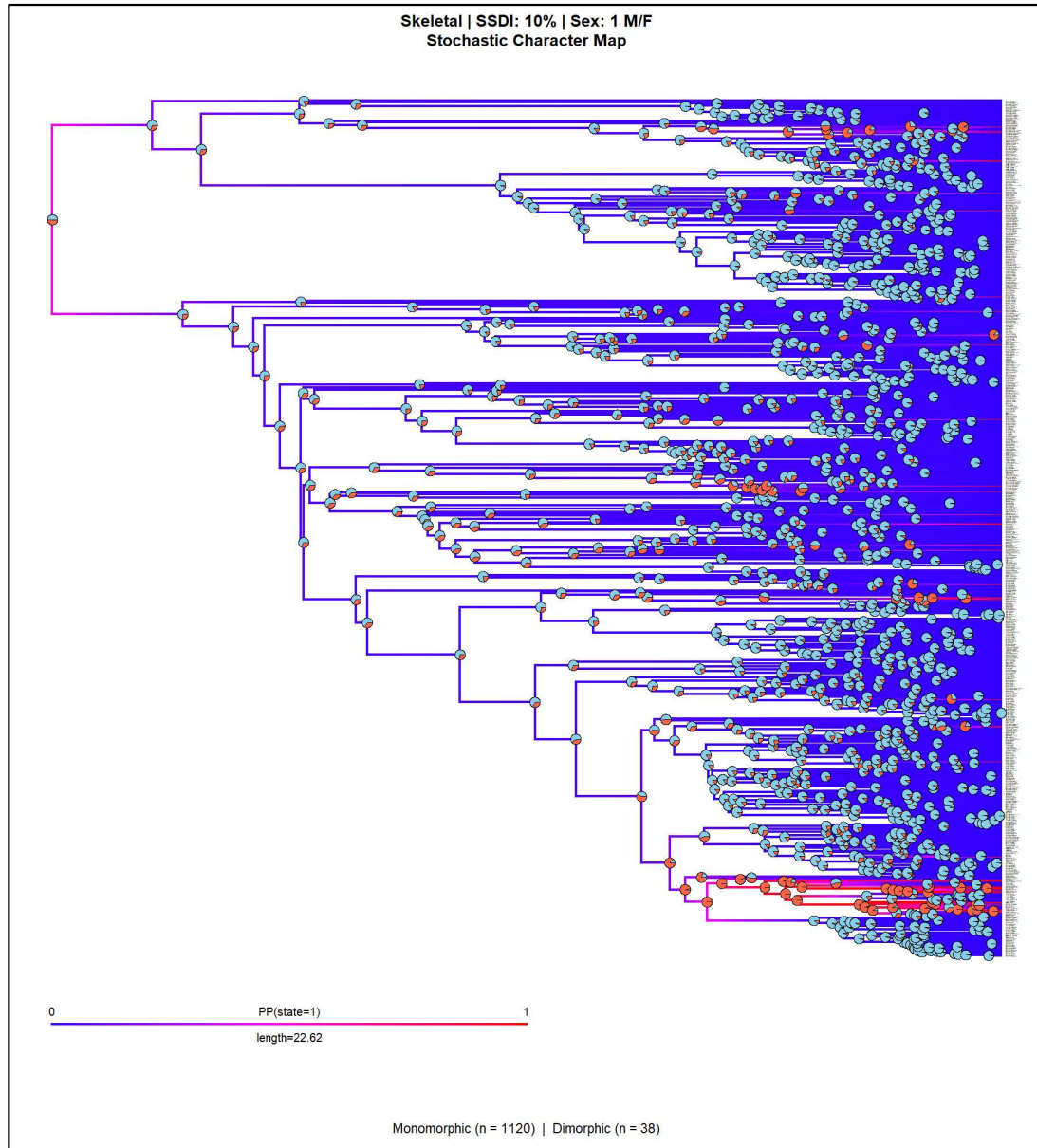


Figure S18. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 1,120) or dimorphic (red, n = 38) state at a given node.

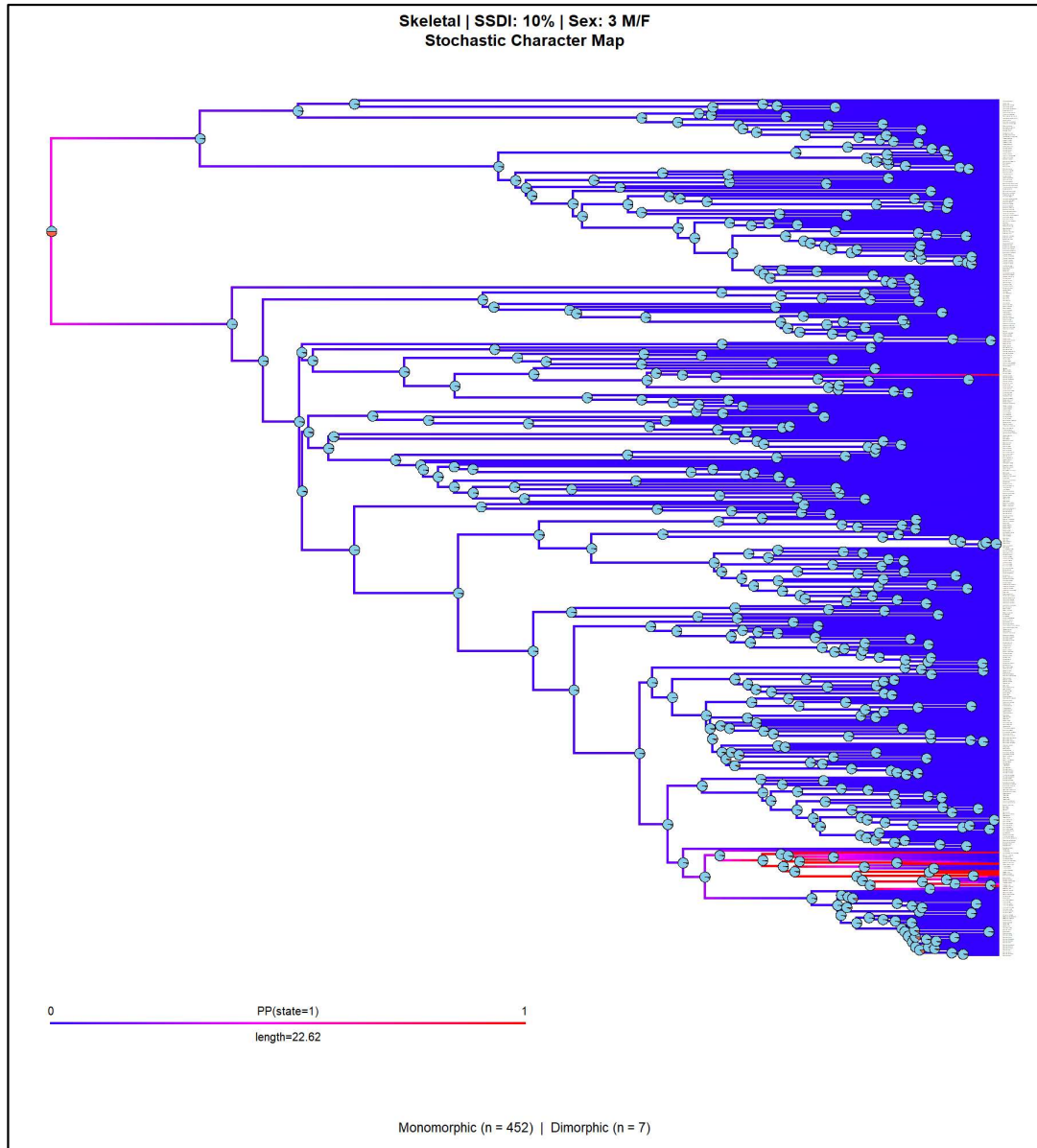


Figure S19. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 452) or dimorphic (red, n = 7) state at a given node.

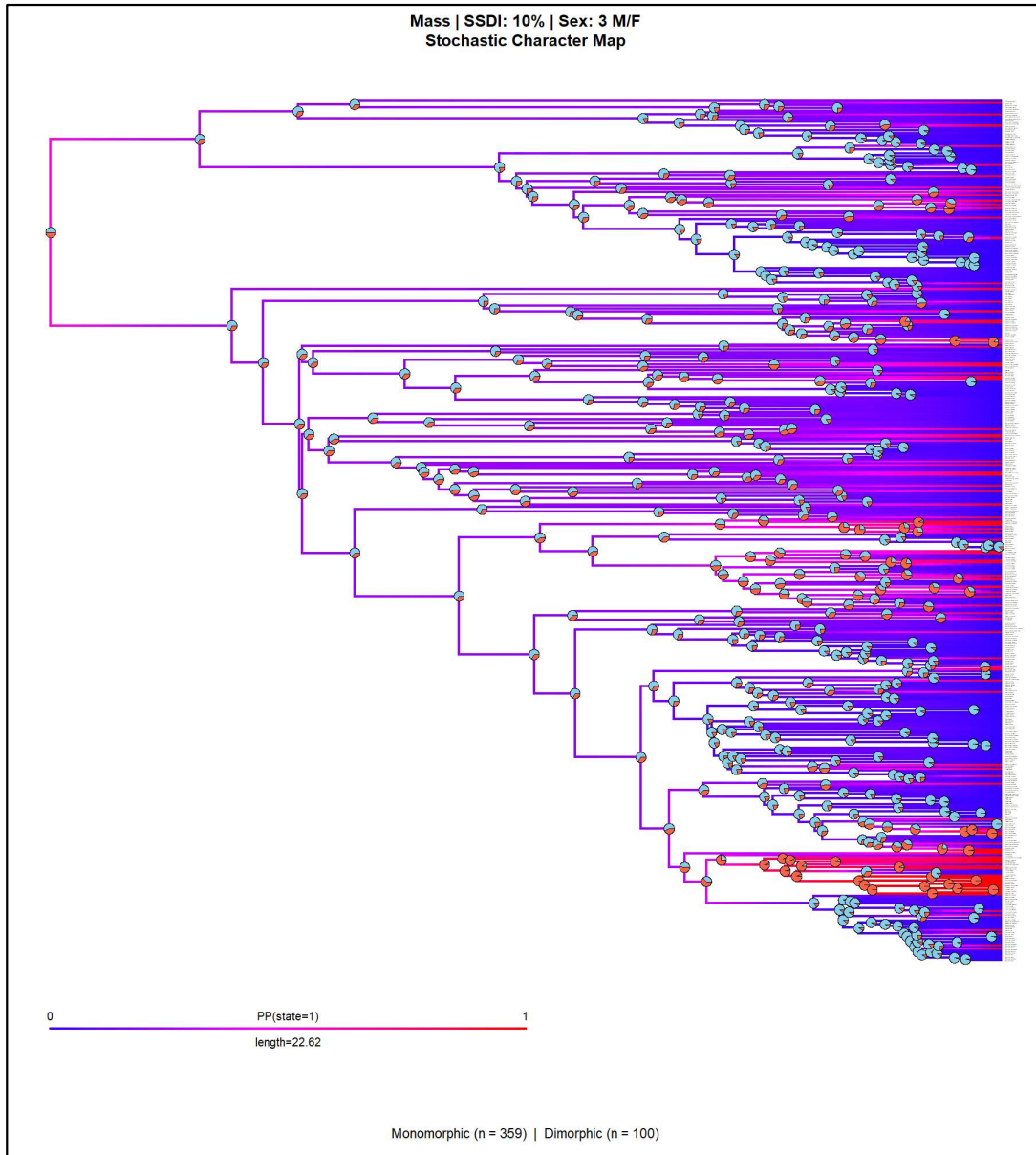


Figure S20. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 359) or dimorphic (red, n = 100) state at a given node.

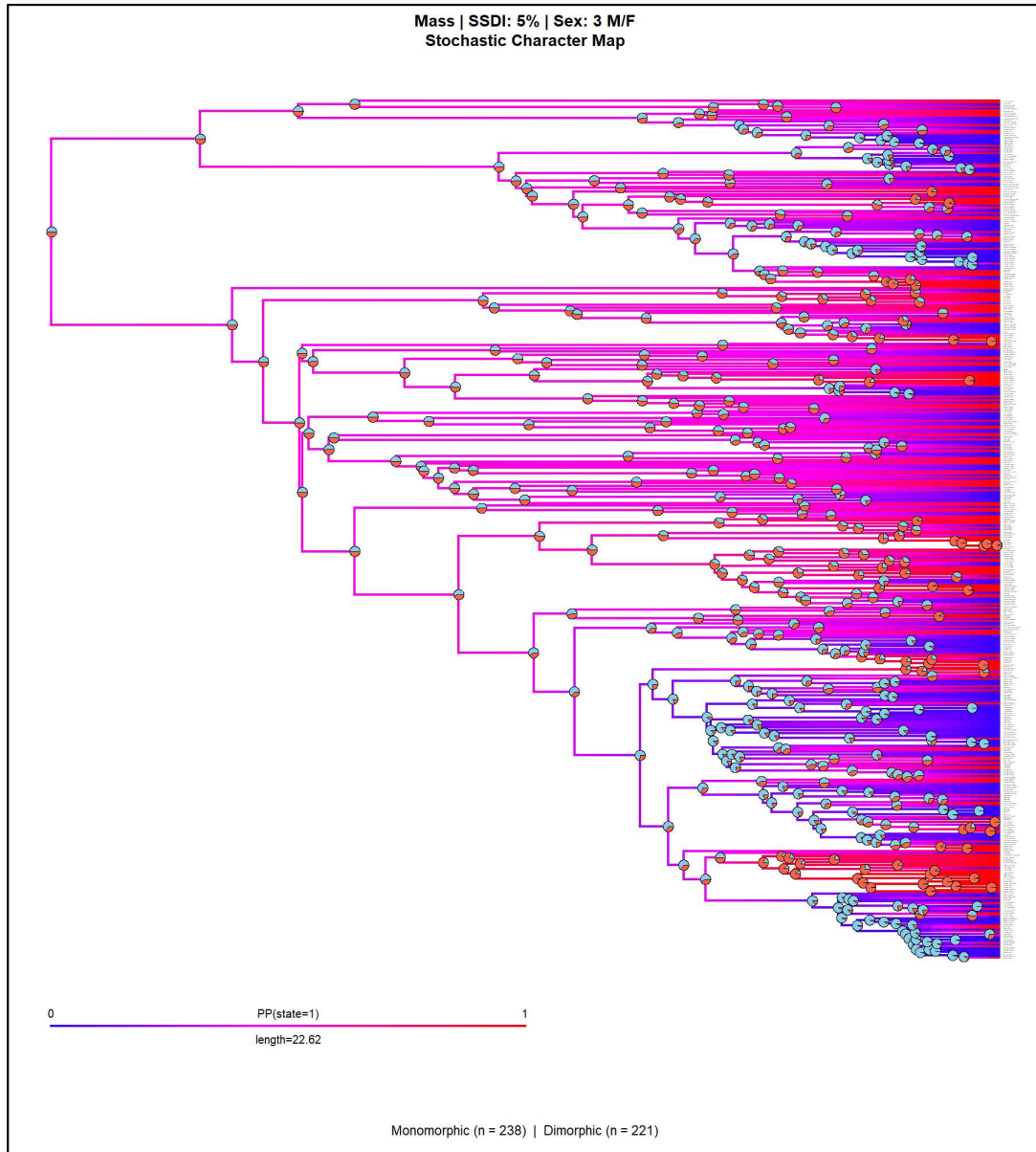


Figure S21. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 238) or dimorphic (red, n = 221) state at a given node.

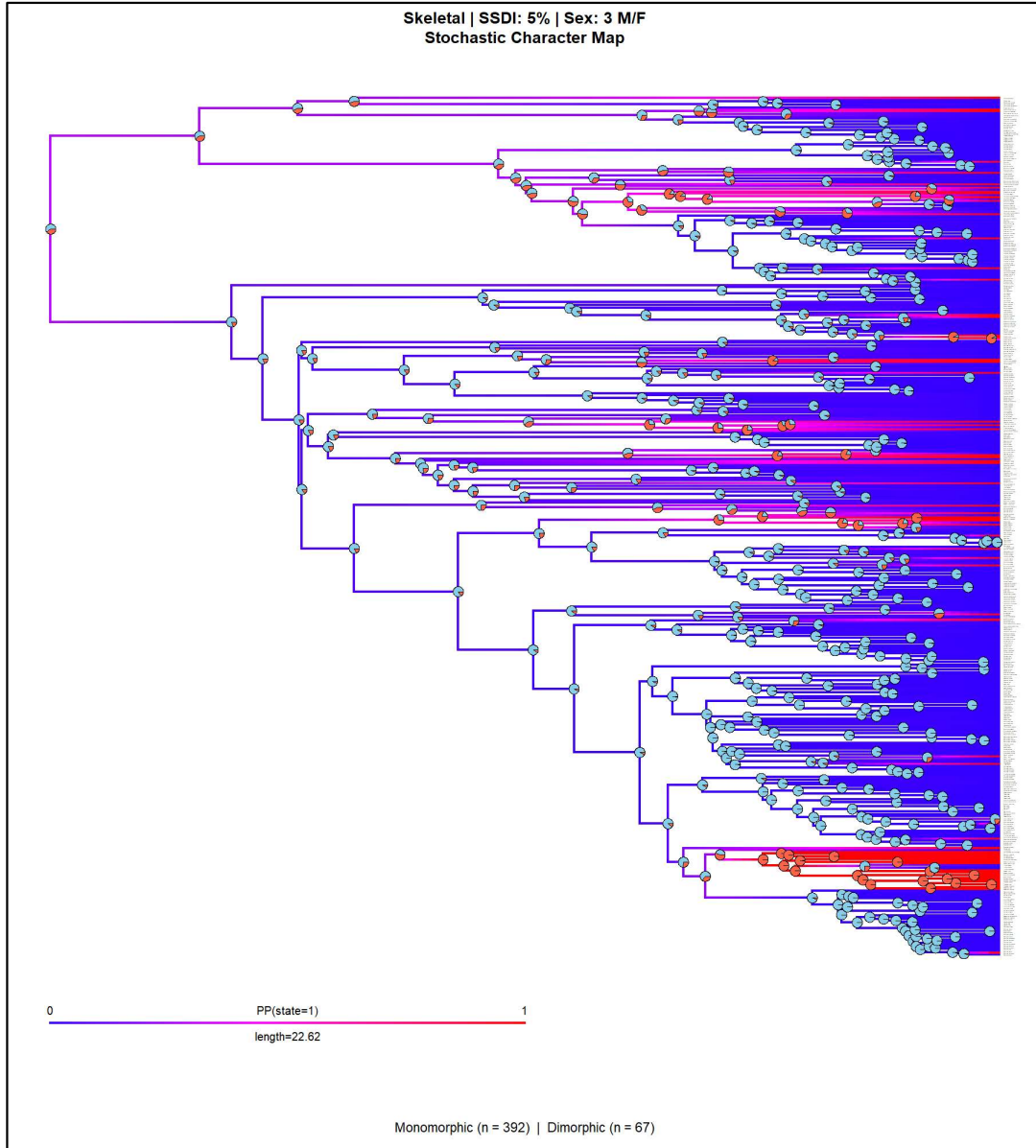


Figure S22. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 392) or dimorphic (red, n = 67) state at a given node.

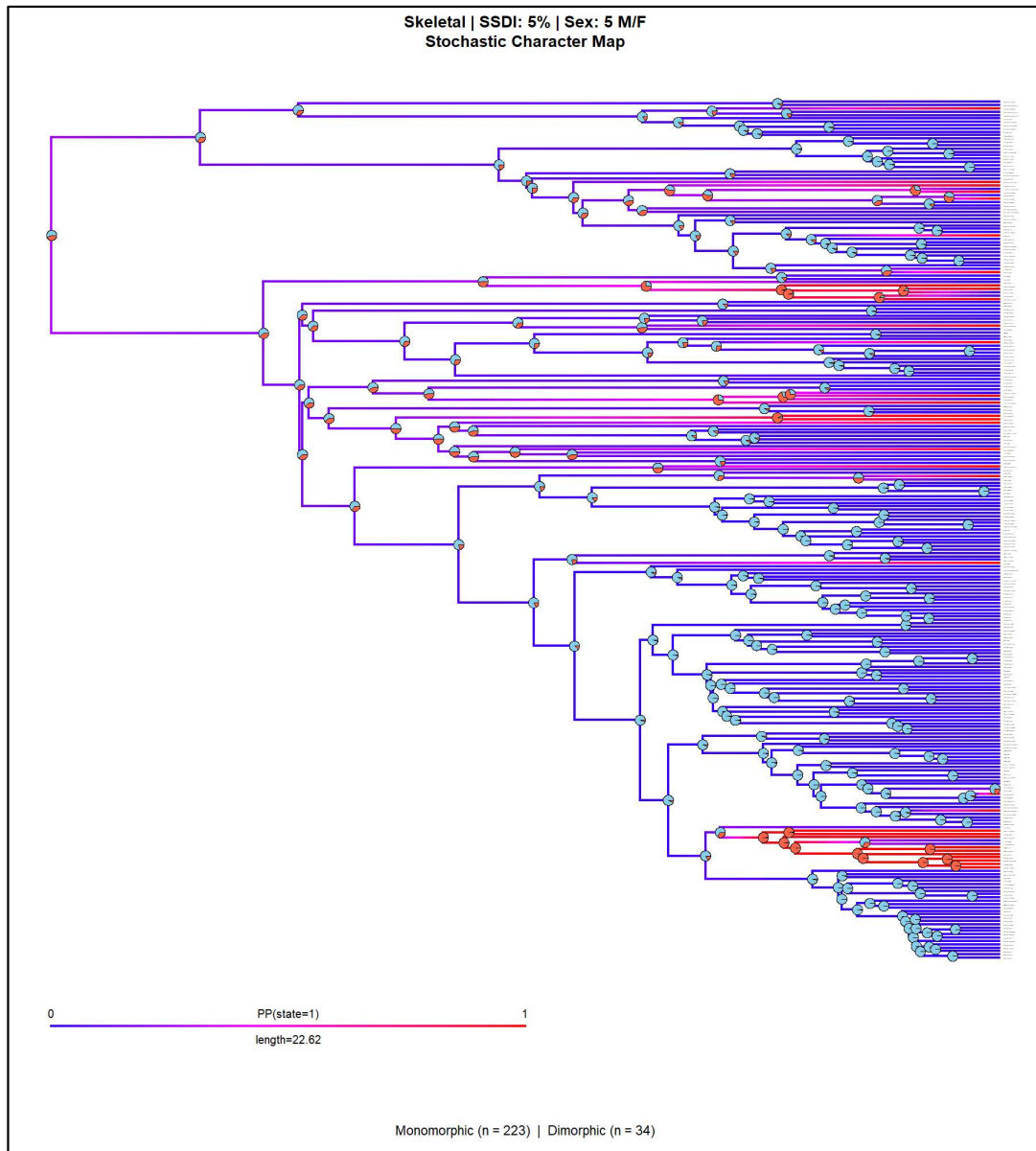


Figure S23. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 223) or dimorphic (red, n = 34) state at a given node.

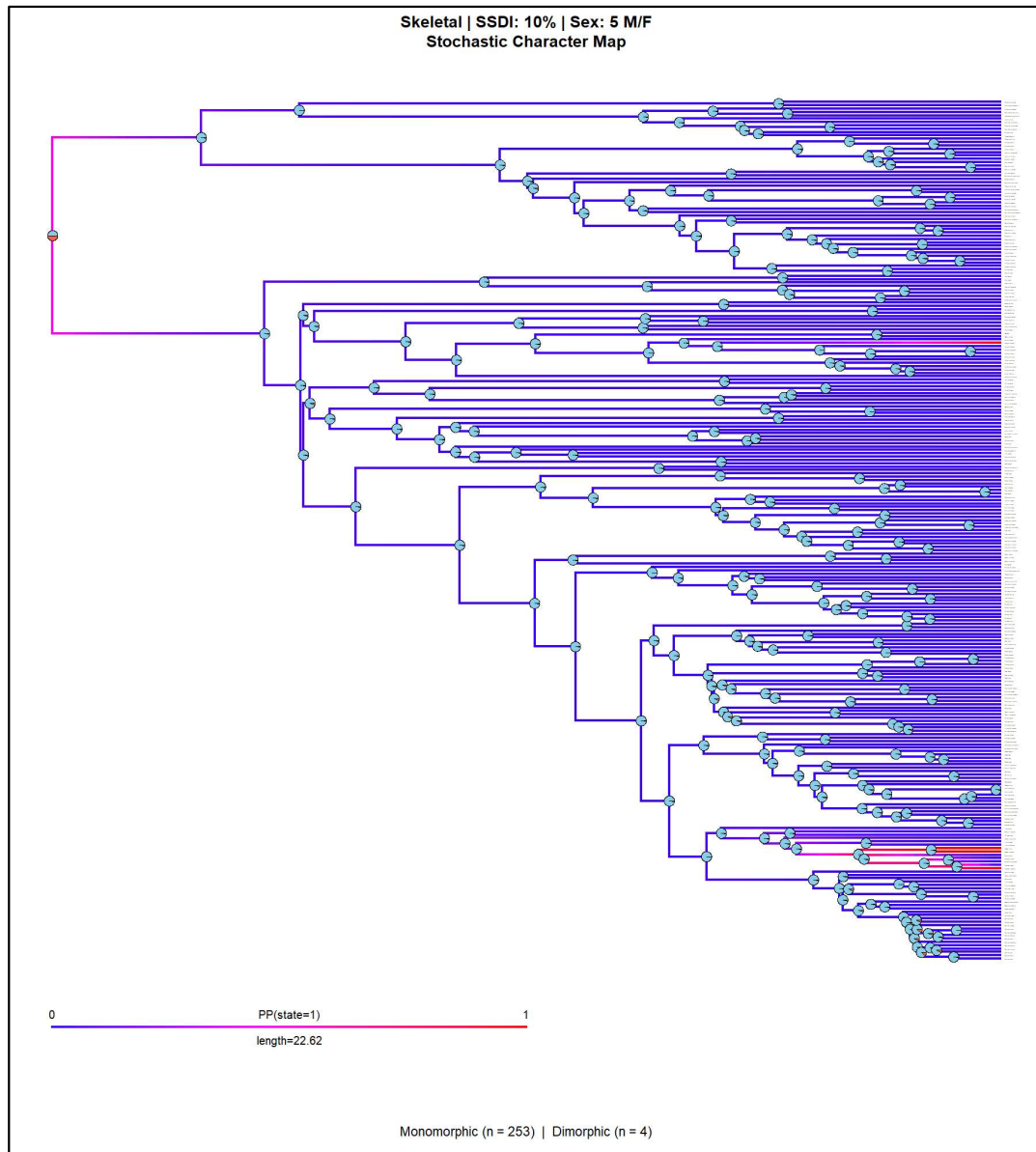


Figure S24. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 253) or dimorphic (red, n = 4) state at a given node.

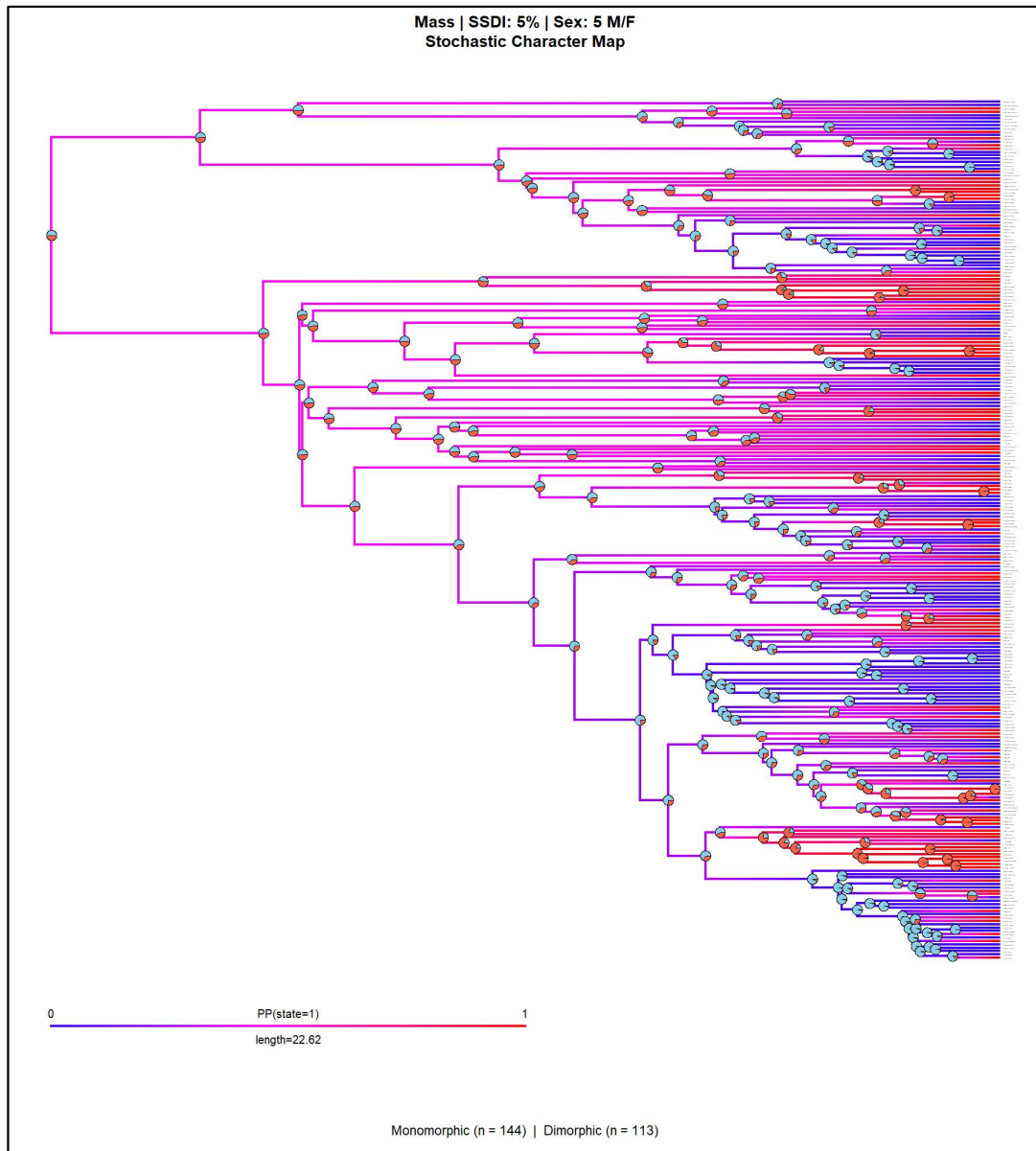


Figure S25. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 144) or dimorphic (red, n = 113) state at a given node.

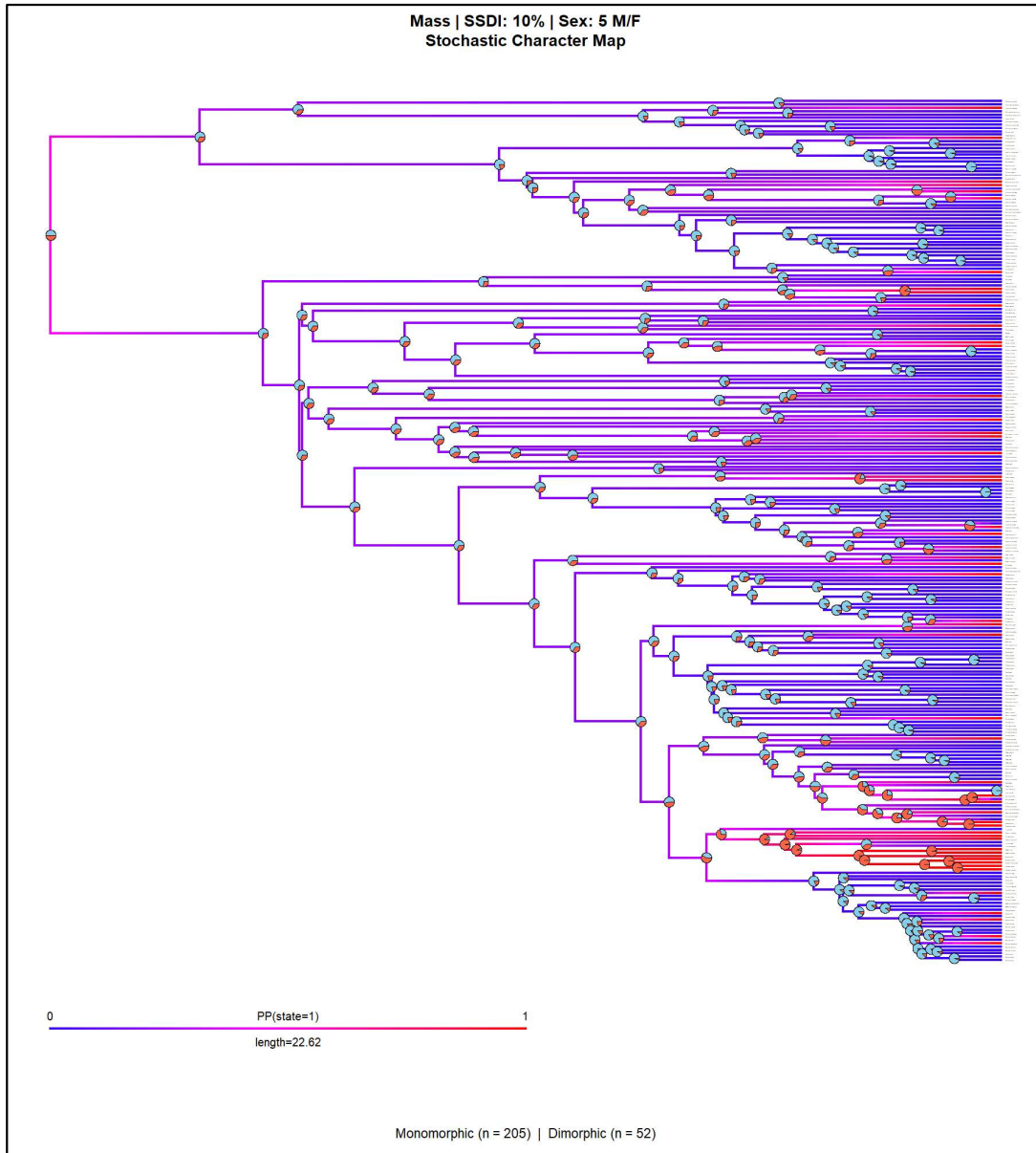


Figure S26. Ancestral state reconstruction under an ARD model across 1,800 simulations of sexual dimorphism across passerine birds using stochastic character mapping. The branches represent the mean probability of being in a sexually dimorphic versus monomorphic state; scale bar = 22.62 million years. The root reflects the Fitzjohn root prior method. The branch colors of blue (0) are high certainty of monomorphic, and red (1) are high certainty of dimorphic, with intermediate colors reflecting uncertainty. Similarly, the pie charts reflect the maximum-likelihood, also under the ARD model, of being in the monomorphic (blue, n = 205) or dimorphic (red, n = 52) state at a given node.

State-Dependent Evolutionary Rates Across All Threshold Combinations								
BMM; Y ~ mass; Wilcoxon paired test; rates summarised by mode								
SSDI [†]	Sex	Species			Sims	BMM Rates (σ^2 / time)		
		N	Mono	Dim		Rate (mono)	Rate (dim)	Fold change p
Skeletal								
5%	1 M/F	1158	886	272	1800	2.56×10^{-4}	2.44×10^{-4}	0.953 6.91e-01
5%	3 M/F	459	392	67	1800	2.84×10^{-4}	3.09×10^{-4}	1.090 < 2e-16
5%	5 M/F	257	223	34	1800	2.58×10^{-4}	3.58×10^{-4}	1.391 < 2e-16
10%	1 M/F	1158	1120	38	1800	2.51×10^{-4}	2.93×10^{-4}	1.167 < 2e-16
10%	3 M/F	459	452	7	1800	2.85×10^{-4}	3.51×10^{-4}	1.229 < 2e-16
10%	5 M/F	257	253	4	1800	2.70×10^{-4}	2.93×10^{-4}	1.086 < 2e-16
Mass								
5%	1 M/F	1158	499	659	1800	2.50×10^{-4}	2.56×10^{-4}	1.026 2.96e-01
5%	3 M/F	459	238	221	1800	2.73×10^{-4}	3.06×10^{-4}	1.123 < 2e-16
5%	5 M/F	257	144	113	1800	2.62×10^{-4}	2.83×10^{-4}	1.082 < 2e-16
10%	1 M/F	1158	800	358	1800	2.59×10^{-4}	2.39×10^{-4}	0.923 < 2e-16
10%	3 M/F	459	359	100	1800	2.87×10^{-4}	2.86×10^{-4}	0.998 < 2e-16
10%	5 M/F	257	205	52	1800	2.60×10^{-4}	3.08×10^{-4}	1.182 < 2e-16
Dichromatism								
NA	NA	1822	1098	724	1800	2.00×10^{-4}	2.61×10^{-4}	1.303 < 2e-16
[†] Teal = Skeletal; Orange = Mass; Purple = Dichromatism. Bold p-values indicate significance at $\alpha = 0.05$. Fold change = mode(dim rate) / mode(mono rate). All models used 1,800 simulations.								

Table S1. State-dependent multivariate evolutionary rates across all datasets and threshold combinations in Passerine birds. Evolutionary rates were summarized by mode and were estimated using Brownian motion multivariate models (BMMs) simulated with stochastic character maps. Each dataset ran 1,800 simulations each. All models ran with mass as a covariate for the 12 skeletal traits ($Y \sim \text{mass}$), with 2 possible underlying states: monomorphic (Mono) or dimorphic (Dim). Rate (mono) and Rate (dim) are modal evolutionary rates, sigma squared per unit time, within each group, by estimating the density distribution of the evolutionary rates. Fold change is the modal dimorphic rate divided by the modal monomorphic rate. The p-value refers to the two-sided Wilcoxon test for the paired rate estimates across simulations. The table is split into 3 datasets: Skeletal (teal), Mass (orange), and Dichromatism (purple). SSDI refers to the sexual size dimorphism index, which has 2 possible thresholds: 5% and 10% differences between the sexes within a

species. Within each SSDI threshold, there are also 3 thresholds for the minimum number of individuals per sex per species: 1, 3, and 5. Species under the skeletal and mass datasets were classified as dimorphic when the SSDI value was greater than or equal to the SSDI threshold and classified as monomorphic when less than the SSDI threshold. Under the dichromatism model, species were classified as monochromatic when their Dichro value was 0, and dichromatic when the absolute value of their Dichro value was positive.