

# Male-biased sexual selection, but not sexual dichromatism, predicts speciation in birds

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Received October 9, 2019

Accepted January 13, 2021

Sexual selection is thought to shape phylogenetic diversity by affecting speciation or extinction rates. However, the net effect of sexual selection on diversification is hard to predict because many of the hypothesized effects on speciation or extinction have opposing signs and uncertain magnitudes. Theoretical work also suggests that the net effect of sexual selection on diversification should depend strongly on ecological factors, though this prediction has seldom been tested. Here, we test whether variation in sexual selection can predict speciation and extinction rates across passerine birds (up to 5812 species, covering most genera) and whether this relationship is mediated by environmental factors. Male-biased sexual selection, and specifically sexual size dimorphism, predicted two of the three measures of speciation rates that we examined. The link we observed between sexual selection and speciation was independent of environmental variability, though species with smaller ranges had higher speciation rates. There was no association between any proxies of sexual selection and extinction rate. Our findings support the view that male-biased sexual selection, as measured by frequent predictors of male-male competition, has shaped diversification in the largest radiation of birds.

**KEY WORDS:** Macroevolution, phylogenetics, sexual selection, speciation.

Sexual selection is a ubiquitous evolutionary process whose effect on phylogenetic diversification is much debated (Lande 1981, 1982; West-Eberhard 1983; Seddon et al. 2008; Cooney et al. 2018; Tsuji and Fukami 2020). Sexual selection can promote speciation because it operates on traits that can create reproductive isolation when they diverge between lineages, such as signals and preferences involved in mate selection (Lande 1981, 1982; Safran et al. 2013), sperm-egg interactions (Swanson and Vacquier 1998), or genital morphology (Sloan and Simmons 2019). Sexual selection could also promote speciation or prevent extinction by purging deleterious mutations (Whitlock and Agrawal 2009), fixing beneficial ones (Whitlock 2000), and accelerating adaptation in different environments (Lorch et al. 2003; Candolin and Heuschele 2008; Cally et al. 2019). Conversely, sexual selection might hinder speciation or make extinction more likely by favoring traits that improve mating success but reduce population fitness (Kokko and Jennions 2008; Rankin et al. 2011; Holman and Kokko 2013; Fromhage and

Jennions 2016). For example, species with costly sexual signals may be less resilient to environmental change (Kokko and Brooks 2003). Extinction risk may also be exacerbated by sexual selection causing maladaptation (gender load) in female traits that are genetically correlated with sexually selected male traits (Pischedda and Chippindale 2006; Bonduriansky and Chenoweth 2009; Harano et al. 2010; Pennell and Morrow 2013; Berger et al. 2014).

Although numerous studies have examined the relationship between sexual selection and speciation or extinction rates (Barraclough et al. 1995; Morrow et al. 2003; Seddon et al. 2008, 2013; Kraaijeveld et al. 2011; Huang and Rabosky 2014), the availability of more complete phenotypic, ecological and phylogenetic data (Jetz et al. 2012), together with significant advances in phylogenetic methods (Rabosky 2014; Harvey Michael et al. 2017), present new opportunities to test whether and how sexual selection drives diversification. Furthermore, the diversity of outcomes and approaches in previous studies suggests that the

association between species diversity and sexual selection is far from clear (reviewed in Tsuji and Fukami 2020).

A possible reason for the above uncertainty regarding the relationship between sexual selection and diversification is that this relationship may strongly depend on the environment. Theoretical work predicts that sexual selection should have a more positive effect on adaptation and population fitness in variable environments relative to stable ones (Long et al. 2012; Connallon and Hall 2016). In stable environments, consistent selection depletes genetic variation at sexually concordant loci (i.e., loci where the same allele is fittest for both sexes). In these environments, genetic variation remains disproportionately at sexually antagonistic loci, leading to stronger gender load and reduced net benefits of sexual selection (Connallon and Hall 2016). By contrast, in spatially or temporally variable environments, sexual selection can enhance local adaptation. For example, in Darwin's finches, divergent beak morphology is an adaptation to local food availability that has been maintained through assortative mating (Huber et al. 2007). Under these circumstances, we predict that the effect of sexual selection on rates of divergence may depend on the variability of the species' environment. Despite the potential interaction between sexual selection and environmental variability in diversification, phylogenetic tests are currently lacking.

Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification (Barraclough et al. 1995; Morrow et al. 2003; Seddon et al. 2008, 2013; Huang and Rabosky 2014) because their biology and phylogenetic relationships are comparatively well known. A 2011 meta-analysis covering 20 primary studies of birds and other taxa found a small but significant positive association between sexual selection and speciation, with the average effect size in birds stronger than in mammals but weaker than in insects or fish (Kraaijeveld et al. 2011). However, there was large variation in effect size estimates across the 20 studies, likely reflecting differences in methodology, such as metrics used to characterize speciation and sexual selection, in addition to true biological differences. More recently, Huang and Rabosky (2014) found no association between sexual dichromatism and speciation ( $n = 918$  species) in a study using spectrophotometric measurements of museum specimens (Armenta et al. 2008) and tip-rate estimates from a molecular-only phylogeny (Jetz et al. 2012). Similarly, Cooney et al. (2017) found no effect of sexual dichromatism on diversification across 1306 pairs of species, using dichromatism scores provided by human observers. More recently, social polygyny (a proxy for sexual selection) was found to have a positive association with speciation rate across 954 species of birds (Iglesias-Carrasco et al. 2019). We summarize the major findings from previous studies testing the association between sexual selection and speciation in birds since Kraaijeveld et al. (2011) meta-analysis (Table 1).

Here, we investigate the association between sexual selection and diversification in birds while building upon previous approaches in multiple ways. We use two measures of the strength of sexual selection: sexual dichromatism (Dale et al. 2015), as well as an index of male-biased sexual selection, which captures (co)variation in sexual size dimorphism, social polygyny, and paternal care. We use these two measures because sexual dichromatism does not always signal the presence of strong sexual selection and vice versa (Dale et al. 2015). For example, male and female dunnocks (*Prunella modularis*) are similarly colored yet sexual selection appears to be strong (Davies and Houston 1986). Furthermore, a recent comparative study found a negative relationship between dichromatism and another sexually selected trait (song) across species, suggesting that a multi-trait focus would improve estimates of sexual selection intensity (Cooney et al. 2018). Additionally, our analysis includes multiple ecological and environmental variables, allowing us to control for potential confounds, to identify environmental factors, including spatial and temporal environmental variability, interact with sexual selection as theory predicts (Connallon and Hall 2016).

We use multiple approaches for quantifying speciation and extinction rates at the tips of phylogenetic trees, including Bayesian analysis of macroevolutionary mixtures (BAMM; Beaulieu and O'Meara 2015; Moore et al. 2016; Rabosky 2016; Rabosky et al. 2017), as well as older but reliable tip-rate statistics, namely diversification rate ( $\lambda_{DR}$ ) and node density ( $\lambda_{ND}$ ) (Jetz et al. 2012). Our results show that (i) a composite measure of sexual selection, but not sexual dichromatism, significantly predicts speciation rates; (ii) the significant association between the composite measure of sexual selection and speciation rate is largely driven by sexual size dimorphism; (iii) species with smaller ranges have higher speciation rates; and (iv) there is no evidence that environmental variables or their interaction with sexual selection have an impact on diversification rates. Therefore, we provide evidence at a very large scale that sexual selection can have positive effects on diversification in the largest radiation of birds. Furthermore, we suggest that the use of sexual dichromatism as the sole proxy for sexual selection should be reconsidered because it appears to be inconsistently associated with the operation of sexual selection.

## Materials and Methods

We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ( $n = 5812$  species; 58% of all birds). Specifically, we (i) compiled datasets for sexual dichromatism/selection strength and environmental variability, (ii) obtained estimates of speciation and extinction rates across passerines, and (iii) conducted phylogenetic generalized least-squares

**Table 1.** Previous studies testing the association between sexual selection and speciation.

Study	Taxa studied	Proxy for sexual selection	Support?	Outcome
Kraaijeveld et al. (2011)	Meta-analysis across all animals	Plumage dichromatism	Yes	Across all birds, evidence in 4/6 studies
Kraaijeveld et al. (2011)	Meta-analysis across all animals	Mating system	Yes	Across all birds, evidence in 4/4 studies
Kraaijeveld et al. (2011)	Meta-analysis across all animals	Size dimorphism	Mixed	Across all birds, evidence in 1/2 studies
Maia et al. (2013)	Starlings ( <i>Sturnidae</i> ), 113 species	Ornamental innovations	Yes	Lineages with derived melanosomes (an ornamental innovation) diversify faster
Huang and Rabosky (2014)	Across birds, ~1000 species	Plumage dichromatism	No	No association between different measures of dichromatism and diversification
Gomes et al. (2016)	Estrildid finches, 134 species	Color ornamentation	No	More ornamented lineages do not speciate more (but ornaments do evolve faster)
Cooney et al. (2017)	Across birds, 1306 pairs of species	Plumage dichromatism	No	Plumage dichromatism does not predict diversification rates, but might reduce the rate of fusion of lineages after secondary contact
Janicke et al. (2018)	Meta-analysis across all animals	Bateman gradient	Yes	Steepness of Bateman gradient in males predicts species richness
Mason et al. (2017)	Thraupids and Furnariids, 581 species	Vocal evolution	Yes	Bursts of speciation and song evolution are coincident
Iglesias-Carrasco et al. (2019)	Across birds, 954 species	Degree of polygyny	Yes	A higher degree of polygyny and rapid molecular evolution are linked with rate of diversification
Hosner et al. (2020)	Gallopheasants, 22 species	Sexual dimorphism (range of traits)	No	No role of sexual selection in relation to diversification
Price-Waldman et al. (2020)	Thraupidae, 355 species	Plumage complexity	Yes	Elevated rates of plumage complexity evolution are associated with higher speciation rates
		Size dimorphism	Yes	Sexual size dimorphism predicts two out of three measures of speciation rates
This study	Across passerines, 5812 species	Plumage dichromatism	No	There was no link between plumage dichromatism (measured from spectral info or RGB values) and any speciation rate

Studies were obtained by searching “Web of Science” for articles published from 2011 for terms containing “speciation,” “diversification,” and “sexual selection.” We summarized all the studies we found relevant and comparable to our study.

(PGLS) regressions. Analyses are documented with reproducible code in the Supporting Information.

## COMPILING DATA FOR SEXUAL SELECTION AND ENVIRONMENTAL STRESS

### *Sexual dichromatism*

We used a previously published measure of sexual dichromatism for 5983 species of passerines (Dale et al. 2015). Briefly, Dale et al. (2015) obtained sex-specific red-green-blue (RGB) values across six body patches (nape, crown, forehead, throat, upper breast, and lower breast) from *Handbook of the Birds of the World* (Del Hoyo et al. 2011). The relative contribution of male and female RGB color values were averaged across body patches and provide “male-like” and “female-like” plumage scores. Here we use the absolute difference between male and female plumage scores as an estimate of sexual dichromatism. Technically, this measures differences in the “degree of maleness” between males and females, rather than sex differences in color per se (i.e., dichromatism in the strict sense). For example, the metric would fail to capture dichromatism when both the male and female possess a single, but differently colored “male-like” patch. However, the metric is highly correlated with dichromatism measured from spectral data (see next).

Additionally, we used another measure of dichromatism corresponding to color distance in avian color space derived from spectral data (Armenta et al. 2008). These measurements include variation in the ultraviolet and bird-visible range and—unlike the RGB measures—are sourced from museum specimens as opposed to illustrations. The spectrophotometry data cover only 581 passerine species (10-fold fewer than the RGB data), although there was a substantial correlation between the two dichromatism measures ( $r = 0.79$ ; Fig. S10).

### *Male-biased sexual selection*

Sexual dichromatism is likely to be imperfectly correlated with variation in the strength of sexual selection across taxa. For this reason, we sourced an additional measure of sexual selection (Dale et al. 2015), referred to here as the “index of male-biased sexual selection.” This index is the first principal component from a phylogenetic principal component analysis (PPCA) of three characteristics positively associated with sexual selection (sexual size dimorphism, social polygyny, and [lack of] paternal care). The variables included in this index have all been positively linked to the intensity of sexual selection, and are usually correlated (Björklund 1990; Owens and Hartley 1998; Dunn et al. 2001), which is why they were combined into a single metric in previous studies (Dale et al. 2015). This measure of male-biased sexual selection is available for only 2465 species, and shows a moderate correlation with the RGB measure of sexual dichromatism ( $r = 0.34$ ; Fig. S12).

### *Environmental variables*

We obtained estimates of species range size using expert range maps (BirdLife International and Handbook of the Birds of the World 2017). The names of 1230 species in the Birdlife database (Hoyo and Collar 2016) have been recently changed, so we manually matched these taxa with the names used in the sexual dichromatism dataset (Hoyo and Collar 2016). For each species’ range, we obtained estimates of climatic conditions by extracting 1000 random point samples of each bioclimatic variable. We extracted 19 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature and precipitation) with 30-sec ( $\sim 1 \text{ km}^2$ ) spatial resolution (Fick and Hijmans 2017). From the 1000 values of each bioclimatic variable, we obtained means and standard deviations for each species. Using the same spatial sampling, we extracted means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial (LIG; 120,000–140,000 years ago) (Otto-Bliesner et al. 2006). To estimate variability in the energy available to species, we obtained the mean and standard deviation of net primary productivity (NPP) values between 2000 and 2015 across each species distribution. Estimates of NPP had 30-sec resolution and were obtained through Moderate Resolution Imaging Spectroradiometer primary production products stage 3 (MOD17A3) (Zhao et al. 2005). We provide these data as a potentially useful data resource (see Supporting Information).

### *Generating biologically relevant predictors for environmental stress*

Given that stressful environments are expected to interact with sexual selection and have a positive effect on adaptation (Cally et al. 2019), we used the extracted environmental variables from each species range size to create predictors of environmental variation/stress. We used (i) the average NPP in each species’ range and (ii) the log-transformed range size as potentially informative predictors of speciation rates. We also used three environmental predictors derived from bioclimatic data. These predictors relate to seasonal climate variation, spatial climate variation, and long-term climate variation. To obtain seasonal climate variation we used (iii) mean values of temperature seasonality (BIO4) for each range. (iv) To estimate levels of spatial environmental variation a species may endure, we used the first principle component (PC1) from a PCA on standard deviations from all bioclimatic variables, excluding temperature and precipitation seasonality (BIO4 and BIO15). PC1 was heavily loaded towards bioclimatic variables relating to temperature, thus PC1 largely reflects the variation in temperature across a species’ range (Table S1). A taxon’s range size often correlates with speciation and extinction rates (Rosenzweig 1995; Castiglione et al. 2017), so we controlled for the correlation between environmental spatial variation and species’

range sizes—where larger ranges have larger variation in PC1—using the residuals of a fitted general additive model (Fig. S1) as a predictor. To obtain long-term variation in climates for each species range, we took ( $v$ ) the first principal component of the absolute difference in the bioclimatic variables between the LIG and current values. Similar to spatial variation, the long-term climate variation is primarily loaded to temperature differences between the LIG and current climates (Table S2 and Fig. S2). The five predictors of environmental variability are not strongly correlated (Fig. S3). Details and R code to generate these predictors can be found within the Supporting Information.

### ESTIMATING EXTINCTION AND SPECIATION

Phylogenetic information was obtained from [www.birdtree.org](http://www.birdtree.org) (Jetz et al. 2012). We used a maximum clade credibility (MCC) tree from 2500 samples of the posterior distribution ( $n = 5965$ ) as the main phylogenetic hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using tip-rate measures (1000 trees) and BAMM (100 trees) (Rabosky 2014). These trees had crown clades with a topology that was heavily constrained on the basis of a previously published study (“Hackett backbone”; Hackett et al. 2008) and were constructed using a pure birth (Yule) model. We calculated three different tip-rate metrics of speciation and one of extinction across all trees.

Diversification is the result of two processes, speciation and extinction through time. To estimate speciation rates, we first obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES; also referred to as diversification rate/DR) is derived from the sum of edge lengths from each tip towards the root, with each edge towards the root having the length down-weighted (Jetz et al. 2012; Quintero and Jetz 2018; Rabosky et al. 2018). Crucially, studies have suggested that DR and ND (henceforth referred to as  $\lambda_{DR}$  and  $\lambda_{ND}$ ) are more reflective estimates of speciation than diversification. Because  $\lambda_{DR}$  and  $\lambda_{ND}$  cannot account for whole-clade extinctions and thus underestimate extinction rate, which makes the composite measure of diversification more dependent on speciation (Belmaker and Jetz 2015; Title and Rabosky 2018). Therefore,  $\lambda_{DR}$  is a measure of speciation rate more heavily weighted to recent speciation events while  $\lambda_{ND}$  measures speciation across the root-to-tip path. These tip-rate measures are alternatives to state-dependent diversification models such as quantitative state speciation-extinction (QuaSSE); but, based on previous simulation studies,  $\lambda_{DR}$  and  $\lambda_{ND}$  are robust and intuitive measures that provide high power and low false discovery rate with large phy-

logenies when incorporated into PGLS models (Harvey Michael et al. 2017).

We used BAMM to model the dynamics of speciation and extinction across the 101 phylogenetic trees (one MCC tree and 100 random draws of the posterior). This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo, MCMC) to generate probability distributions of evolutionary rate-shift configurations with variable speciation and extinction rates (Rabosky 2014). These models provide tip-rate estimates of speciation and extinction rate that can be easily used in comparative analyses. The parameters of the 100 BAMM runs are detailed in full in the Supporting Information; briefly, we used a time-variable model with the prior expected number of evolutionary rate shifts set at 100 and prior rates set from the initial tip-level estimates of speciation and extinction using the `BAMMtools` R package (Rabosky et al. 2014). BAMM models were run independently for the 101 phylogenetic trees for 100 million generations. Given the computationally intensive nature of BAMM, runs were conducted across multiple CPUs. Important BAMM parameters (log-likelihood and the number of rate shifts) reached convergence with effective sample size of MCMC samples surpassing 200; an arbitrary value, above which posterior distributions can often be accurately inferred (Tables S3 and S4). Further details of BAMM parameters and output are available in the Supporting Information, with tip-rate means and variances provided. Additionally, given the variability in BAMM estimates, we also provide analysis of BAMM shift configurations and tip-rate estimates from our run on the MCC tree and within a BAMM run on the MCC tree from a genetic-only phylogeny across all birds (Harvey et al. 2017). All analyses were conducted on log rates.

### PHYLOGENETIC COMPARATIVE ANALYSIS

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we used PGLS models in the `nlme` package (Pinheiro et al. 2018). First, we conducted model selection to compare models in which  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ , or  $\mu_{BAMM}$  were the response variable: these tip-rate estimates all came from the same MCC tree (derived from 2500 draws of the posterior distribution; Jetz et al. 2012). For models of  $\lambda_{BAMM}$  and  $\mu_{BAMM}$ , we used the inverse of the variance associated with each tip-rate estimate as weights, to account for the variable precision of the estimates provided by BAMM. For each response variable, we conducted model selection to compare models with different combinations of predictor variables. The most complex model in each set under comparison contained one of the measures of sexual selection (sexual dichromatism or the index of male-biased sexual selection), all of the environmental measures (i.e., log-transformed range size, seasonal temperature variation, spatial temperature variation, long-term temperature variation, and NPP), and all of the two-way

interactions between sexual selection and each of the environmental measures. The simpler models contained all of the same main effects, but had fewer two-way interaction terms (potentially none). Model selection was done in MuMIn using the dredge function (Bartoń 2017). Using the terms from the top-ranked model (ranked by Akaike's information criterion (AICc)), we ran the equivalent model for each of the 1000 phylogenetic trees used to derive  $\lambda_{DR}$ ,  $\lambda_{ND}$  and each of the 100 trees used to derive  $\lambda_{BAMM}$  and  $\mu_{BAMM}$ . Additionally, we investigated the effect of the individual variables used to derive the index of male-biased sexual selection on speciation rate. For these PGLS models we replaced the composite index score with the individual biological variable (sexual size dimorphism, social polygyny and [lack of] paternal care) and ran the equivalent model for 300 phylogenetic trees used to derive  $\lambda_{DR}$ ,  $\lambda_{ND}$ , and 100 trees used to derive  $\lambda_{BAMM}$ .

Across all our analyses we corrected for the phylogenetic signal. Our models used the unique response variables and correlation structure for a given phylogenetic tree. Specifically, for models using tip-rate metrics ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ), we estimated the phylogenetic signal independently for each of the 1000 trees/models. Phylogenetic signal was estimated as Pagel's  $\lambda$  (Pagel 1999) using the `corPagel` function in the `ape` package (Paradis et al. 2004). Alternatively, for models using speciation and extinction estimates derived using BAMM ( $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ), we found that  $\lambda$  was consistently estimated at 1 and hence assumed Brownian motion (using the `corBrownian` function) to estimate the correlation structure. This method enabled us to present model estimates for an MCC tree alongside 1000/100 trees from the posterior distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three datasets corresponding to each measure of sexual selection: dichromatism derived from RGB values of images ( $n = 5812$ ); dichromatism from spectrophotometry ( $n = 581$ ) and the index of male-biased sexual selection ( $n = 2465$ ).

Finally, using the subset of species with an index of male-biased sexual selection, we conducted a phylogenetic path analysis using the `phylopath` R package (Bijl 2018). The phylogenetic path analysis was used to assess causal paths between variables unable to be modeled within the univariate response of PGLS. That is, a phylogenetic path analysis allowed us to model relationships between the predictor variables used in our PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection, and range size to have effects on each other and not just on speciation rate. To minimize path complexity, we used temperature seasonality (BIO4) as the single measure for environmental variability,  $\lambda_{DR}$  as the single measure of speciation, and the tip rates from the MCC tree. Further details of the path analysis, including our rationale for each path's directions, can be found within the Supporting Information along with all other analyses and the relevant R code to reproduce results.

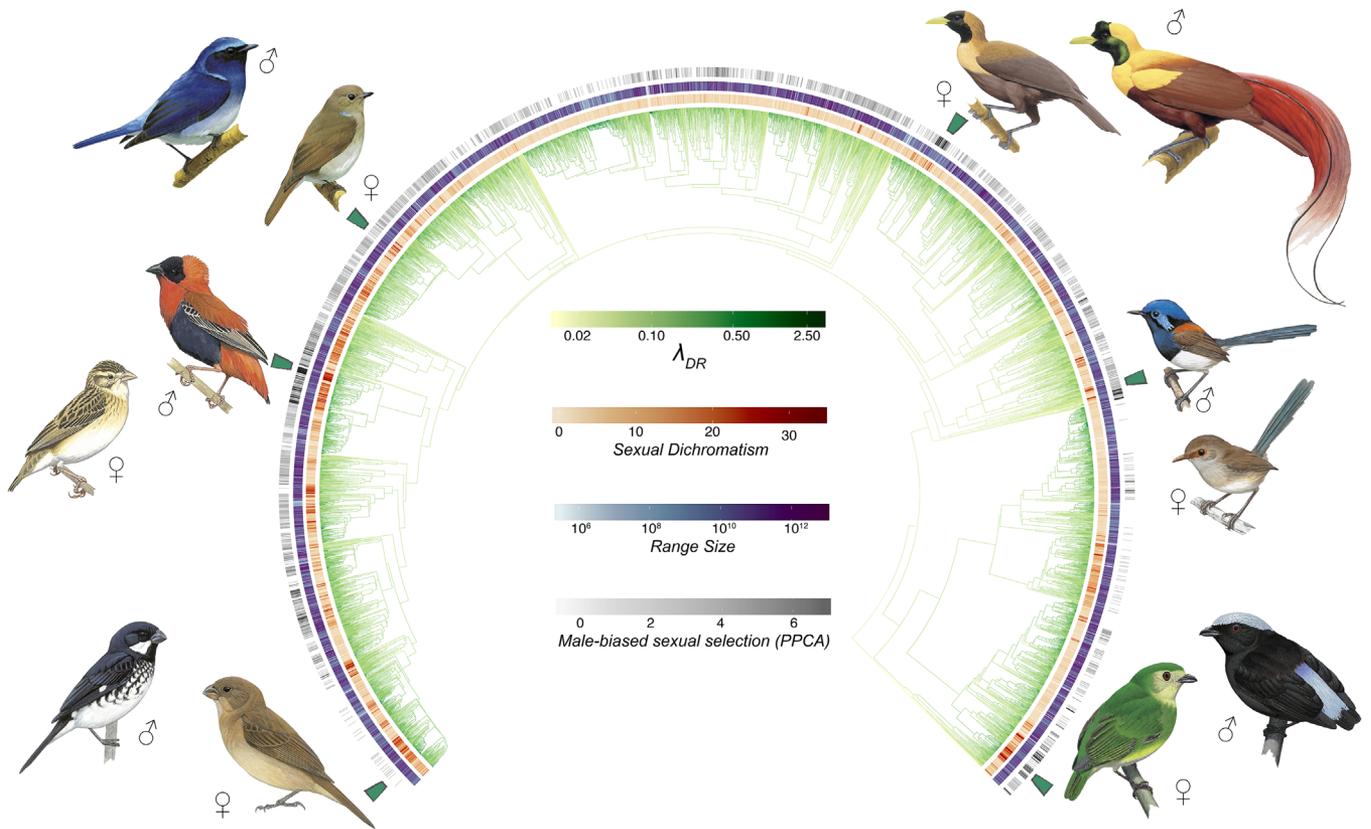
## Results

### MALE-BIASED SEXUAL SELECTION, BUT NOT SEXUAL DICHROMATISM, AFFECTS SPECIATION

We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ( $n = 5812$  species; 58% of all birds; Fig. 1). We found a significant positive association between the index of male-biased sexual selection ( $n = 2465$ ) and  $\lambda_{DR}$  from the MCC tree ( $\beta = 3.89 \times 10^{-2}$ ,  $P = 0.01$ ; Fig. 2B). However, this association was not significant for the other two measures of speciation rate ( $\lambda_{ND}$ :  $\beta = 4.38 \times 10^{-4}$ ,  $P = 0.35$ ;  $\lambda_{BAMM}$ :  $\beta = 9.42 \times 10^{-4}$ ,  $P = 0.76$ ; Fig. 2B). When we took into account phylogenetic uncertainty by running the models using 1000 trees, the distribution of estimates from PGLS models was similar to the estimate from the MCC tree: among the 1000 trees there was a positive association between sexual selection and  $\lambda_{DR}$  (highest posterior density [HPD] interval =  $4.51 \times 10^{-3}$ ,  $5.72 \times 10^{-2}$ ), and the distribution skewed towards a positive association between sexual selection and  $\lambda_{ND}$  (HPD interval =  $-5.04 \times 10^{-4}$ ,  $1.58 \times 10^{-3}$ ) as well as the 100 models using  $\lambda_{BAMM}$  (HPD interval =  $-1.30 \times 10^{-2}$ ,  $3.09 \times 10^{-2}$ ; Table S15).

We investigated which of the three variables comprising the index of male-biased sexual selection was driving the association observed with  $\lambda_{DR}$ . Our results over 300 trees showed that this pattern is mainly driven by the sexual size dimorphism component (HPD interval =  $8.53 \times 10^{-1}$ , 3.11), with the effects of other components overlapping zero; paternal care (HPD interval =  $-1.78 \times 10^{-1}$ ,  $7.90 \times 10^{-3}$ ) and mating system (HPD interval =  $-7.35 \times 10^{-2}$ ,  $4.32 \times 10^{-2}$ ). Importantly, the association between sexual size dimorphism and speciation rates is also present when using  $\lambda_{ND}$  (HPD interval =  $1.80 \times 10^{-1}$ ,  $6.38 \times 10^{-1}$ ), but not when using  $\lambda_{BAMM}$  (HPD interval =  $-1.49$ ,  $7.45 \times 10^{-1}$ ; Fig. 3).

In contrast to male-biased sexual selection, we found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation. Sexual dichromatism showed no association with  $\lambda_{DR}$  ( $\beta = -1.28 \times 10^{-3}$ ,  $P = 0.15$ ; Figs. 1 and 2A),  $\lambda_{ND}$  ( $\beta = -5.75 \times 10^{-5}$ ,  $P = 0.08$ ; Fig. 2A), or  $\lambda_{BAMM}$  ( $\beta = -1.43 \times 10^{-5}$ ,  $P = 0.87$ ; Fig. 2A). PGLS analyses using sexual dichromatism ( $n = 581$ ) measured by spectrophotometry (Armenta et al. 2008) yielded results concordant with the full dataset; that is, no association between sexual dichromatism and speciation (Fig. S11). Our results from models based on the MCC tree are largely corroborated by model estimates from PGLS analyses of the rates and correlation structures from 1000 trees (for  $\lambda_{DR}$ ,  $\lambda_{ND}$ ) and 100 trees for  $\lambda_{BAMM}$ . The HPD intervals show model estimates are distributed around zero when using complete taxon sampling models and RGB measures of sexual dichromatism ( $\lambda_{DR}$ : HPD interval =  $-1.63 \times 10^{-3}$ ,  $1.66 \times 10^{-3}$ ,  $\lambda_{ND}$ : HPD interval =  $-4.26 \times 10^{-5}$ ,  $5.50 \times 10^{-5}$ ; Fig. 2A, Table S8).



**Figure 1.** Speciation rate ( $\lambda_{DR}$ ) across all passerine birds ( $n = 5965$ ) with estimates of sexual dichromatism, range size available for 5812 species and an index of male-biased sexual selection available for 2465 species. Across these species there was a small but significant negative association between  $\lambda_{DR}$  and log-range size as well as a significant positive association between  $\lambda_{DR}$  and male-biased sexual selection but no significant association between  $\lambda_{DR}$  and sexual dichromatism based on RGB measures.  $\lambda_{DR}$  are those from the MCC tree and images of birds are from the *Handbook of the Birds of the World*. Clockwise the six species are *Sporophila bouvronides*, *Euplectes franciscanus*, *Phainopepla nitens*, *Paradisaea rubra*, *Malurus pulcherrimus*, and *Lepidothrix coeruleocapilla*. Edge colors for the terminal branch correspond to  $\lambda_{DR}$  but all precluding branches have been generated for graphical purposes using ancestral character state estimation (Revell 2012) and should not be interpreted. Illustrations are reproduced by the permission of Lynx Editions.

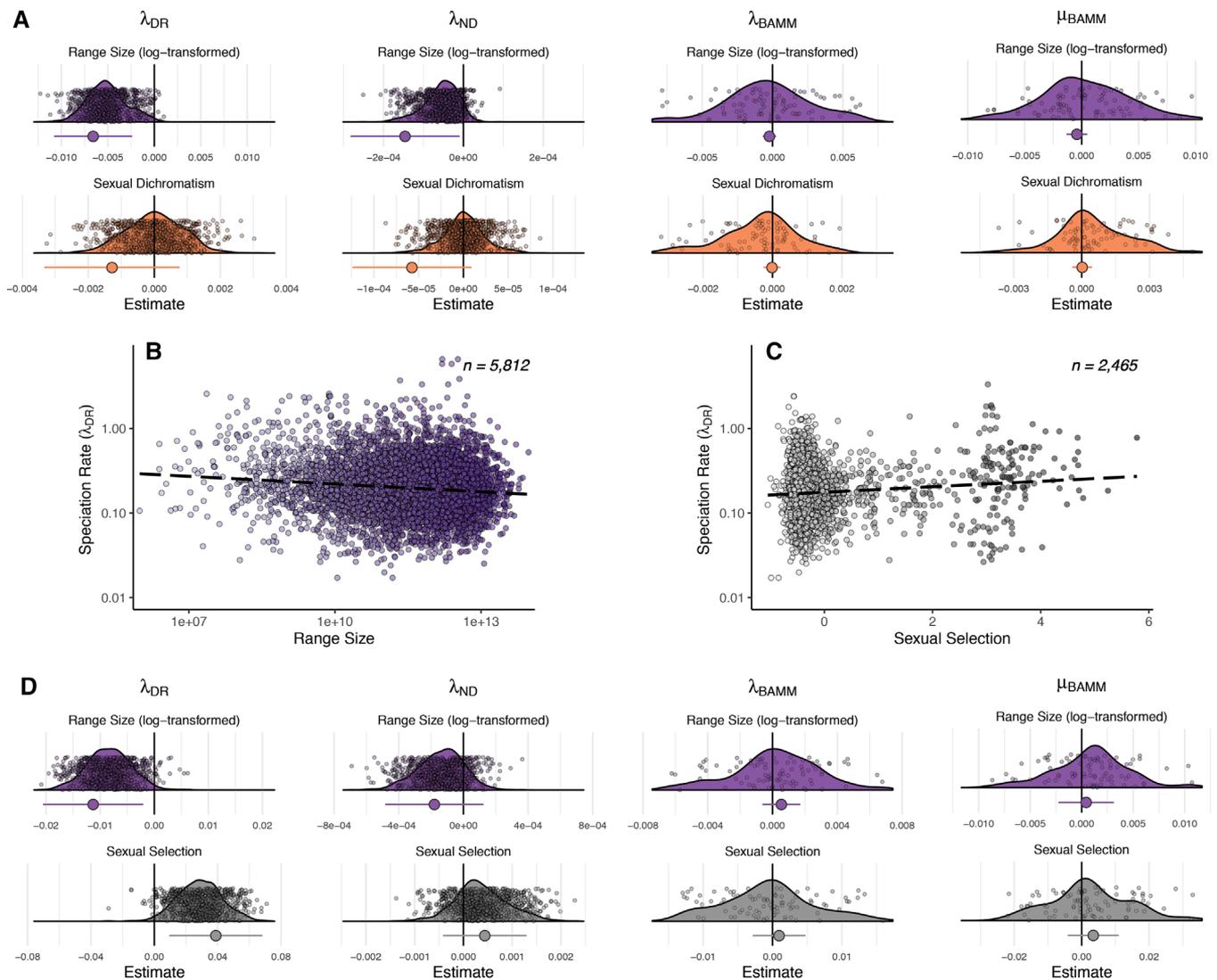
For PGLS models using spectrophotometry-based measures of sexual dichromatism, the estimates from the 100 trees in the  $\lambda_{DR}$  models are positively skewed (HPD interval =  $-1.78 \times 10^{-2}$ ,  $3.49 \times 10^{-2}$ ) but normally distributed around zero for  $\lambda_{ND}$  and  $\lambda_{BAMM}$  (Table S12).

Our analyses also show that the differences in results between sexual dichromatism and male-biased sexual selection (i.e., association with speciation rates only for the latter) were not due to differences in the size of the datasets used (5812 species vs. 2465; Fig. S17). No interaction terms were present in the top models ( $\Delta AICc > 4$ ) for any measure of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) or sexual selection (RGB values, spectrophotometry and the index of male-biased sexual selection;  $\Delta AICc > 4$ ; Tables S5, S6, S11, and S14). Thus, we found no evidence that the effect of sexual selection on speciation is dependent on our measures of environmental variation or range size. Furthermore, we found no evidence that these environmental factors—seasonal temperature variation, long-term temperature variation, spatial tempera-

ture variation, and NPP—predict speciation independently from sexual dichromatism/selection (Figs. 2 and S11).

### SPECIES WITH SMALLER RANGES HAVE INCREASED RATES OF SPECIATION

Based on  $\lambda_{DR}$  and  $\lambda_{ND}$  tip-rate metrics of speciation, we found a negative association between range size and speciation; that is, species with smaller ranges show marginally higher values for  $\lambda_{DR}$  and  $\lambda_{ND}$ . This negative association was small but significant for models using the MCC tree ( $\lambda_{DR}$ :  $\beta = -6.58 \times 10^{-3}$ ,  $P = 1.48 \times 10^{-3}$ ;  $\lambda_{ND}$ :  $\beta = -1.46 \times 10^{-4}$ ,  $P = 0.03$ ; Figs. 1 and 2A). This association was also evident across the estimates from models using the 1000 trees ( $\lambda_{DR}$ : HPD interval =  $-8.87 \times 10^{-3}$ ,  $-6.61 \times 10^{-4}$ ;  $\lambda_{ND}$ : HPD interval =  $-1.51 \times 10^{-4}$ ,  $1.72 \times 10^{-5}$ ; Fig. 2A). Subset models with reduced sample size and different measures of sexual selection—but the same measure of range size—showed equivocal evidence that range size is negatively associated with speciation. Range size is



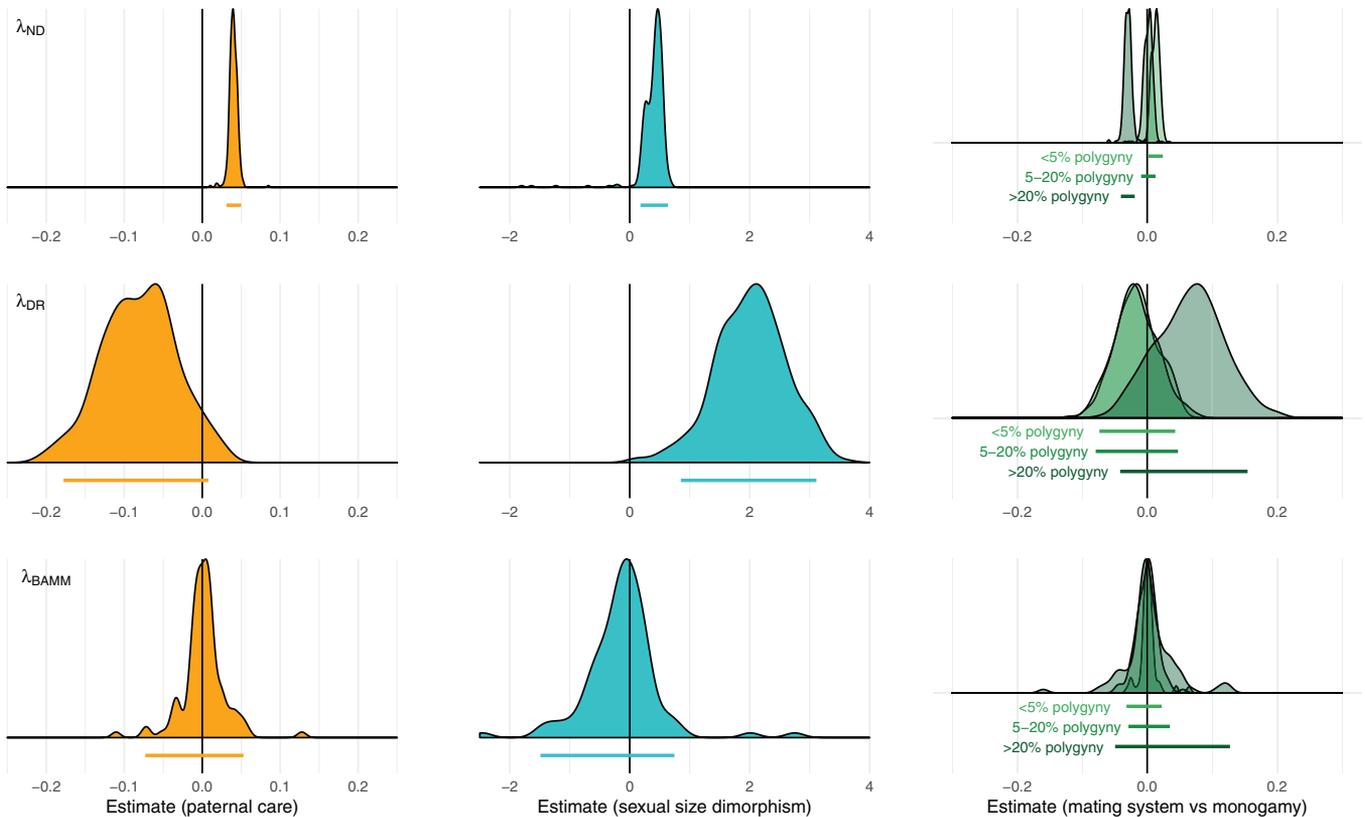
**Figure 2.** Model estimates (A) showing the effect size (i.e., slope) of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset (RGB values,  $n = 5812$ ). (B) The scatter plot of speciation rate ( $\lambda_{DR}$ ) and log-range size with the model estimate presented as a dashed line. (C) The scatter plot of speciation rate ( $\lambda_{DR}$ ) and male-biased sexual selection ( $n = 2465$ ). Similar to (A), (D) presents model estimates for PGLS analyses using a restricted dataset with measures of an index of male-biased sexual selection ( $n = 2465$ ) and shows the effect of log-range size and male-biased sexual selection on speciation and extinction rates. Both datasets were used for analyses with three measures of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) and one measure of extinction ( $\mu_{BAMM}$ ) as response variables. The numerical values for the model estimates using the MCC tree and HPD intervals of estimates from 1000 randomly sampled trees (for  $\lambda_{DR}$  and  $\lambda_{ND}$ ) or 100 randomly sampled trees for  $\lambda_{BAMM}$  and  $\mu_{BAMM}$  can be found in the Supporting Information. Density curves are based on model estimates from 1000/100 trees and the circle below with error bars is the estimate and 95% confidence intervals (CIs) from the MCC tree. For this figure, we removed outliers from estimates coming from the 100 randomly sampled trees for BAMM models to be able to visualize the MCC 95% CIs.

significantly associated with  $\lambda_{DR}$  (Fig. 2B) using data subset for species with an index of male-biased sexual selection ( $n = 2465$ ) but not  $\lambda_{ND}$  or  $\lambda_{BAMM}$ . Models using data subset for spectrophotometry-based dichromatism ( $n = 581$ ) gave non-significant estimates for the effect of range size on all measures of speciation (Fig. S11, Tables S12 and S13). Because the range size dataset is the same across the three data subsets, we draw

our conclusions from the models with the highest power using near-complete taxon sampling ( $n = 5812$ ).

#### PHYLOGENETIC PATH ANALYSIS

Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS (Figs. 4 and S14). There was a modest effect of male-biased sexual selection on



**Figure 3.** Estimates of the effect of individual sexual selection components included in the PPCA (paternal care, sexual size dimorphism, and mating system) on three measures of speciation rate ( $\lambda_{DR}$ ,  $\lambda_{ND}$ , and  $\lambda_{BAMM}$ ). Estimates are presented as density intervals from PGLS models on 300 phylogenetic trees that used species with available data for these sexual selection measures ( $n = 2465$ ). The bar under each density ridge is the 95% HPD interval. Given that the mating system is a categorical variable, model estimates for three polygynous mating system levels are in reference to a strictly monogamous mating system (0% polygyny).

sexual dimorphism ( $\beta = 0.22$ ). Additionally, temperature seasonality weakly affected sexual dimorphism ( $\beta = 0.07$ ) and strongly affected range size ( $\beta = 0.52$ ). This suggests an indirect effect of temperature seasonality on  $\lambda_{DR}$  ( $\beta_{\text{indirect}} = -0.02$ ; Fig. 4), given the negative association we identified between  $\lambda_{DR}$  and range size in PGLS models.

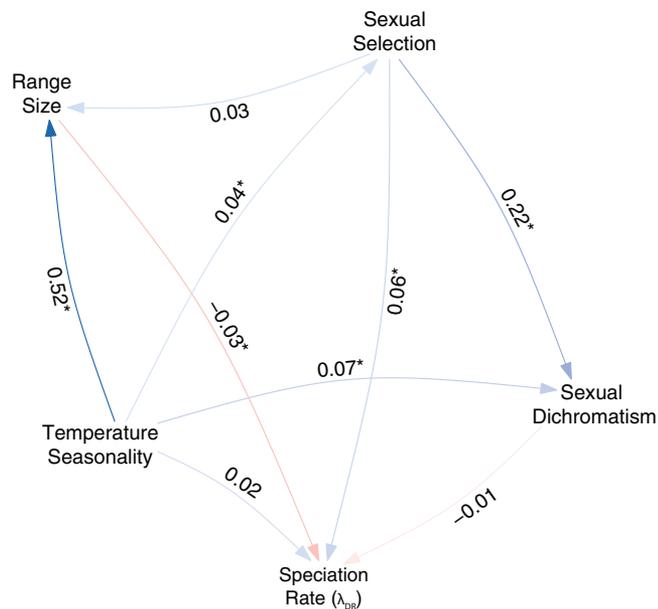
### EXTINCTION RATE

We found no evidence that extinction ( $\mu_{BAMM}$ ) was impacted by the extent of sexual dichromatism for full-taxon sampling ( $\beta = 2.38 \times 10^{-5}$ ,  $P = 0.93$ ; Fig. 2A), nor spectrophotometry-based measures of sexual dichromatism (Fig. S11, Tables S12 and S13) or male-biased sexual selection (Fig. 2b, Tables S15 and S16).

### VARIABILITY ACROSS PHYLOGENETIC TREES AND SPECIATION RATE MEASURES

Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially in the BAMM rates ( $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ), where the 95% HPD interval across PGLS model estimates from 100 trees was often  $>20$  times larger

than the 95% confidence interval for estimates from a single PGLS model using the MCC tree. This contrasts with variation across trees for the other rate estimates ( $\lambda_{DR}$  and  $\lambda_{ND}$ ), where the 95% HPD interval of model estimates for PGLS models using 1000 trees was near-equivalent to the 95% confidence interval calculated for PGLS model estimates of the MCC tree (Table S9). The great majority of earlier studies have based their estimates on a single consensus tree due to the computational requirements of BAMM. However, our results suggest that BAMM estimates between alternative, similarly plausible phylogenies vary substantially. Mean measures of speciation rate across 100 trees were positively correlated between measures ( $\lambda_{DR} - \lambda_{BAMM}$ :  $r = 0.75$ ,  $\lambda_{DR} - \lambda_{ND}$ :  $r = 0.65$ ,  $\lambda_{ND} - \lambda_{BAMM}$ :  $r = 0.51$ ; Fig. S15). The calculation of BAMM rates can be affected by the settings of the run and the use of different priors. We therefore compared the estimate of our MCC tree with that of previously published analyses on birds and found a high correlation ( $r = 0.81$ ; Figs. S6 and S8; Harvey et al. 2017). Full details of the BAMM results are presented as Supporting Information.



**Figure 4.** Path analysis of evolutionary and ecological variables. Arrows represent direct effects with the direction of effect corresponding to colors (blue = positive; red = negative). The numeric values are standardized regression slopes and the asterisks indicates that the 95% confidence intervals of this estimate do not overlap with zero. The confidence intervals were obtained from 500 bootstrapped iterations and the data used in this analysis were subset to species with both sexual dichromatism and an index of male-biased sexual selection measures ( $n = 2465$ ).

## Discussion

We found evidence that the composite index of male-biased sexual selection, but not measures of sexual dichromatism, is correlated with the rate of speciation in passerine birds. The absence of a detectable correlation between sexual dichromatism and speciation rate was consistent across different measures of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ , and  $\lambda_{BAMM}$ ) and both measures of dichromatism (spectral and RGB), and it cannot be explained by a difference in statistical power or sampling. These findings reaffirm the conclusions of previous, smaller studies in which sexual dichromatism was measured using spectrophotometry (Huang and Rabosky 2014) or human observers (Cooney et al. 2017). The correlation between speciation rate and the index of male-biased sexual selection (which encapsulates variation in sexual size dimorphism, social polygyny, and paternal care) was statistically significant for  $\lambda_{DR}$ , but not for  $\lambda_{ND}$  and  $\lambda_{BAMM}$ . This pattern seems to be mainly driven by an association between sexual size dimorphism and speciation. Interestingly, we also found a consistent negative relationship between range size and speciation rate, at least when this rate was quantified using  $\lambda_{DR}$  and  $\lambda_{ND}$ . None of the bioclimatic measures of environmental variability that we investigated (i.e., temperature seasonality,

long-term temperature variation, and spatial temperature variation) were significantly associated speciation rate, nor mediated the relationship between sexual selection and diversification.

The difference in findings between the analyses of sexual dichromatism versus the index of male-biased sexual selection is noteworthy because the majority of earlier studies used dichromatism alone as their proxy for sexual selection (e.g., Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014). Given our findings, and the modest correlation between dichromatism and the sexual selection index ( $r = 0.34$ ; Dale et al. 2015), we suggest that sexual dichromatism may not be a robust proxy for sexual selection (Cooney et al. 2018). Although dichromatism almost certainly provides some insight into the operation of sexual selection, it may be too indirect a measure to detect any association with speciation rate, even with large sample size. There are several reasons why the use of sexual dichromatism as a proxy for sexual selection is problematic. Sexual dichromatism can evolve for reasons other than sexual selection, such as when males and females occupy different ecological niches (Wallace 1889; Kottler 1980; Slatkin 1984; Shine 1989) or experience different selective pressures in contexts other than competition for mates (Price and Eaton 2014). For example, in fairy-wrens (*Malurus spp.*) female coloration has probably evolved in response to spatial variation in predation pressure, affecting dichromatism (Medina et al. 2017). In fact, our path analysis detected a weak relationship between environment and sexual dichromatism, where sexual dichromatism was positively predicted by temperature seasonality (a measure of environmental variation).

In line with some theoretical predictions and previous studies (Kraaijeveld et al. 2011), we found that male-biased sexual selection increases speciation rate, at least when speciation is measured by  $\lambda_{DR}$ . Many of the species that have both high scores of male-biased sexual selection and high diversification rates belong to the genera *Ploceus*, *Euplectes* (Ploceidae) and *Paradisaea* (Paradiaseidae). Multiple weaver species (Ploceidae) are polygynous and lack paternal care, and both weavers and birds of paradise have strong size dimorphism. The association between speciation rates and principal component scores that we report seems to be mainly driven by sexual size dimorphism and, to a lesser extent, paternal care. Speciation rates (both  $\lambda_{DR}$  and  $\lambda_{ND}$ ) are higher in species with larger sexual dimorphism and  $\lambda_{DR}$  also has a tendency to be higher in species with no paternal care. Size dimorphism is often thought to arise as a consequence of intrasexual competition, where one of the sexes (males in most birds) has to compete for access to the other sex, leading to selection for larger body sizes and thus greater dimorphism (Björklund 1990; Owens and Hartley 1998). Therefore, competition between males could be the underlying driver of the high speciation rates that we detect in some clades.

Sexual dimorphism due to competition within sexes contrasts with the drivers of sexual dichromatism. Plumage dichromatism can evolve as a consequence of female cryptic choice and be related to extra-pair fertilizations, but not necessarily paternal care or mating system (Owens and Hartley 1998). It can also arise as a result of selection on the level of crypsis of the sex that cares for offspring (Dale et al. 2015). The fact that traits linked with competition (such as size dimorphism) are the ones associated with higher  $\lambda_{DR}$  values—rather than sexual dichromatism—supports the general view that antagonistic interactions and sexual conflict can lead to increased diversity (Bonduriansky 2011; Qvarnström et al. 2012; Tinghitella et al. 2018; Tsuji and Fukami 2020). Moreover, body size is a trait that influences multiple aspects of the physiology and ecology of a species. Differences in body size (as a result of sexual selection) could be linked to changes in diet, vulnerability to predators or environmental tolerance (Damuth 1993; Liow et al. 2008; Bonduriansky 2011), and such differences could ultimately increase the likelihood of divergence between young lineages. In mammals, sexual selection is suggested to have driven the evolution of large body size, which in turn has allowed diversification of ecological strategies in the clade, and higher speciation rates (McLain 1993; Bonduriansky 2011).

We also found that the association between sexual selection and speciation appears to be independent of NPP and spatiotemporal variation in the environment. The lack of an effect of these environmental variables on speciation rate has several possible interpretations. Firstly, the effects of sexual selection on adaptation and speciation may depend on the type of environmental variability under which the species is evolving. Specifically, speciation rates might be impacted by genetic constraints on adaptation, that vary across environments. Theory suggests that sexual antagonism (which is often exacerbated in species with strong sexual selection) may be lower in habitats experiencing cyclical environmental variation (e.g., seasonality), relative to those experiencing directional change in the environment (Connallon and Hall 2016). Another possibility is that the environmental predictors we chose may not account for the key ecological sources of selection that interact with sexual selection to drive speciation. For example, our study does not include direct measure of food availability or the severity of predation and parasitism, which are both hypothesized to affect sexual selection and speciation (reviewed in Maan and Seehausen 2011). Finally, it is possible that environmental variability genuinely has little effect on speciation rates, at least in the taxa investigated here.

We found that species with smaller ranges have elevated speciation rates. This result is similar to a study of 329 amphibian genera, which found higher diversification rates in taxa with smaller range size (Greenberg and Mooers 2017). Intuitively, large range size should promote speciation by creating more op-

portunities for geographic barriers to form (Rosenzweig 1995; Castiglione et al. 2017). However, the opposite pattern is also plausible because birds with limited dispersal or more specialized niches can have more fragmented populations, which would promote vicariant divergence and higher speciation rates (Jablonski and Roy 2003; Birand et al. 2012; Claramunt et al. 2012). Moreover, species that have recently split as a consequence of vicariant divergence might have smaller ranges as a result of the split of the ancestral lineage, leading to a link between smaller ranges and shorter divergence times. It is also possible that high speciation rates cause smaller range sizes, rather than the other way around, for example, because repeatedly speciating lineages tend to fill niches in ways that hinder the geographical expansion of new species (Rosenzweig 1995; Weir and Price 2011; Price and Eaton 2014). However, species undergoing adaptive radiation in new habitats are unlikely to be limited by competition for resources from existing taxa. One further explanation for the negative association between range size and sexual dichromatism/sexual selection is the potential bias of taxonomic classification, whereby oversplitting of species in clades with large ranges leads to increased recent phylogenetic branching as well as smaller ranges.

In addition to speciation, sexual selection is hypothesized to affect extinction. Using the model-based approach of BAMM, we found no association between the estimated extinction rate and sexual dichromatism, male-biased sexual selection, or our measures of environmental variability. However, these extinction results should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from phylogenies, principally because different combinations of speciation and extinction rates can give rise to similar patterns of diversity (see Rabosky 2016). Phylogenetic methods such as BAMM allow for speciation and extinction rates to be estimated using moderately sized phylogenies, although the ability of BAMM to model evolutionary rate shifts and extinction rates is debated (see Beaulieu and O'Meara 2015; Moore et al. 2016; Rabosky 2016; Rabosky et al. 2017). Additionally, while several tip-rate estimates exist for speciation rate (e.g.,  $\lambda_{DR}$  and  $\lambda_{ND}$ ), tip-rate estimates of extinction rate are difficult to obtain without complex Bayesian models that are sensitive to sampling bias (Davis et al. 2013). Although extinction rates can be inferred from alternative sources, such as the fossil record (Martins et al. 2018), direct observation extinction, or International Union for Conservation of Nature (IUCN) red list status (Greenberg and Mooers 2017), each approach has its limitations. Across the passerine bird phylogeny, we found that BAMM often produced homogeneous speciation and extinction rates for smaller clades showing few rate shifts, which might reduce our power to detect small differences in extinction rates among closely related taxa (Rabosky et al. 2017; Title and Rabosky 2018). Thus, this methodological constraint

likely decreases our ability to accurately measure the correlation between metrics of sexual selection and the probability of extinction.

One outcome of our analyses was that different measures of speciation rates presented different results. This is not completely surprising because each of the rates is calculated differently (Title and Rabosky 2018). For instance,  $\lambda_{DR}$  is weighted more toward speciation events close to the tips and allows more rate heterogeneity compared to  $\lambda_{BAMM}$  estimates. Rate shifts are unlikely to be detected in smaller clades in BAMM, meaning that it is not uncommon for whole genera to have the same rate. Using the  $\lambda_{DR}$  metric, only sister species are guaranteed to have the same rate. This leads to greater variation in  $\lambda_{DR}$  relative to the  $\lambda_{BAMM}$  estimates, which is suggested to be an advantage when studying diversification patterns (Quintero et al. 2015). Additionally,  $\lambda_{BAMM}$  estimates were more sensitive to phylogenetic uncertainty and were 20 times more variable across trees compared to  $\lambda_{DR}$  estimates. We cannot completely reject the idea that the lack of association between  $\lambda_{BAMM}$  and sexual selection could be the result of low statistical power, due to the combination of both low variation across species in the speciation rates and high levels of variation in the estimates across trees.

To summarize, we have shown that sexual size dimorphism (a putative proxy for male-biased sexual selection), but not sexual dichromatism, predicts speciation in passerines, that the magnitude of this effect is modest, and that this relationship is not markedly affected by environmental variability. We have also shown that there is no evidence of an association between sexual selection and extinction rates. Overall, our findings imply that male-male competition could be the mechanism driving increased speciation rates in birds, that sexual dichromatism may not be a reliable proxy for sexual selection, and that alternative measures of sexual selection are more directly related to diversification.

#### AUTHOR CONTRIBUTIONS

All authors contributed to conception, design, and approach to analyses; JGC and JD compiled the data; JGC and IM conducted analyses; JGC wrote the first draft of the manuscript; all authors contributed substantially to further manuscript revisions.

#### ACKNOWLEDGMENTS

We thank Adnan Moussalli for his assistance in conducting BAMM runs across 100 phylogenetic trees, Ignacio Quintero for providing BAMM results for comparison and for discussion of the results, as well as Chris Cooney for comments on the manuscript.

#### DATA ARCHIVING

We have sought to make the data and Supporting Information (including R code) freely accessible to readers. The code and Supporting Information for this manuscript are available on GitHub and as an attached HTML document (Supporting Information) for reviewers. Data

are archived in the adjoined GitHub repository and the environmental dataset collated for this manuscript is available on Dryad: <https://doi.org/10.5061/dryad.573n5tb6n>.

#### CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Associate Editor: Dr. Rebecca Fuller

## Supporting Information

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Supporting Information