

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

3

4 **Abstract**

5 Sexual selection is thought to shape phylogenetic diversity by affecting speciation or extinction rates.  
6 However, the net effect of sexual selection on diversification is hard to predict *a priori*, because many of  
7 the hypothesised effects on speciation or extinction have opposing signs and uncertain magnitudes. **The-**  
8 **oretical work also suggests that the net effect of sexual selection on diversification should**  
9 **depend strongly on ecological factors, though this prediction has seldom been tested. Here,**  
10 **we test whether variation in sexual selection can predict speciation and extinction rates**  
11 **across passerine birds (up to 5,812 species, covering most genera) and whether this relation-**  
12 **ship is mediated by environmental factors. Male-biased sexual selection, and specifically**  
13 **sexual size dimorphism, predicted two of the three measures of speciation rates that we**  
14 **examined.** The link we observed between sexual selection and speciation was independent of envi-  
15 **ronmental variability, though species with smaller ranges had higher speciation rates. There was no**  
16 **association between any proxies of sexual selection and extinction rate. Our findings support the view**  
17 **that male-biased sexual selection, as measured by predictors of male-male competition, has**  
18 **shaped diversification in the largest radiation of birds.**

## 19 INTRODUCTION

20 Sexual selection is a ubiquitous evolutionary process whose effect on phylogenetic diversification is much  
21 debated (Lande 1981, 1982; West-Eberhard 1983; Seddon et al. 2008; Cooney et al. 2018; Tsuji  
22 and Fukami 2020). Sexual selection can promote speciation because it operates on traits that can create  
23 reproductive isolation when they diverge between lineages, such as signals and preferences involved in mate  
24 selection (Lande 1981, 1982; Safran et al. 2013), sperm-egg interactions (Swanson and Vacquier 1998), or  
25 genital morphology (Sloan and Simmons 2019). Sexual selection could also promote speciation or prevent  
26 extinction by purging deleterious mutations (Whitlock and Agrawal 2009), fixing beneficial ones (Whitlock  
27 2000), and accelerating adaptation in different environments (Lorch et al. 2003; Candolin and Heuschele  
28 2008; Cally et al. 2019). Conversely, sexual selection might hinder speciation or make extinction more likely  
29 by favouring traits that improve mating success but reduce population fitness (Kokko and Jennions 2008;  
30 Rankin et al. 2011; Holman and Kokko 2013; Fromhage and Jennions 2016). For example, species with  
31 costly sexual signals may be less resilient to environmental change (Kokko and Brooks 2003). Extinction risk  
32 may also be exacerbated by sexual selection causing maladaptation ('gender load') in female traits that are  
33 genetically correlated with sexually-selected male traits (Pischedda and Chippindale 2006; Bonduriansky and  
34 Chenoweth 2009; Harano et al. 2010; Pennell and Morrow 2013; Berger et al. 2014).

35 Although numerous studies have examined the relationship between sexual selection and speciation or  
36 extinction rates (Barracough et al. 1995; Morrow et al. 2003; Seddon et al. 2008, 2013; Kraaijeveld et al.  
37 2011; Huang and Rabosky 2014), the availability of more complete phenotypic, ecological and phylogenetic  
38 data (Jetz et al. 2012), together with significant advances in phylogenetic methods (Rabosky 2014; Harvey  
39 Michael et al. 2017), present new opportunities to test whether and how sexual selection drives diversification.  
40 **Furthermore, the diversity of outcomes and approaches in previous studies suggests that the**  
41 **association between species diversity and sexual selection is far from clear (reviewed in Tsuji**  
42 **and Fukami (2020)).**

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

57 Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification (Bar-  
58 raclough 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 characterise 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 1,306 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).

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 (Dale et al. 2015), 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 coloured 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 driving diversification, and to test whether environmental factors 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; Rabosky 2016; Moore et al. 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, since it appears to be inconsistently associated with the operation of sexual selection.

## 95 MATERIALS AND METHODS

96 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ( $n = 5,812$  97 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 (PGLS) regressions. Analyses are documented with reproducible code in the Supplementary Information.

## Compiling data for sexual selection and environmental stress

### Sexual dichromatism

We used a previously-published measure of sexual dichromatism for 5,983 species of passerines (Dale et al. 2015). Briefly, Dale et al. (Dale et al. 2015) obtained sex-specific RGB (red-green-blue) 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 colour 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 male-ness’ between males and females, rather than sex differences in colour *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 coloured ‘male-like’ patch. However, the metric is highly correlated with dichromatism measured from spectral data (see below). Additionally, we used another measure of dichromatism corresponding to colour distance in avian colour 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 covers only 581 passerine species (10-fold fewer than the RGB data), although there was a substantial correlation between the two dichromatism measures ( $r = 0.79$ ; Figure S10).

### Male-biased sexual selection

Because sexual dichromatism is presumably imperfectly correlated with variation in the strength of sexual selection across taxa, 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 2,465 species, and shows a moderate correlation with the RGB measure of sexual dichromatism ( $r = 0.34$ ; Figure S12).

130 Environmental variables

131 We obtained estimates of species range size using expert range maps (BirdLife International and Handbook  
132 of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the Birdlife database  
133 (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual dichromatism  
134 dataset (Dale et al. 2015). From these distributions, we obtained estimates of climatic conditions that  
135 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19  
136 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature  
137 and precipitation) with 30-second ( $\sim 1 \text{ km}^2$ ) spatial resolution (Fick and Hijmans 2017). From these values,  
138 we obtained means and standard deviations for each species. Using the same spatial sampling, we extracted  
139 means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial  
140 (LIG; 120,000 - 140,000 years ago) (Otto-Bliesner et al. 2006). To estimate variability in the energy available  
141 to species, we obtained the mean and standard deviation of net primary productivity (NPP) values between  
142 2000 - 2015 across each species distribution. Estimates of NPP had 30-second resolution and were obtained  
143 through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production products stage 3  
144 (MOD17A3) (Zhao et al. 2005). Using these data, which we provide as a potentially useful data resource (see  
145 Supplementary Information), we generated five predictors of speciation associated with different patterns in  
146 environmental variability (see below).

147 Generating biologically relevant predictors for environmental stress

148 Given that stressful environments are expected to interact with sexual selection and have a positive effect on  
149 adaptation (Cally et al. 2019), we used the extracted environmental variables from each species range size to  
150 create predictors of environmental variation/stress. Firstly we used (i) the average NPP in each species' range  
151 and (ii) the log-transformed range size as potentially informative predictors of speciation rates. We also used  
152 three environmental predictors derived from bioclimatic data. These predictors relate to seasonal climate  
153 variation, spatial climate variation and long-term climate variation. To obtain seasonal climate variation we  
154 used (iii) mean values of temperature seasonality (BIO4) for each range. (iv) To estimate levels of spatial  
155 environmental variation a species may endure, we used the first principle component (PC1) from a PCA  
156 on standard deviations from all bioclimatic variables, excluding temperature and precipitation seasonality  
157 (BIO4 and BIO15). PC1 was heavily loaded towards bioclimatic variables relating to temperature, thus  
158 PC1 **largely reflects the variation in temperature across a species' range (Table S1)**. **A taxon's range**  
159 **size often correlates with speciation and extinction rates (Rosenzweig 1995; Castiglione et al.**  
160 **2017)**, so we controlled for the correlation between environmental spatial variation and species' range sizes —  
161 where larger ranges have larger variation in PC1 — by using the residuals of a fitted general additive model  
162 (GAM; Figure S1) as a predictor. To obtain long-term variation in climates for each species range we take  
163 (v) the first principal component of the absolute difference in the bioclimatic variables between the LIG  
164 and current values. Similarly to spatial variation, the long-term climate variation is primarily loaded to  
165 temperature differences between the LIG and current climates (Table S2, Figure S2). The five predictors  
166 of environmental variability are not strongly correlated (Figure S3). Details and R code to generate these  
167 predictors can be found within the Supplementary Information.

168 Estimating extinction and speciation

169 Phylogenetic information was obtained from [www.birdtree.org](http://www.birdtree.org) (Jetz et al. 2012). We used a maximum clade  
170 credibility (MCC) tree from 2,500 samples of the posterior distribution ( $n = 5,965$ ) as the main phylogenetic  
171 hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without  
172 genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using  
173 tip-rate measures (1,000 trees) and BAMM (100 trees) (Rabosky 2014). **These trees had crown clades**  
174 **with a topology that was heavily constrained on the basis of a previously published study**  
175 (“Hackett backbone”; Hackett et al. 2008) and were constructed using a pure birth (Yule)  
176 model. We calculated three different tip-rate metrics of speciation and one of extinction across all trees.

177 **Diversification is the result of two processes, speciation and extinction through time. To**  
178 **estimate speciation rates, we first obtained two tip-rate metrics of speciation using statistics**  
179 **derived from the properties of the nodes and branches along root-to-tip paths of the phylogeny.**  
180 Node density (ND) is a simple statistic calculating the density of nodes from the phylogenetic root to the  
181 tip, while the log-transformed equal splits (logES; also referred to as diversification rate/DR) is derived  
182 **from the sum of edge lengths from each tip towards the root, with each edge towards the**  
183 **root having the length down-weighted** (Jetz et al. 2012; Quintero and Jetz 2018; Rabosky  
184 et al. 2018). Crucially, studies have suggested that DR and ND (henceforth referred to as  $\lambda_{DR}$  and  
185  $\lambda_{ND}$ ) are more reflective estimates of speciation than diversification; this is because  $\lambda_{DR}$  and  $\lambda_{ND}$  cannot  
186 account for whole-clade extinctions and thus under-estimate extinction rate, which makes the composite  
187 measure of diversification more dependent on speciation (Belmaker and Jetz 2015; Title and Rabosky 2018).  
188 Therefore,  $\lambda_{DR}$  is a measure of speciation rate more heavily weighted to recent speciation events while  $\lambda_{ND}$   
189 measures speciation across the root-to-tip path. These tip-rate measures are alternatives to state-dependent  
190 diversification models such as Quantitative State Speciation-Extinction (QuaSSE); but, based on previous  
191 simulation studies,  $\lambda_{DR}$  and  $\lambda_{ND}$  are robust and intuitive measures that provide high power and low false  
192 discovery rate with large phylogenies when incorporated into Phylogenetic Generalized Least Squares (PGLS)  
193 models (Harvey Michael et al. 2017).

194 We used BAMM to model the dynamics of speciation and extinction across the **101 phylogenetic trees**  
195 **(one MCC tree and 100 random draws of the posterior)**. This software uses a Bayesian approach  
196 (reversible-jump Markov Chain Monte Carlo) to generate probability distributions of evolutionary rate-shift  
197 configurations with variable speciation and extinction rates (Rabosky 2014). **These models provide**  
198 **tip-rate estimates of speciation and extinction rate that can be easily used in comparative**  
199 **analyses.** The parameters of the 100 BAMM runs are detailed in full in the Supplementary Information;  
200 briefly, we used a time-variable model with the prior expected number of evolutionary rate  
201 shifts set at 100 and prior rates set from the initial speciation and extinction values using the  
202 BAMMtools R package (Rabosky et al. 2014). BAMM models were run independently for the  
203 101 phylogenetic trees for 100 million generations, and given the computationally intensive  
204 nature of BAMM, runs were conducted across multiple CPUs. Important BAMM parameters  
205 (log-likelihood and number of rate shifts) reached convergence with effective sample size (ESS)  
206 of MCMC (Markov Chain Monte Carlo) samples surpassing 200; an arbitrary value, above  
207 which posterior distributions can often be accurately inferred (Table S3, Table S4). Further details  
208 of BAMM parameters and output are available in the Supplementary 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 phylogenetic least squares (PGLS) models in the `nlme` package (Pinheiro et al. 2018). Firstly, 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 2,500 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 2-way interactions between sexual selection and each of the environmental measures. The simpler models contained all of the same main effects, but had fewer 2-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 AICc), we ran the equivalent model for each of the 1,000 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 pgl 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 — Pagel's  $\lambda$  (Pagel 1999) — using the `corPagel` function in the `ape` package (Paradis et al. 2004) independently for each of the 1,000 trees/models. Alternatively, for models using speciation and extinction estimates derived using BAMM ( $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ) we found  $\lambda$  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 1,000/100 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 ( $n = 5,812$ ); dichromatism from spectrophotometry ( $n = 581$ ) and the index of male-biased sexual selection ( $n = 2,465$ ).

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 modelled within the univariate response of PGLS. That is, a

249 phylogenetic path analysis allowed us to model relationships between the predictor variables used in our  
250 PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection, and range size to  
251 have effects on each other and not just on speciation rate. To minimise path complexity we used temperature  
252 seasonality (BIO4) as the single measure for environmental variability,  $\lambda_{DR}$  as the single measure of speciation  
253 and the tip-rates from the MCC tree. Further details of the path analysis, including our rationale for each  
254 path's directions, can be found within the Supplementary Information along with all other analyses and the  
255 relevant R code to reproduce results.

## 256 RESULTS

### 257 Male-biased sexual selection, but not sexual dichromatism, affects speciation

258 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ( $n = 5,812$   
259 species; 58% of all birds; Figure 1). To do this, we tested the association between speciation/extinction and  
260 sexual selection, environmental variability and their interaction using phylogenetic least squares (PGLS)  
261 models with  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  or  $\mu_{BAMM}$  as the response variable. These are three different tip-rate metrics  
262 of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) and one of extinction ( $\mu_{BAMM}$ , see Methods for details). Predictors  
263 included one measure of sexual selection (one of two measures of sexual dichromatism or the index of  
264 male-biased sexual selection), four measures of environmental variation, range size and 2-way interactions  
265 between the measure of sexual selection and each of the environmental measures including range size, with  
266 subsequent model simplification using AIC model selection. **In all cases the best model had a  $\Delta$  AICc  
267 above 20 against the second model, and an evidence ratio above 100.**

268 We found a significant positive association between the index of male-biased sexual selection ( $n = 2,465$ ) and  
269  $\lambda_{DR}$  maximum credibility (MCC) tree ( $\beta = 3.89 \times 10^{-2}$ ,  $p = 0.01$ ; Figure 2b). However, this association  
270 was not significant for the other two measures of speciation rate ( $\lambda_{ND}$ :  $\beta = 4.38 \times 10^{-4}$ ,  $p = 0.35$ ;  $\lambda_{BAMM}$ :  
271  $\beta = 9.42 \times 10^{-4}$ ,  $p = 0.76$ ; Figure 2b). When we took into account phylogenetic uncertainty by running  
272 the models using 1,000 trees, the distribution of estimates from PGLS models was similar to the estimate  
273 from the MCC tree: among the 1,000 trees there was a positive association between sexual selection and  $\lambda_{DR}$   
274 (highest posterior density (HPD) Interval =  $4.51 \times 10^{-3}$ ,  $5.72 \times 10^{-2}$ ), and the distribution skewed towards a  
275 positive association between sexual selection and  $\lambda_{ND}$  (HPD Interval =  $-5.04 \times 10^{-4}$ ,  $1.58 \times 10^{-3}$ ; ) as well  
276 as the 100 models using  $\lambda_{BAMM}$  (HPD Interval =  $-1.30 \times 10^{-2}$ ,  $3.09 \times 10^{-2}$ ; Table S15).

277 Given that this male-biased sexual selection index comprises of three different (but correlated)  
278 variables, we investigated which of these variables was driving the association observed with  
279  $\lambda_{DR}$ . Our results over 300 trees showed that this pattern is mainly driven by the sexual size  
280 dimorphism component (HPD Interval =  $8.53 \times 10^{-1}$ , 3.11), with the effects of other components  
281 overlapping zero; paternal care (HPD Interval =  $-1.78 \times 10^{-1}$ ,  $7.90 \times 10^{-3}$ ) and mating system  
282 (HPD Interval =  $-7.35 \times 10^{-2}$ ,  $4.32 \times 10^{-2}$ ). Importantly, the association between sexual size  
283 dimorphism and speciation rates is also present when using  $\lambda_{ND}$  (HPD Interval =  $1.80 \times 10^{-1}$ ,  
284  $6.38 \times 10^{-1}$ ), but not when using  $\lambda_{BAMM}$  (HPD Interval = -1.49,  $7.45 \times 10^{-1}$ , Figure 3).

285 In contrast to male-biased sexual selection, we found no evidence that species with increased sexual dichro-

286 matism have higher or lower rates of speciation. Sexual dichromatism showed no association with  $\lambda_{DR}$   
287 ( $\beta = -1.28 \times 10^{-3}$ ,  $p = 0.15$ ; Figure 2a, Figure 1),  $\lambda_{ND}$  ( $\beta = -5.75 \times 10^{-5}$ ,  $p = 0.08$ ; Figure 2a) or  
288  $\lambda_{BAMM}$  ( $\beta = -1.43 \times 10^{-5}$ ,  $p = 0.87$ ; Figure 2a). PGLS analyses using sexual dichromatism ( $n = 581$ )  
289 measured by spectrophotometry (Armenta et al. 2008) yielded results concordant with the full dataset; i.e. no  
290 association between sexual dichromatism and speciation (Figure S11). Our results from models based on  
291 the MCC tree are largely corroborated by model estimates from PGLS analyses of the rates and correlation  
292 structures from 1,000 trees (for  $\lambda_{DR}$ ,  $\lambda_{ND}$ ) and 100 trees for  $\lambda_{BAMM}$ . The HPD intervals show model  
293 estimates are distributed around zero when using complete taxon sampling models and RGB measures of  
294 sexual dichromatism ( $\lambda_{DR}$ : HPD Interval =  $-1.63 \times 10^{-3}$ ,  $1.66 \times 10^{-3}$ ,  $\lambda_{ND}$ : HPD Interval =  $-4.26 \times 10^{-5}$ ,  
295  $5.50 \times 10^{-5}$ , Figure 2a, Table S8). For PGLS models using spectrophotometry-based measures of sexual  
296 dichromatism, the estimates from the 100 trees in the  $\lambda_{DR}$  models are positively skewed (HPD Interval =  
297  $-1.78 \times 10^{-2}$ ,  $3.49 \times 10^{-2}$ ) but normally distributed around zero for  $\lambda_{ND}$  and  $\lambda_{BAMM}$  (Table S12).

298 **Our analyses also show that the differences in results between sexual dichromatism and male-**  
299 **biased sexual selection (i.e. association with speciation rates only for the latter) were not due**  
300 **to differences in the size of the datasets used (5,812 species vs. 2,465, Figure S17).** No interaction  
301 terms were present in the top models ( $\Delta \text{AICc} > 4$ ) for any measure of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) or  
302 sexual selection (RGB values, spectrophotometry and the index of male-biased sexual selection;  $\Delta \text{AICc} > 4$ ;  
303 Table S5, Table S6, Table S10, Table S13). Thus we found no evidence that the effect of sexual selection on  
304 speciation is dependent on our measures of environmental variation or range size. Furthermore, we found no  
305 evidence that these environmental factors — seasonal temperature variation, long-term temperature variation,  
306 spatial temperature variation, and Net Primary Productivity (NPP) — predict speciation independently  
307 from sexual dichromatism/selection (Figure 2, Figure S11).

### 308 Species with smaller ranges have increased rates of speciation

309 Based on  $\lambda_{DR}$  and  $\lambda_{ND}$  tip-rate metrics of speciation, we found a negative association between range size  
310 and speciation; that is, species with smaller ranges show marginally higher values for  $\lambda_{DR}$  and  $\lambda_{ND}$ . This  
311 negative association was small but significant for models using the MCC tree ( $\lambda_{DR}$ :  $\beta = -6.58 \times 10^{-3}$ ,  $p$   
312 = 0;  $\lambda_{ND}$ :  $\beta = -1.46 \times 10^{-4}$ ,  $p = 0.03$ ; Figure 2a, Figure 1). This association was also evident across the  
313 estimates from models using the 1,000 trees ( $\lambda_{DR}$ : HPD Interval =  $-8.87 \times 10^{-3}$ ,  $-6.61 \times 10^{-4}$ ;  $\lambda_{ND}$ : HPD  
314 Interval =  $-1.51 \times 10^{-4}$ ,  $1.72 \times 10^{-5}$ ; Figure 2a). Subset models with reduced sample size and different  
315 measures of sexual selection — but the same measure of range size — showed equivocal evidence that range  
316 size is negatively associated with speciation. Range size is **significantly associated with  $\lambda_{DR}$**  (Figure 2b)  
317 using data subset for species with an index of male-biased sexual selection ( $n = 2,465$ ) but not  $\lambda_{ND}$  or  
318  $\lambda_{BAMM}$ . Models using data subset for spectrophotometry-based dichromatism ( $n = 581$ ) gave non-significant  
319 estimates for the effect of range size on all measures of speciation (Figure S11, Table S11, Table S12). Because  
320 the range size dataset is the same across the three data subsets we draw our conclusions from the models  
321 with the highest power using near-complete taxon sampling ( $n = 5,812$ ).

## 322 Phylogenetic path analysis

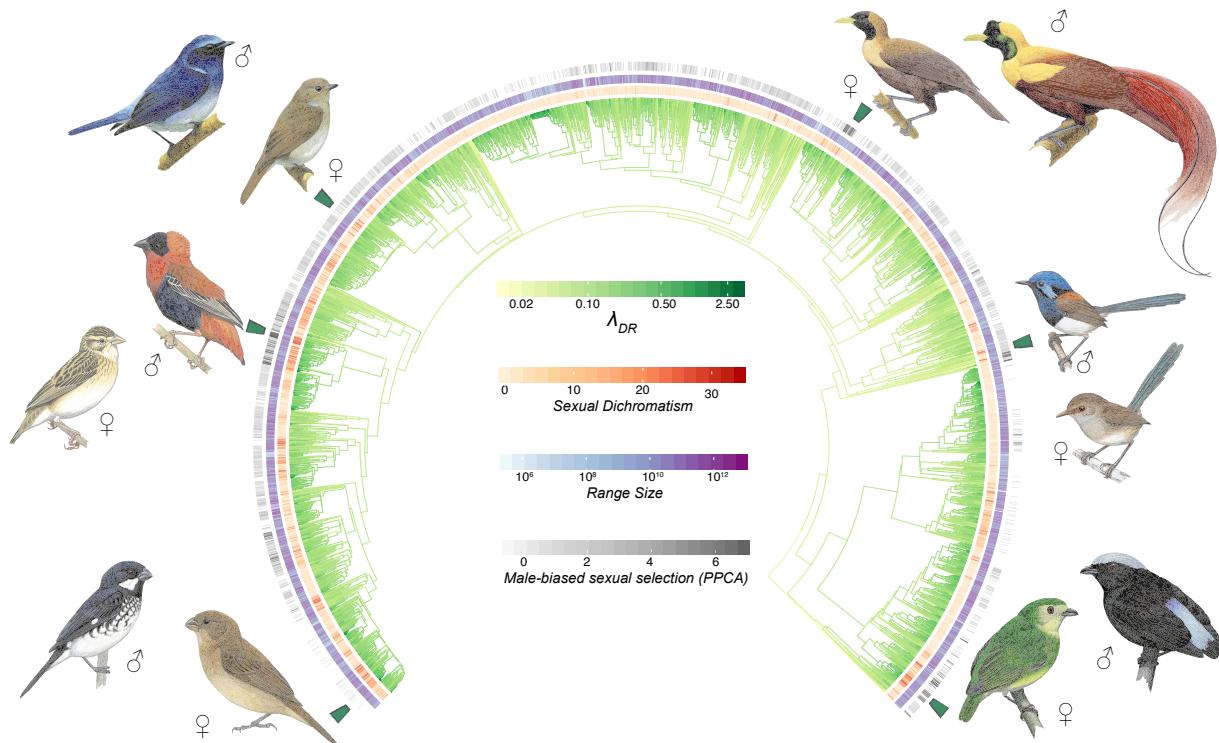
323 Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS  
324 (Figure 4; Figure S14). There was a modest effect of male-biased sexual selection on sexual dimorphism ( $\beta$   
325 = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism ( $\beta$  = 0.07) and strongly  
326 affected range size ( $\beta$  = 0.52). This suggests an indirect effect of temperature seasonality on  $\lambda_{DR}$  ( $\beta_{indirect}$  =  
327 -0.02; Figure 4), given the negative association we identified between  $\lambda_{DR}$  and range size in PGLS models.

## 328 Extinction rate

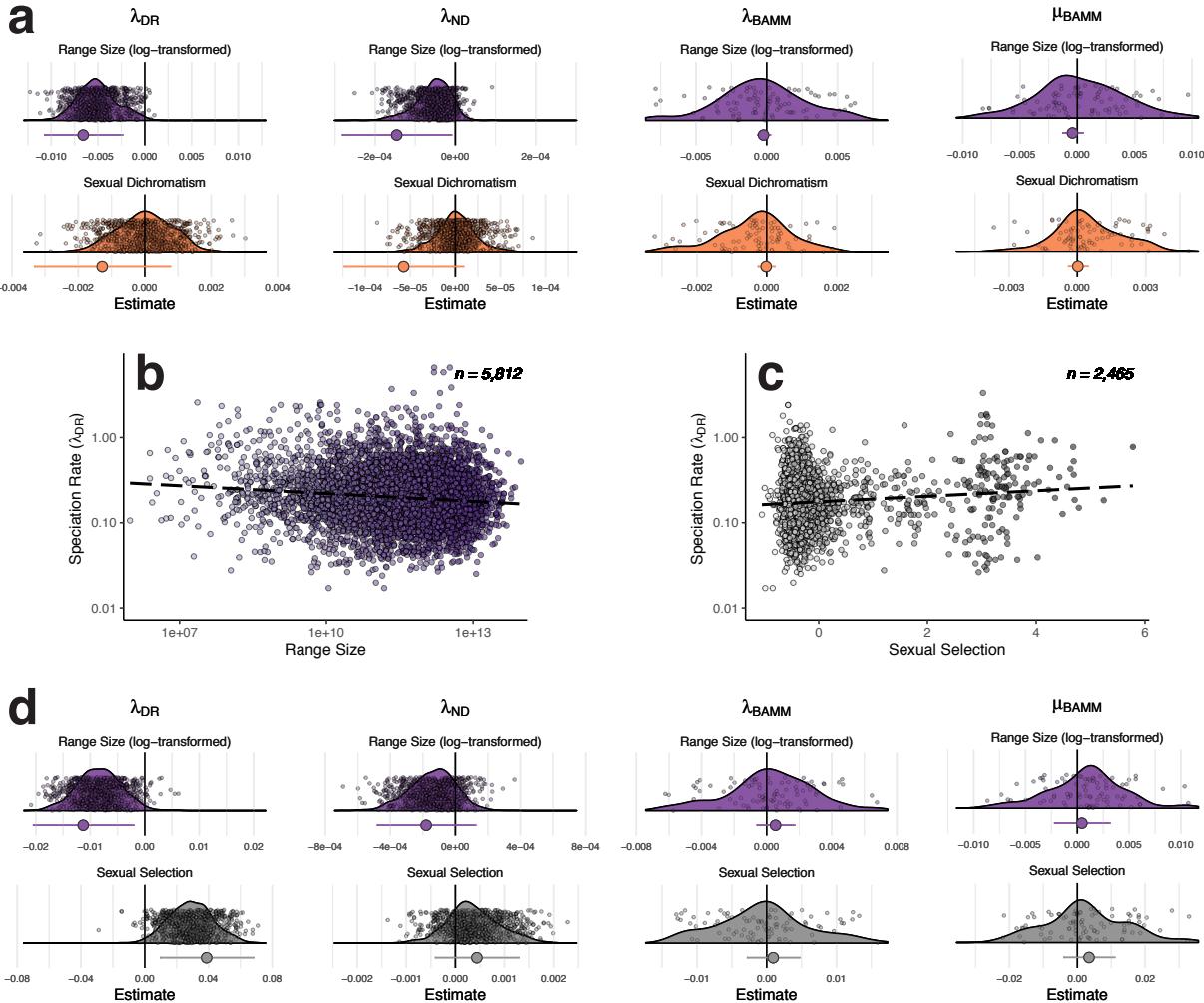
329 We found no evidence that extinction ( $\mu_{BAMM}$ ) was impacted by the extent of sexual dichromatism for  
330 full-taxon sampling ( $\beta = 2.38 \times 10^{-5}$ ,  $p = 0.93$ ; Figure 2a), nor spectrophotometry-based measures of sexual  
331 dichromatism (Figure S11, Table S11, Table S12) or male-biased sexual selection (Figure 2b, Table S14, Table  
332 S15).

## 333 Variability across phylogenetic trees and speciation rate measures

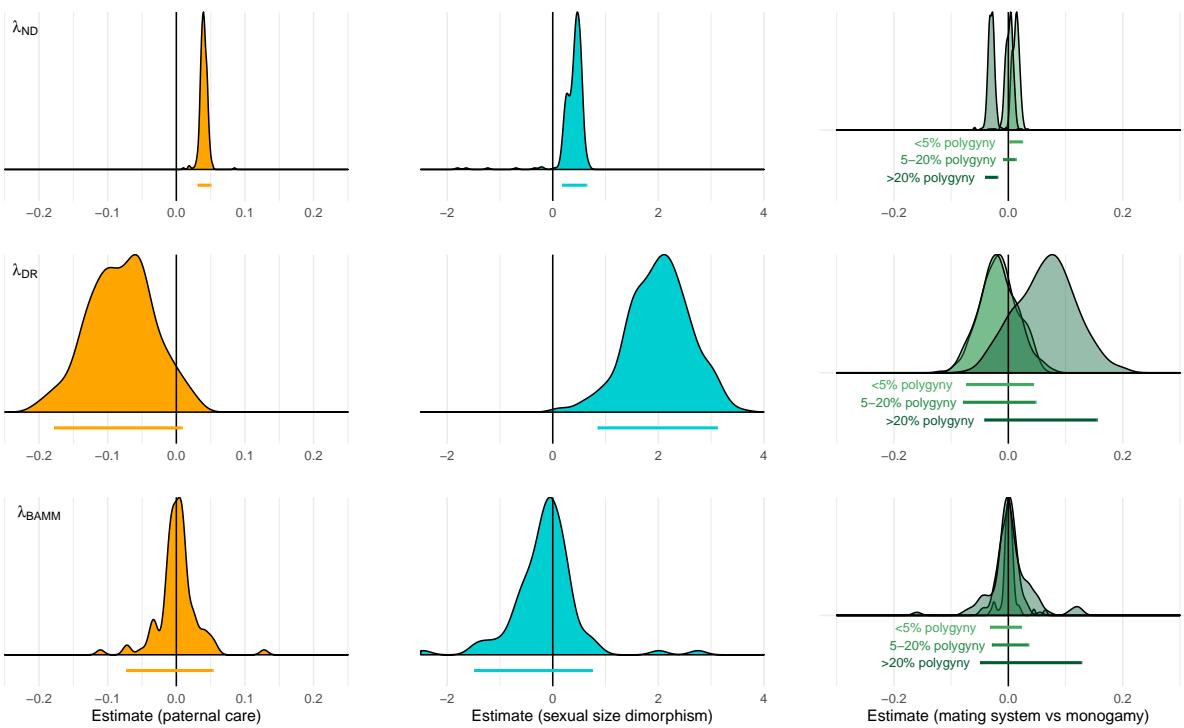
334 Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially in  
335 the BAMM rates ( $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ), where the 95 % HPD interval across PGLS model estimates from  
336 100 trees was often > 20 times larger than the 95 % confidence interval for estimates from a single PGLS  
337 model using the MCC tree. This contrasts with variation across trees for the other rate estimates ( $\lambda_{DR}$  and  
338  $\lambda_{ND}$ ), where the 95 % HPD interval of model estimates for pglS models using 1,000 trees was near-equivalent  
339 to the 95 % confidence interval calculated for PGLS model estimates of the MCC tree (Table S9). Given the  
340 computational requirements of BAMM, the great majority of earlier studies have based their estimates on a  
341 single consensus tree, **and so it is concerning that there are such large differences in the BAMM**  
342 **estimates between alternative, similarly plausible phylogenies.** Mean measures of speciation rate  
343 across 100 trees were positively correlated between measures ( $\lambda_{DR}$  -  $\lambda_{BAMM}$ :  $r=0.75$ ,  $\lambda_{DR}$  -  $\lambda_{ND}$ :  $r=0.65$ ,  
344  $\lambda_{ND}$  -  $\lambda_{BAMM}$ :  $r=0.51$ ; Figure S15). Given that the calculation of BAMM rates can be affected by the  
345 settings of the run and the use of different priors, we compared the estimate of our MCC tree with that of  
346 previous published analyses on birds, and found a high correlation ( $r=0.81$ , Figure S8, Harvey et al. (2017)).  
347 Full details of the BAMM results are presented as supplementary materials.



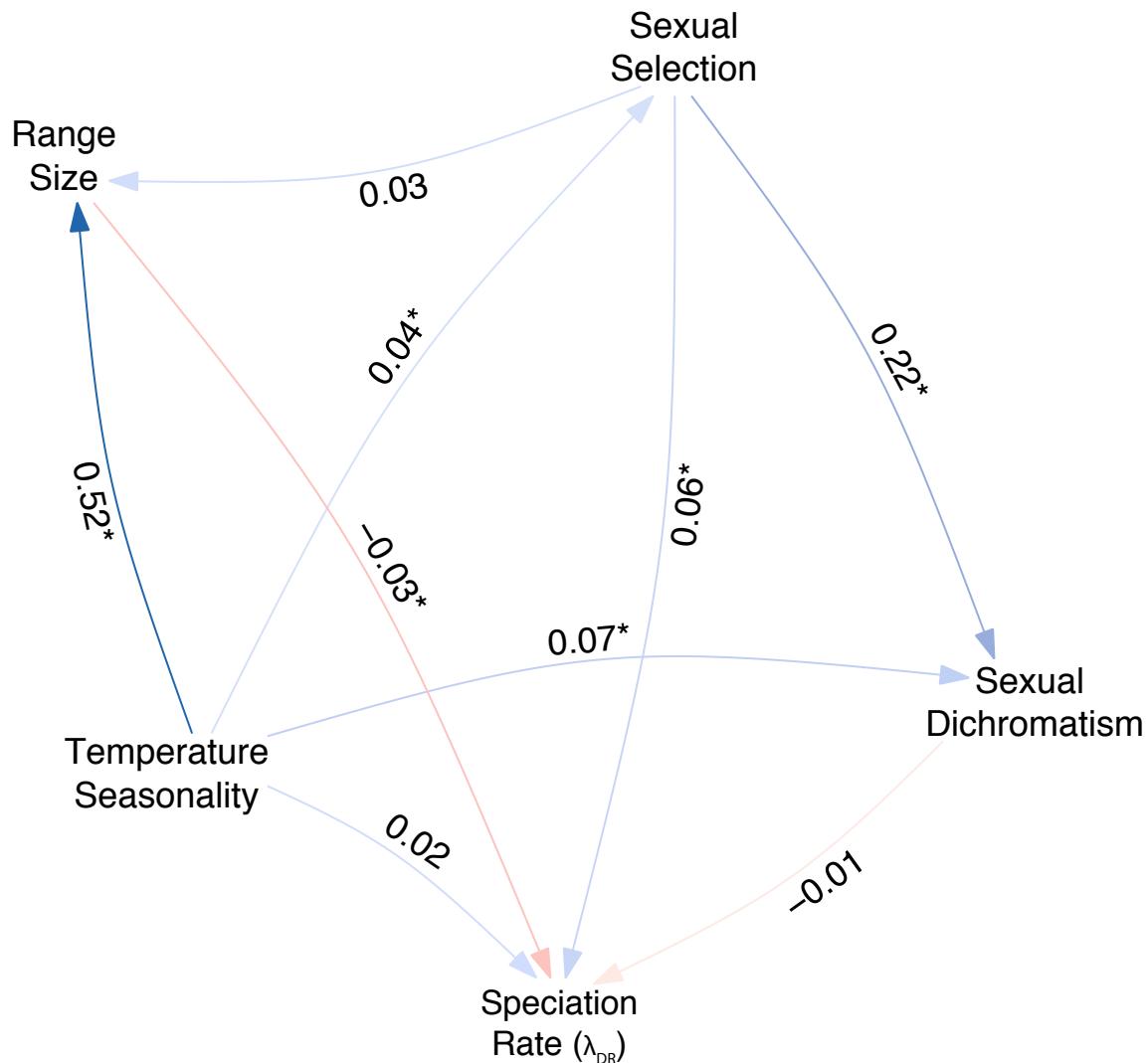
**Figure 1:** Speciation rate ( $\lambda_{DR}$ ) across all passerine birds ( $n = 5,965$ ) with estimates of sexual dichromatism, range size available for 5,812 species and an index of male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative 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*, *Lepidothrix coeruleocapilla*. Edge colours for the terminal branch correspond to  $\lambda_{DR}$  but all precluding branches have been generated for graphical purposes using ancestral character state estimation and should not be interpreted. Illustrations reproduced by permission of Lynx Editions.



**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,  $n = 5,812$ ). (b) depicts the scatter plot of speciation rate ( $\lambda_{DR}$ ) and log-range size with the model estimate presented as a dashed line. (c) shows the scatter plot of speciation rate ( $\lambda_{DR}$ ) and male-biased sexual selection ( $n = 2,465$ ). Similar to (a), (d) presents model estimates for PGLS analyses using a restricted dataset with measures of an index of male-biased sexual selection ( $n = 2,465$ ) 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 1,000 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 Supplementary Information. Density curves are based on model estimates from 1,000/100 trees and the circle below with error bars is the estimate and 95% CIs from the MCC tree. For this figure we removed outliers from estimates coming from the 100 randomly sampled trees for BAMM models in order to be able to visualise the MCC 95% CIs.



**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 ( $n = 2,465$ ). The bar under each density ridge is the 95 % Highest Posterior Density Interval. Given that the mating system variable is categorical, model estimates for three polygynous mating system levels are in reference to a strictly monogamous mating system (0% polygyny)



**Figure 4:** Path analysis of evolutionary and ecological variables. Arrows represent direct effects with the direction of effect corresponding to colours (blue = positive, red = negative). The numeric values are standardised 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 was subset to species with both sexual dichromatism and an index of male-biased sexual selection measures ( $n = 2,465$ ).

## 348 DISCUSSION

349 We found evidence that the composite index of male-biased sexual selection, but not measures of sexual  
350 dichromatism, is correlated with the rate of speciation in passerine birds. The absence of a detectable  
351 correlation between sexual dichromatism and speciation rate was consistent across different measures of  
352 speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$  and  $\lambda_{BAMM}$ ) and both measures of dichromatism (spectral and RGB), **and it cannot**  
353 **be explained by a difference in statistical power or sampling**. These findings reaffirm the conclusions  
354 of previous, smaller studies in which sexual dichromatism was measured using spectrophotometry (Huang and  
355 Rabosky 2014) or human observers (Cooney et al. 2017). The correlation between speciation rate and the  
356 index of male-biased sexual selection (which encapsulates variation in sexual size dimorphism, social polygyny,  
357 and paternal care) was statistically significant for  $\lambda_{DR}$ , but not for  $\lambda_{ND}$  and  $\lambda_{BAMM}$ . **This pattern**  
358 **seems to be mainly driven by an association between sexual size dimorphism and speciation**.  
359 Interestingly, we also found a consistent negative relationship between range size and speciation rate, at  
360 least when this rate was quantified using  $\lambda_{DR}$  and  $\lambda_{ND}$ . None of the bioclimatic measures of environmental  
361 variability that we investigated (i.e., temperature seasonality, long-term temperature variation, and spatial  
362 temperature variation) **were significantly associated speciation rate, nor mediated the relationship**  
363 **between sexual selection and diversification**.

364 The difference in findings between the analyses of sexual dichromatism *versus* the index of male-biased  
365 sexual selection is noteworthy, because the majority of earlier studies used dichromatism alone as their proxy  
366 for sexual selection (e.g., Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al.  
367 2013; Huang and Rabosky 2014). Given our findings, and the modest correlation between dichromatism  
368 and the sexual selection index ( $r = 0.34$ ; Dale et al. 2015), we suggest that sexual dichromatism may  
369 not be a robust proxy for sexual selection (Cooney et al. 2018). Although dichromatism almost certainly  
370 provides some insight into the operation of sexual selection, it may be too indirect a measure to detect any  
371 association with speciation rate, even with large sample size. There are several reasons why the use of sexual  
372 dichromatism as a proxy for sexual selection is problematic. Sexual dichromatism can evolve for reasons  
373 other than sexual selection, such as when males and females occupy different ecological niches (Wallace  
374 1889; Kottler 1980; Slatkin 1984; Shine 1989) or experience different selective pressures in contexts other  
375 than competition for mates (Price and Eaton 2014). For example, in superb fairy-wrens (*Malurus cyaneus*)  
376 female colouration has probably evolved in response to spatial variation in predation pressure, increasing  
377 dichromatism (Medina et al. 2017). **In fact, our path analysis detected a weak relationship between**  
378 **environment and sexual dichromatism, where sexual dichromatism was positively predicted**  
379 **by temperature seasonality (a measure of environmental variation)**.

380 In line with some theoretical predictions and previous studies (Kraaijeveld et al. 2011) we found that  
381 male-biased sexual selection increases speciation rate, at least when speciation is measured by  $\lambda_{DR}$ . **Many of**  
382 **the species that have both high scores of male-biased sexual selection and high diversification**  
383 **rates belong to the genera *Ploceus*, *Euplectes* (Ploceidae) and *Paradisaea* (Paradiaseidae)**.  
384 Multiple weaver species (Ploceidae) are polygynous and lack paternal care, and both weavers  
385 and birds of paradise have strong size dimorphism. The association between speciation rates  
386 and principal component scores that we report seems to be mainly driven by sexual size  
387 dimorphism and, to a lesser extent, paternal care. Speciation rates (both  $\lambda_{DR}$  and  $\lambda_{ND}$ ) are  
388 higher in species with larger sexual dimorphism and  $\lambda_{DR}$  also has a tendency to be higher

389 in species with no paternal care. Size dimorphism is often thought to arise as a consequence  
390 of intrasexual competition, where one of the sexes (males in most birds) has to compete for  
391 access to the other sex, leading to selection for larger body sizes and thus greater dimorphism  
392 (Björklund 1990; Owens and Hartley 1998). Therefore, competition between males could be  
393 the underlying driver of the high speciation rates that we detect in some clades.

394 Sexual dimorphism due to competition within sexes contrasts with the drivers of sexual dichro-  
395 matism. Plumage dichromatism can evolve as a consequence of female cryptic choice and be  
396 related to extra-bond fertilizations, but not necessarily paternal care or mating system (Owens  
397 and Hartley 1998). It can also arise as a result of selection on the level of crypsis of the sex  
398 that cares for offspring (Dale et al. 2015). The fact that traits linked with competition (such as  
399 size dimorphism) are the ones associated with higher  $\lambda_{DR}$  values – rather than sexual dichro-  
400 matism – supports the general view that antagonistic interactions and sexual conflict can lead  
401 to increased diversity (Hoskin and Higgle 2010; Bonduriansky 2011; Tsuji and Fukami 2020).  
402 Moreover, body size is a trait that influences multiple aspects of the physiology and ecology of  
403 a species. Differences in body size (as a result of sexual selection) could be linked to changes  
404 in diet, vulnerability to predators or environmental tolerance (Damuth 1993; Liow et al. 2008;  
405 Bonduriansky 2011), and such differences could ultimately increase the likelihood of diver-  
406 gence between young lineages. In mammals, sexual selection is suggested to have driven the  
407 evolution of large body size which in turn has allowed diversification of ecological strategies  
408 in the clade, and higher speciation rates (McLain 1993; Bonduriansky 2011).

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

423 We found that species with smaller ranges have elevated speciation rates. This result is similar  
424 to a study of 329 amphibian genera, which found higher diversification rates in taxa with smaller range  
425 size (Greenberg and Mooers 2017). Intuitively, large range size should promote speciation by creating more  
426 opportunities for geographic barriers to form (Rosenzweig 1995; Castiglione et al. 2017). However, the  
427 opposite pattern is also plausible because birds with limited dispersal or more specialised niches can have more  
428 fragmented populations, which would promote vicariant divergence and higher speciation rates (Jablonski  
429 and Roy 2003; Birand et al. 2012; Claramunt et al. 2012). Moreover, species that have recently split as a  
430 consequence of vicariant divergence might have smaller ranges as a result of the split of the ancestral lineage,

431 leading to link between smaller ranges and shorter divergence times. It is also possible that high speciation  
432 rates cause smaller range sizes, rather than the other way around, for example because repeatedly-speciating  
433 lineages tend to fill niches in ways that hinder the geographical expansion of new species (Rosenzweig 1995;  
434 Weir and Price 2011; Price and Eaton 2014). However, species undergoing adaptive radiation in new habitats  
435 are unlikely to be limited by competition for resources from existing taxa. **One further explanation for**  
436 **the negative association between range size and sexual dichromatism/sexual selection is the**  
437 **potential bias of taxonomic classification, whereby over-splitting of species in clades with large**  
438 **ranges leads to increased recent phylogenetic branching as well as smaller ranges.**

439 In addition to speciation, sexual selection is hypothesised to affect extinction. Using the model-based  
440 approach of BAMM, we found no association between the estimated extinction rate and sexual dichromatism,  
441 male-biased sexual selection, or our measures of environmental variability. However, these extinction results  
442 should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from  
443 phylogenies, principally because different combinations of speciation and extinction rates can give rise to  
444 similar patterns of diversity (see Rabosky 2016). Phylogenetic methods such as BAMM allow for speciation  
445 and extinction rates to be estimated using moderately-sized phylogenies, although the ability of BAMM to  
446 model evolutionary rate shifts and extinction rates is debated (see, Beaulieu and O'Meara 2015; Rabosky  
447 2016; Moore et al. 2016; Rabosky et al. 2017). Additionally, while several tip-rate estimates exist for  
448 speciation rate (e.g.,  $\lambda_{DR}$  and  $\lambda_{ND}$ ), tip-rate estimates of extinction rate are difficult to obtain without  
449 complex Bayesian models which are sensitive to sampling bias (Davis et al. 2013). Although extinction rates  
450 can be inferred from alternative sources, such as the fossil record (Martins et al. 2018), direct observation  
451 extinction, or IUCN red list status (Greenberg and Mooers 2017), each approach has its limitations. Across  
452 the passerine bird phylogeny, we found that BAMM often produced homogeneous speciation and extinction  
453 rates for smaller clades showing few rate shifts, which might reduce our power to detect small differences  
454 in extinction rates among closely-related taxa (Rabosky et al. 2017; Title and Rabosky 2018). Thus, this  
455 methodological constraint likely decreases our ability to accurately measure the correlation between metrics  
456 of sexual selection and the probability of extinction.

457 One outcome of our analyses was that different measures of speciation rates presented different results.  
458 This is not completely surprising, because each of the rates is calculated differently (Title and Rabosky  
459 2018). For instance,  $\lambda_{DR}$  is weighted more towards speciation events close to the tips and allows more  
460 rate heterogeneity compared to  $\lambda_{BAMM}$  estimates. **Rate shifts are unlikely to be detected in smaller**  
461 **clades in BAMM, meaning that it is not uncommon for whole genera to have the same rate.**  
462 **Using the  $\lambda_{DR}$  metric, only sister species are guaranteed to have the same rate.** This leads to  
463 greater variation in  $\lambda_{DR}$  relative to the  $\lambda_{BAMM}$  estimates, which is suggested to be an advantage  
464 when studying diversification patterns (Quintero et al. 2015). Additionally,  $\lambda_{BAMM}$  estimates  
465 were also more sensitive to phylogenetic uncertainty when compared to  $\lambda_{DR}$ , and estimates  
466 are 20 times more variable across trees in  $\lambda_{BAMM}$  compared to  $\lambda_{DR}$ . We cannot completely  
467 reject the idea that the lack of association between  $\lambda_{BAMM}$  and sexual selection could be the  
468 result of low statistical power, due to the combination of both low variation across species in  
469 the speciation rates and high levels of variation in the estimates across trees.

470 To summarise, we have shown that sexual size dimorphism (a putative proxy for male-biased sexual selection),  
471 but not sexual dichromatism, predicts speciation in passerines, that the magnitude of this effect is modest,  
472 and that this relationship is not markedly affected by environmental variability. We have also shown that

473 there is no evidence of an association between sexual selection and extinction rates. Overall, our findings  
474 imply that male-male competition could be the mechanism driving increased speciation rates in birds, that  
475 sexual dichromatism may not a reliable proxy for sexual selection, and that alternative measures of sexual  
476 selection are more directly related to diversification.

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