

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

## 18 INTRODUCTION

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

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

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

54 Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification (Bar-  
55 racough et al. 1995; Morrow et al. 2003; Seddon et al. 2008, 2013; Huang and Rabosky 2014) because  
56 their biology and phylogenetic relationships are comparatively well-known. A 2011 meta-analysis covering 20  
57 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). **We summarize the major findings from previous studies testing the association between sexual selection and speciation in birds and other taxa 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 (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, 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; 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.

**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
		Mating system	Yes	Across all birds, evidence in 4/4 studies
		Size dimorphism	Mixed	Across all birds, evidence in 1/2 studies
Maia et al. (2013)	Starlings (Sturnidae), 113 species	Ornamental innovations	Yes	Lineages with derived melanosomes (an ornamental innovation) diversify faster
Huang & 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	Colour 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
This study	Across passerines, 5812 species	Size dimorphism	Yes	Sexual size dimorphism predicts two out of three measures of speciation rates
		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 summarised all the studies we found relevant and comparable to our study.

## 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  
 98 and environmental variability, (ii) obtained estimates of speciation and extinction rates across passerines,  
 99 and (iii) conducted phylogenetic generalized least-squares (PGLS) regressions. Analyses are documented  
 100 with reproducible code in the [Supplementary Information](#).

## 101 Compiling data for sexual selection and environmental stress

### 102 Sexual dichromatism

103 We used a previously-published measure of sexual dichromatism for 5,983 species of passerines (Dale et  
 104 al. 2015). Briefly, Dale et al. (Dale et al. 2015) obtained sex-specific RGB (red-green-blue) values across  
 105 six body patches (nape, crown, forehead, throat, upper breast, and lower breast) from *Handbook of the*  
 106 *Birds of the World* (Del Hoyo et al. 2011). The relative contribution of male and female RGB colour values  
 107 were averaged across body patches and provide 'male-like' and 'female-like' plumage scores. Here we use  
 108 the absolute difference between male and female plumage scores as an estimate of sexual dichromatism.  
 109 Technically, this measures differences in the 'degree of male-ness' between males and females, rather than  
 110 sex differences in colour *per se* (i.e. dichromatism in the strict sense). For example, the metric would fail to

111 capture dichromatism when both the male and female possess a single, but differently coloured ‘male-like’  
112 patch. However, the metric is highly correlated with dichromatism measured from spectral data (see below).  
113 Additionally, we used another measure of dichromatism corresponding to colour distance in avian colour space  
114 derived from spectral data (Armenta et al. 2008). These measurements include variation in the ultraviolet  
115 and bird-visible range and — unlike the RGB measures — are sourced from museum specimens as opposed  
116 to illustrations. The spectrophotometry data covers only 581 passerine species (10-fold fewer than the RGB  
117 data), although there was a substantial correlation between the two dichromatism measures ( $r = 0.79$ ; [Figure S10](#)).  
118

119 Male-biased sexual selection

120 **Sexual dichromatism is likely to be imperfectly correlated with variation in the strength of**  
121 **sexual selection across taxa.** For this reason, we sourced an additional measure of sexual  
122 **selection (Dale et al. 2015)**, referred to here as the ‘index of male-biased sexual selection’. This  
123 index is the first principal component from a phylogenetic principal component analysis (PPCA) of three  
124 characteristics positively associated with sexual selection (sexual size dimorphism, social polygyny and [lack  
125 of] paternal care). The variables included in this index have all been positively linked to the intensity of  
126 sexual selection, and are usually correlated (Björklund 1990; Owens and Hartley 1998; Dunn et al. 2001),  
127 which is why they were combined into a single metric in previous studies (Dale et al. 2015). This measure of  
128 male-biased sexual selection is available for only 2,465 species, and shows a moderate correlation with the  
129 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  
132 and Handbook of the Birds of the World 2017). The names of 1,230 species in the Birdlife  
133 database (Hoyo and Collar 2016) have been recently changed, so we manually matched these  
134 taxa with the names used in the sexual dichromatism dataset (Hoyo and Collar 2016). For  
135 each species’ range, we obtained estimates of climatic conditions by extracting 1,000 random  
136 point samples of each bioclimatic variable. We extracted 19 present-day bioclimatic variables  
137 (representing a variety of biologically relevant annual trends in temperature and precipitation)  
138 with 30-second (~1 km<sup>2</sup>) spatial resolution (Fick and Hijmans 2017). From the 1000 values  
139 of each bioclimatic variable, we obtained means and standard deviations for each species.  
140 Using the same spatial sampling, we extracted means and standard deviations of bioclimatic  
141 variables from the paleoclimate during the last interglacial (LIG; 120,000 - 140,000 years ago)  
142 (Otto-Bliesner et al. 2006). To estimate variability in the energy available to species, we  
143 obtained the mean and standard deviation of net primary productivity (NPP) values between  
144 2000 - 2015 across each species distribution. Estimates of NPP had 30-second resolution and  
145 were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary  
146 production products stage 3 (MOD17A3) (Zhao et al. 2005). We provide these data as a  
147 potentially useful data resource (see [Supplementary Information](#)).

148 Generating biologically relevant predictors for environmental stress

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

169 Estimating extinction and speciation

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

178 Diversification is the result of two processes, speciation and extinction through time. To estimate speciation  
179 rates, we first obtained two tip-rate metrics of speciation using statistics derived from the properties of  
180 the nodes and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic  
181 calculating the density of nodes from the phylogenetic root to the tip, while the log-transformed equal  
182 splits (logES; also referred to as diversification rate/DR) is derived from the sum of edge lengths from each  
183 tip towards the root, with each edge towards the root having the length down-weighted (Jetz et al. 2012;  
184 Quintero and Jetz 2018; Rabosky et al. 2018). Crucially, studies have suggested that DR and ND (henceforth  
185 referred to as  $\lambda_{DR}$  and  $\lambda_{ND}$ ) are more reflective estimates of speciation than diversification. Because  $\lambda_{DR}$   
186 and  $\lambda_{ND}$  cannot account for whole-clade extinctions and thus under-estimate extinction rate, which makes

187 the composite measure of diversification more dependent on speciation (Belmaker and Jetz 2015; Title and  
 188 Rabosky 2018). Therefore,  $\lambda_{DR}$  is a measure of speciation rate more heavily weighted to recent speciation  
 189 events while  $\lambda_{ND}$  measures speciation across the root-to-tip path. These tip-rate measures are alternatives  
 190 to state-dependent diversification models such as Quantitative State Speciation-Extinction (QuaSSE); but,  
 191 based on previous simulation studies,  $\lambda_{DR}$  and  $\lambda_{ND}$  are robust and intuitive measures that provide high  
 192 power and low false discovery rate with large phylogenies when incorporated into Phylogenetic Generalized  
 193 Least Squares (PGLS) models (Harvey Michael et al. 2017).

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

## 212 Phylogenetic comparative analysis

213 To test the association between speciation/extinction and sexual selection, environmental variability and their  
 214 interaction, we used phylogenetic least squares (PGLS) models in the **nlme** package (Pinheiro et al. 2018).  
 215 Firstly, we conducted model selection to compare models in which  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  or  $\mu_{BAMM}$  were the  
 216 response variable: these tip-rate estimates all came from the same MCC tree (derived from 2,500 draws of  
 217 the posterior distribution (Jetz et al. 2012)). For models of  $\lambda_{BAMM}$  and  $\mu_{BAMM}$ , we used the inverse of  
 218 the variance associated with each tip rate estimate as weights, to account for the variable precision of the  
 219 estimates provided by BAMM. For each response variable, we conducted model selection to compare models  
 220 with different combinations of predictor variables. The most complex model in each set under comparison  
 221 contained one of the measures of sexual selection (sexual dichromatism or the index of male-biased sexual  
 222 selection), all of the environmental measures (i.e. log-transformed range size, seasonal temperature variation,  
 223 spatial temperature variation, long-term temperature variation, and NPP), and all of the 2-way interactions  
 224 between sexual selection and each of the environmental measures. The simpler models contained all of the  
 225 same main effects, but had fewer 2-way interaction terms (potentially none). Model selection was done in  
 226 **MuMin** using the **dredge** function (Barton 2017). Using the terms from the top-ranked model (ranked by

227 AICc), we ran the equivalent model for each of the 1,000 phylogenetic trees used to derive  $\lambda_{DR}$ ,  $\lambda_{ND}$  and  
 228 each of the 100 trees used to derive  $\lambda_{BAMM}$  and  $\mu_{BAMM}$ . Additionally, we investigated the effect of the  
 229 individual variables used to derive the index of male-biased sexual selection on speciation rate. For these pgls  
 230 models we replaced the composite index score with the individual biological variable (sexual size dimorphism,  
 231 social polygyny and [lack of] paternal care) and ran the equivalent model for 300 phylogenetic trees used to  
 232 derive  $\lambda_{DR}$ ,  $\lambda_{ND}$  and 100 trees used to derive  $\lambda_{BAMM}$ .

233 Across all our analyses we corrected for the phylogenetic signal. Our models used the unique response  
 234 variables and correlation structure for a given phylogenetic tree. Specifically, for models using  
 235 tip-rate metrics ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ) we estimated the phylogenetic signal independently for each of  
 236 the 1,000 trees/models. Phylogenetic signal was estimated as Pagel's  $\lambda$  (Pagel 1999) using  
 237 the `corPage1` function in the `ape` package (Paradis et al. 2004). Alternatively, for models using  
 238 speciation and extinction estimates derived using BAMM ( $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ), we found that  $\lambda$  was  
 239 consistently estimated at 1 and hence assumed Brownian motion (using the `corBrownian` function) to estimate  
 240 the correlation structure. This method enabled us to present model estimates for an MCC tree alongside  
 241 1,000/100 trees from the posterior distribution of trees to account for phylogenetic uncertainty. This approach  
 242 was repeated on three datasets corresponding to each measure of sexual selection: dichromatism derived  
 243 from RGB values of images ( $n = 5,812$ ); dichromatism from spectrophotometry ( $n = 581$ ) and the index of  
 244 male-biased sexual selection ( $n = 2,465$ ).

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

## 255 RESULTS

256 Male-biased sexual selection, but not sexual dichromatism, affects speciation

257 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ( $n = 5,812$  species; 58% of all birds; [Figure 1](#)). We found a significant positive association  
 258 between the index of male-biased sexual selection ( $n = 2,465$ ) and  $\lambda_{DR}$  from the maximum clade credibility  
 259 (MCC) tree ( $\beta = 3.89 \times 10^{-2}$ ,  $p = 0.01$ ; [Figure 2b](#)). However, this association was not significant for the  
 260 other two measures of speciation rate ( $\lambda_{ND}$ :  $\beta = 4.38 \times 10^{-4}$ ,  $p = 0.35$ ;  $\lambda_{BAMM}$ :  $\beta = 9.42 \times 10^{-4}$ ,  $p = 0.76$ ;  
 261 [Figure 2b](#)). When we took into account phylogenetic uncertainty by running the models using 1,000 trees,  
 262 the distribution of estimates from PGLS models was similar to the estimate from the MCC tree: among  
 263 the 1,000 trees there was a positive association between sexual selection and  $\lambda_{DR}$  (highest posterior density  
 264

(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 =  $-1.49$ ,  $7.45 \times 10^{-1}$ , [Figure 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  $\lambda_{DR}$  ( $\beta = -1.28 \times 10^{-3}$ ,  $p = 0.15$ ; [Figure 2a](#), [Figure 1](#)),  $\lambda_{ND}$  ( $\beta = -5.75 \times 10^{-5}$ ,  $p = 0.08$ ; [Figure 2a](#)) or  $\lambda_{BAMM}$  ( $\beta = -1.43 \times 10^{-5}$ ,  $p = 0.87$ ; [Figure 2a](#)). PGLS analyses using sexual dichromatism ( $n = 581$ ) measured by spectrophotometry (Armenta et al. 2008) yielded results concordant with the full dataset; i.e. no association between sexual dichromatism and speciation ([Figure 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 1,000 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 =  $-4.26 \times 10^{-5}$ ,  $5.50 \times 10^{-5}$ , [Figure 2a](#), [Table S8](#)). 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 (5,812 species vs. 2,465, [Figure 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;  $\Delta AICc > 4$ ; [Table S5](#), [Table S6](#), [Table S11](#), [Table 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 temperature variation, and Net Primary Productivity (NPP) — predict speciation independently from sexual dichromatism/selection ([Figure 2](#), [Figure 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 ( $\lambda_{DR}$ :  $\beta = -6.58 \times 10^{-3}$ ,  $p = 1.48 \times 10^{-3}$ ;  $\lambda_{ND}$ :  $\beta = -1.46 \times 10^{-4}$ ,  $p = 0.03$ ; [Figure 2a](#), [Figure 1](#)). This association was also evident across the estimates from models using the 1,000 trees ( $\lambda_{DR}$ : HPD Interval =  $-8.87 \times 10^{-3}$ ,  $-6.61 \times 10^{-4}$ ;  $\lambda_{ND}$ :

304 HPD Interval =  $-1.51 \times 10^{-4}$ ,  $1.72 \times 10^{-5}$ ; [Figure 2a](#)). Subset models with reduced sample size and different  
 305 measures of sexual selection — but the same measure of range size — showed equivocal evidence that range  
 306 size is negatively associated with speciation. Range size is significantly associated with  $\lambda_{DR}$  ([Figure 2b](#)) using  
 307 data subset for species with an index of male-biased sexual selection ( $n = 2,465$ ) but not  $\lambda_{ND}$  or  $\lambda_{BAMM}$ .  
 308 Models using data subset for spectrophotometry-based dichromatism ( $n = 581$ ) gave non-significant estimates  
 309 for the effect of range size on all measures of speciation ([Figure S11](#), [Table S12](#), [Table S13](#)). Because the  
 310 range size dataset is the same across the three data subsets, we draw our conclusions from the models with  
 311 the highest power using near-complete taxon sampling ( $n = 5,812$ ).

## 312 Phylogenetic path analysis

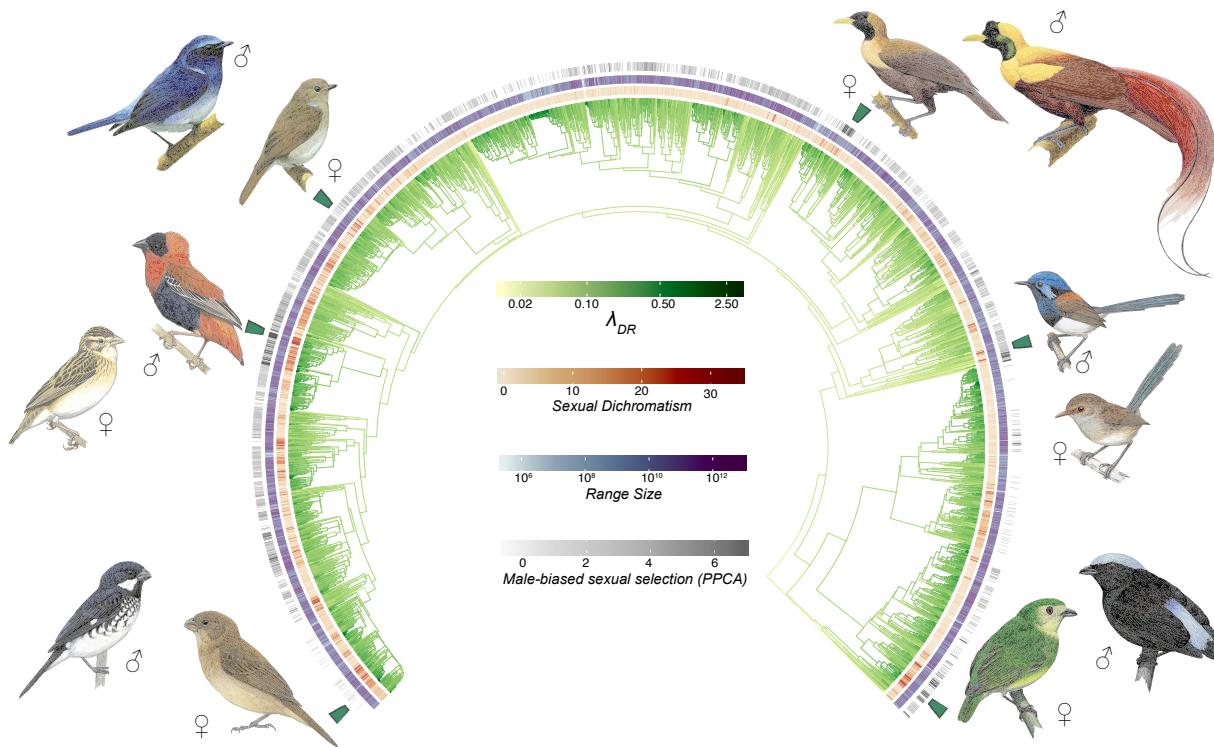
313 Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS  
 314 ([Figure 4](#); [Figure S14](#)). There was a modest effect of male-biased sexual selection on sexual dimorphism ( $\beta$   
 315 = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism ( $\beta = 0.07$ ) and strongly  
 316 affected range size ( $\beta = 0.52$ ). This suggests an indirect effect of temperature seasonality on  $\lambda_{DR}$  ( $\beta_{indirect} =$   
 317 -0.02; [Figure 4](#)), given the negative association we identified between  $\lambda_{DR}$  and range size in PGLS models.

## 318 Extinction rate

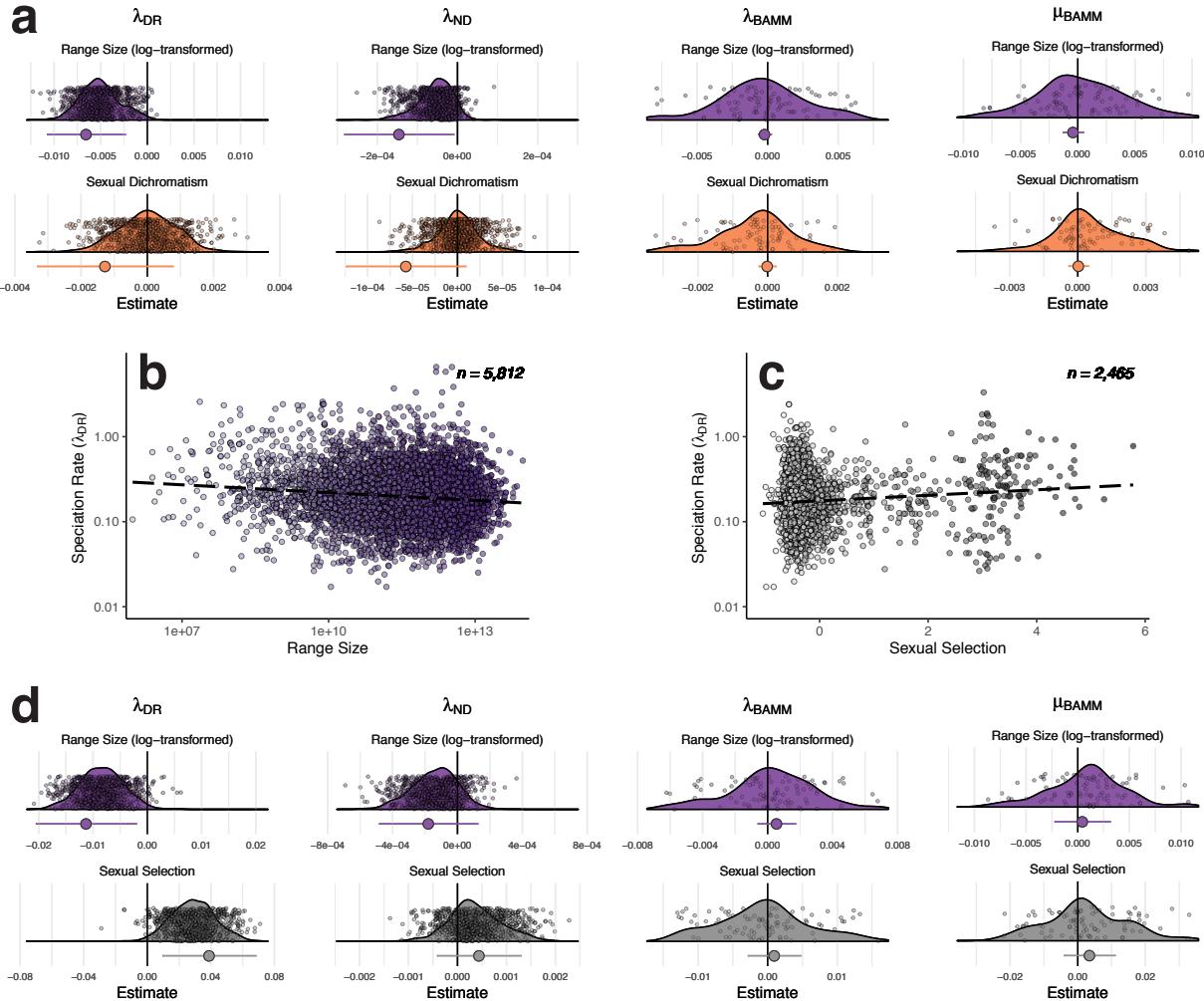
319 We found no evidence that extinction ( $\mu_{BAMM}$ ) was impacted by the extent of sexual dichromatism for  
 320 full-taxon sampling ( $\beta = 2.38 \times 10^{-5}$ ,  $p = 0.93$ ; [Figure 2a](#)), nor spectrophotometry-based measures of sexual  
 321 dichromatism ([Figure S11](#), [Table S12](#), [Table S13](#)) or male-biased sexual selection ([Figure 2b](#), [Table S15](#), [Table  
 322 S16](#)).

## 323 Variability across phylogenetic trees and speciation rate measures

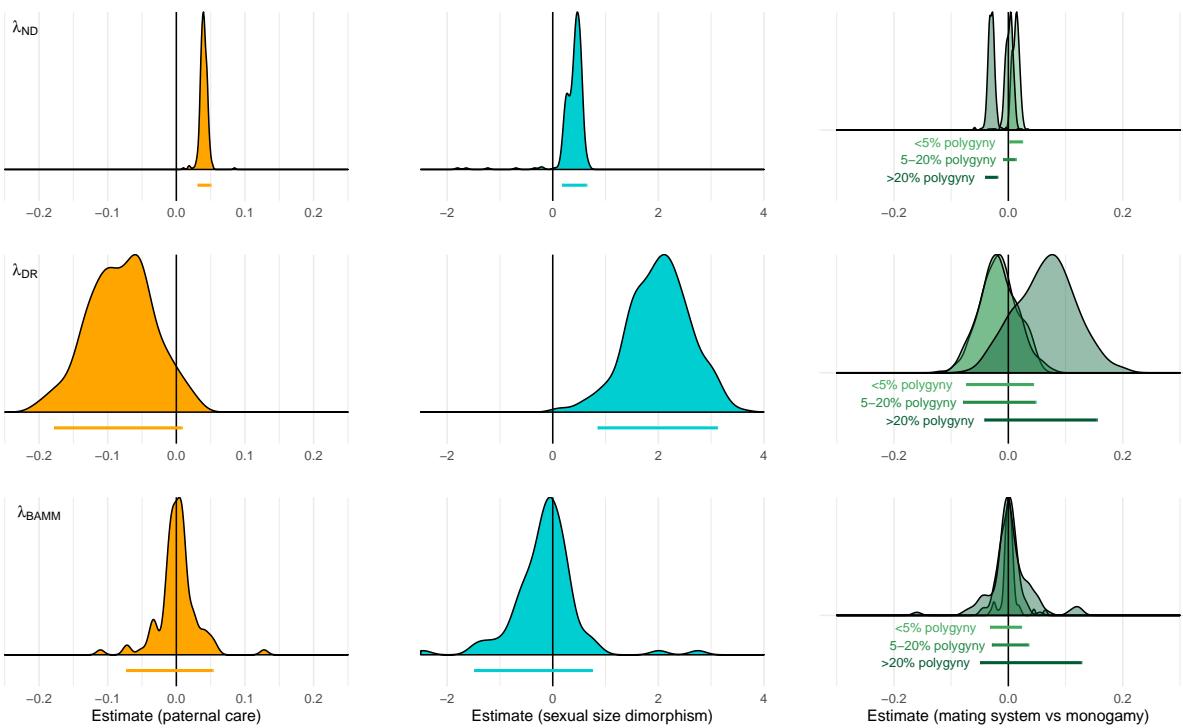
324 Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially  
 325 in the BAMM rates ( $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ), where the 95 % HPD interval across PGLS model estimates  
 326 from 100 trees was often > 20 times larger than the 95 % confidence interval for estimates from a single  
 327 PGLS model using the MCC tree. This contrasts with variation across trees for the other rate estimates  
 328 ( $\lambda_{DR}$  and  $\lambda_{ND}$ ), where the 95 % HPD interval of model estimates for pgls models using 1,000 trees was  
 329 near-equivalent to the 95 % confidence interval calculated for PGLS model estimates of the MCC tree ([Table  
 330 S9](#)). **The great majority of earlier studies have based their estimates on a single consensus tree**  
 331 **due to the computational requirements of BAMM. However, our results suggest that BAMM**  
 332 **estimates between alternative, similarly plausible phylogenies vary substantially.** Mean measures  
 333 of speciation rate across 100 trees were positively correlated between measures ( $\lambda_{DR}$  -  $\lambda_{BAMM}$ :  $r=0.75$ ,  $\lambda_{DR}$   
 334 -  $\lambda_{ND}$ :  $r=0.65$ ,  $\lambda_{ND}$  -  $\lambda_{BAMM}$ :  $r=0.51$ ; [Figure S15](#)). The calculation of BAMM rates can be affected by  
 335 the settings of the run and the use of different priors. We therefore compared the estimate of our MCC tree  
 336 with that of previous published analyses on birds and found a high correlation ( $r=0.81$ , [Figure S6](#), [Figure S8](#),  
 337 Harvey et al. (2017)). Full details of the BAMM results are presented as supplementary materials.



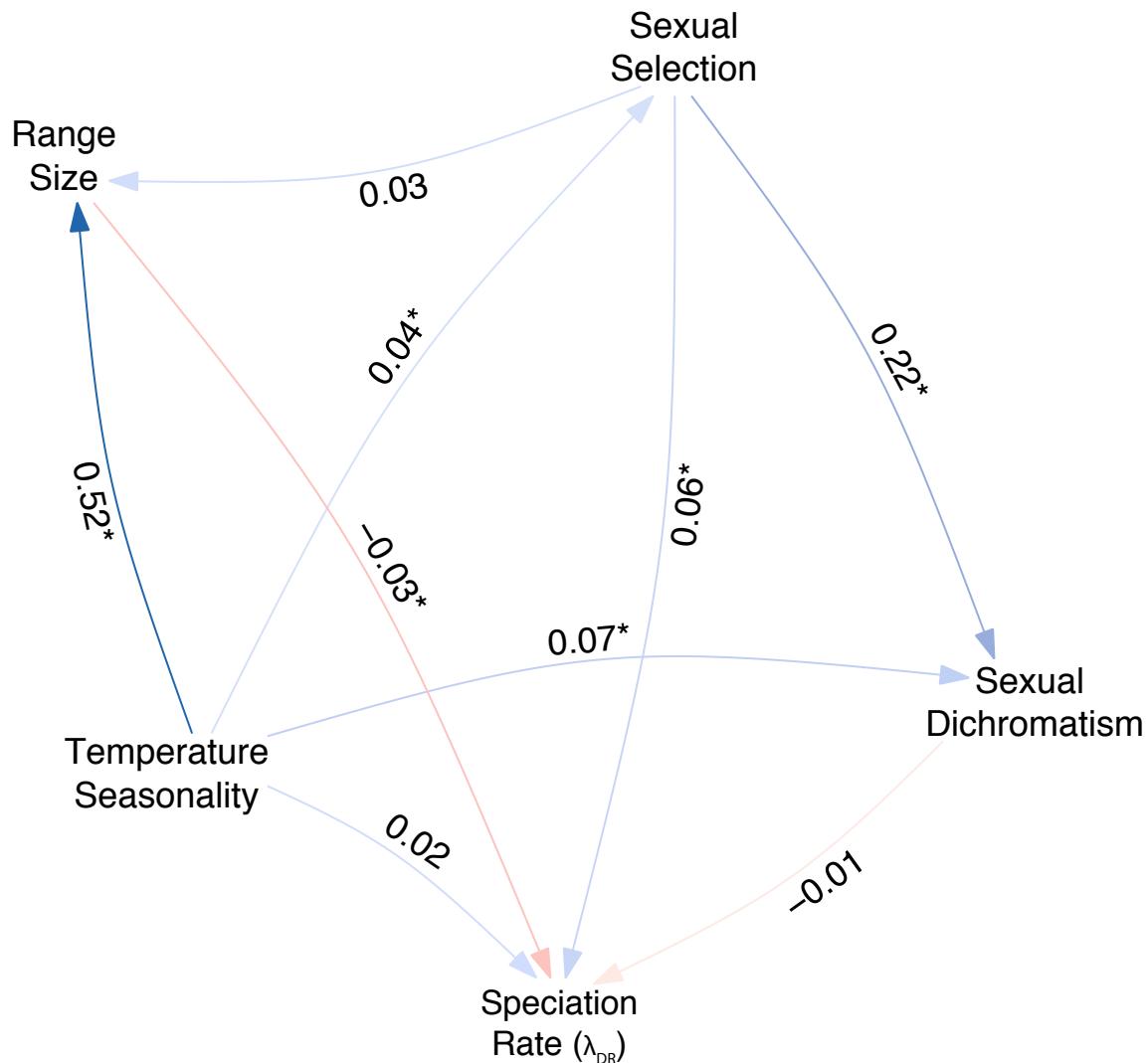
**Figure 1:** Speciation rate ( $\lambda_{DR}$ ) across all passerine birds ( $n = 5,965$ ) with estimates of sexual dichromatism, range size available for 5,812 species and an index of male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative 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 (Revell 2012) 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 is a categorical variable, 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 ( $n = 2,465$ ).

## 338 DISCUSSION

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

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

370 In line with some theoretical predictions and previous studies (Kraaijeveld et al. 2011) we found that  
371 male-biased sexual selection increases speciation rate, at least when speciation is measured by  $\lambda_{DR}$ . Many of  
372 the species that have both high scores of male-biased sexual selection and high diversification rates belong to  
373 the genera *Ploceus*, *Euplectes* (Ploceidae) and *Paradisaea* (Paradiaseidae). Multiple weaver species (Ploceidae)  
374 are polygynous and lack paternal care, and both weavers and birds of paradise have strong size dimorphism.  
375 The association between speciation rates and principal component scores that we report seems to be mainly  
376 driven by sexual size dimorphism and, to a lesser extent, paternal care. Speciation rates (both  $\lambda_{DR}$  and  $\lambda_{ND}$ )  
377 are higher in species with larger sexual dimorphism and  $\lambda_{DR}$  also has a tendency to be higher in species  
378 with no paternal care. Size dimorphism is often thought to arise as a consequence of intrasexual competition,

379 where one of the sexes (males in most birds) has to compete for access to the other sex, leading to selection  
380 for larger body sizes and thus greater dimorphism (Björklund 1990; Owens and Hartley 1998). Therefore,  
381 competition between males could be the underlying driver of the high speciation rates that we detect in some  
382 clades.

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

397 We also found that the association between sexual selection and speciation appears to be independent of  
398 net primary productivity and spatiotemporal variation in the environment. The lack of an effect of these  
399 environmental variables on speciation rate has several possible interpretations. Firstly, the effects of sexual  
400 selection on adaptation and speciation may depend on the type of environmental variability under which the  
401 species is evolving. Specifically, speciation rates might be impacted by genetic constraints on adaptation,  
402 that vary across environments. Theory suggests that sexual antagonism (which is often exacerbated in  
403 species with strong sexual selection) may be lower in habitats experiencing cyclical environmental variation  
404 (e.g. seasonality), relative to those experiencing directional change in the environment (Connallon and Hall  
405 2016). Another possibility is that the environmental predictors we chose may not account for the key ecological  
406 sources of selection that interact with sexual selection to drive speciation. For example, our study does  
407 not include direct measure of food availability or the severity of predation and parasitism, which are both  
408 hypothesised to affect sexual selection and speciation (reviewed in Maan and Seehausen 2011). Finally, it  
409 is possible that environmental variability genuinely has little effect on speciation rates, at least in the taxa  
410 investigated here.

411 We found that species with smaller ranges have elevated speciation rates. This result is similar to a study of  
412 329 amphibian genera, which found higher diversification rates in taxa with smaller range size (Greenberg  
413 and Mooers 2017). Intuitively, large range size should promote speciation by creating more opportunities  
414 for geographic barriers to form (Rosenzweig 1995; Castiglione et al. 2017). However, the opposite pattern  
415 is also plausible because birds with limited dispersal or more specialised niches can have more fragmented  
416 populations, which would promote vicariant divergence and higher speciation rates (Jablonski and Roy 2003;  
417 Birand et al. 2012; Claramunt et al. 2012). Moreover, species that have recently split as a consequence of  
418 vicariant divergence might have smaller ranges as a result of the split of the ancestral lineage, leading to a  
419 link between smaller ranges and shorter divergence times. It is also possible that high speciation rates cause  
420 smaller range sizes, rather than the other way around, for example because repeatedly-speciating lineages

421 tend to fill niches in ways that hinder the geographical expansion of new species (Rosenzweig 1995; Weir  
422 and Price 2011; Price and Eaton 2014). However, species undergoing adaptive radiation in new habitats  
423 are unlikely to be limited by competition for resources from existing taxa. One further explanation for the  
424 negative association between range size and sexual dichromatism/sexual selection is the potential bias of  
425 taxonomic classification, whereby over-splitting of species in clades with large ranges leads to increased recent  
426 phylogenetic branching as well as smaller ranges.

427 In addition to speciation, sexual selection is hypothesised to affect extinction. Using the model-based  
428 approach of BAMM, we found no association between the estimated extinction rate and sexual dichromatism,  
429 male-biased sexual selection, or our measures of environmental variability. However, these extinction results  
430 should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from  
431 phylogenies, principally because different combinations of speciation and extinction rates can give rise to  
432 similar patterns of diversity (see Rabosky 2016). Phylogenetic methods such as BAMM allow for speciation  
433 and extinction rates to be estimated using moderately-sized phylogenies, although the ability of BAMM to  
434 model evolutionary rate shifts and extinction rates is debated (see, Beaulieu and O'Meara 2015; Rabosky  
435 2016; Moore et al. 2016; Rabosky et al. 2017). Additionally, while several tip-rate estimates exist for  
436 speciation rate (e.g.,  $\lambda_{DR}$  and  $\lambda_{ND}$ ), tip-rate estimates of extinction rate are difficult to obtain without  
437 complex Bayesian models which are sensitive to sampling bias (Davis et al. 2013). Although extinction rates  
438 can be inferred from alternative sources, such as the fossil record (Martins et al. 2018), direct observation  
439 extinction, or IUCN red list status (Greenberg and Mooers 2017), each approach has its limitations. Across  
440 the passerine bird phylogeny, we found that BAMM often produced homogeneous speciation and extinction  
441 rates for smaller clades showing few rate shifts, which might reduce our power to detect small differences  
442 in extinction rates among closely-related taxa (Rabosky et al. 2017; Title and Rabosky 2018). Thus, this  
443 methodological constraint likely decreases our ability to accurately measure the correlation between metrics  
444 of sexual selection and the probability of extinction.

445 One outcome of our analyses was that different measures of speciation rates presented different results.  
446 This is not completely surprising, because each of the rates is calculated differently (Title and Rabosky  
447 2018). For instance,  $\lambda_{DR}$  is weighted more towards speciation events close to the tips and allows more rate  
448 heterogeneity compared to  $\lambda_{BAMM}$  estimates. Rate shifts are unlikely to be detected in smaller clades in  
449 BAMM, meaning that it is not uncommon for whole genera to have the same rate. Using the  $\lambda_{DR}$  metric,  
450 only sister species are guaranteed to have the same rate. This leads to greater variation in  $\lambda_{DR}$  relative to the  
451  $\lambda_{BAMM}$  estimates, which is suggested to be an advantage when studying diversification patterns (Quintero et  
452 al. 2015). **Additionally,  $\lambda_{BAMM}$  estimates were more sensitive to phylogenetic uncertainty and**  
453 **were 20 times more variable across trees compared to  $\lambda_{DR}$  estimates.** We cannot completely reject  
454 the idea that the lack of association between  $\lambda_{BAMM}$  and sexual selection could be the result of low statistical  
455 power, due to the combination of both low variation across species in the speciation rates and high levels of  
456 variation in the estimates across trees.

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

<sup>463</sup> selection are more directly related to diversification.

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