

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
7 of the hypothesised effects on speciation or extinction have opposing signs and uncertain magnitudes.
8 Theoretical work also suggests that the net effect of sexual selection on diversification should depend
9 strongly on ecological factors, though this prediction has seldom been tested. Here, we test whether
10 variation in sexual selection can predict speciation and extinction rates across passerine birds (up to
11 5,812 species, covering most genera) and whether this relationship is mediated by environmental factors.
12 Male-biased sexual selection, and specifically sexual size dimorphism, predicted two of the three measures
13 of speciation rates that we examined. The link we observed between sexual selection and speciation
14 was independent of environmental variability, though species with smaller ranges had higher speciation
15 rates. There was no association between any proxies of sexual selection and extinction rate. Our findings
16 support the view that male-biased sexual selection, as measured by frequent predictors of male-male
17 competition, has 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 **See Table 1 for a review of the major findings from previous studies testing the association
42 between sexual selection and speciation.**

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

56 Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification (Bar-
57 racough 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 (λ_{DR}) and node density (λ_{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: Review of 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)	Yes	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

94 MATERIALS AND METHODS

95 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ($n = 5,812$ 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](#).

100 Compiling data for sexual selection and environmental stress

101 Sexual dichromatism

102 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).

112 Additionally, we used another measure of dichromatism corresponding to colour distance in avian colour space
113 derived from spectral data (Armenta et al. 2008). These measurements include variation in the ultraviolet
114 and bird-visible range and — unlike the RGB measures — are sourced from museum specimens as opposed
115 to illustrations. The spectrophotometry data covers only 581 passerine species (10-fold fewer than the RGB
116 data), although there was a substantial correlation between the two dichromatism measures ($r = 0.79$; [Figure S10](#)).
117

118 Male-biased sexual selection

119 Because sexual dichromatism is presumably imperfectly correlated with variation in the strength of sexual
120 selection across taxa, we sourced an additional measure of sexual selection (Dale et al. 2015), referred to here
121 as the ‘index of male-biased sexual selection’. This index is the first principal component from a phylogenetic
122 principal component analysis (PPCA) of three characteristics positively associated with sexual selection
123 (sexual size dimorphism, social polygyny and [lack of] paternal care). The variables included in this index
124 have all been positively linked to the intensity of sexual selection, and are usually correlated (Björklund 1990;
125 Owens and Hartley 1998; Dunn et al. 2001), which is why they were combined into a single metric in previous
126 studies (Dale et al. 2015). This measure of male-biased sexual selection is available for only 2,465 species,
127 and shows a moderate correlation with the RGB measure of sexual dichromatism ($r = 0.34$; [Figure S12](#)).

128 Environmental variables

129 We obtained estimates of species range size using expert range maps (BirdLife International
130 and Handbook of the Birds of the World 2017). The names of 1,230 species in the Birdlife
131 database (Hoyo and Collar 2016) have been recently changed, so we manually matched these
132 taxa with the names used in the sexual dichromatism dataset (Hoyo and Collar 2016). For
133 each species’ range, we obtained estimates of climatic conditions by extracting 1,000 random
134 point samples of each bioclimatic variable. We extracted 19 present-day bioclimatic variables
135 (representing a variety of biologically relevant annual trends in temperature and precipitation)
136 with 30-second (~1 km²) spatial resolution (Fick and Hijmans 2017). From the 1000 values
137 of each bioclimatic variable, we obtained means and standard deviations for each species.
138 Using the same spatial sampling, we extracted means and standard deviations of bioclimatic
139 variables from the paleoclimate during the last interglacial (LIG; 120,000 - 140,000 years ago)
140 (Otto-Bliesner et al. 2006). To estimate variability in the energy available to species, we
141 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
143 were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary
144 production products stage 3 (MOD17A3) (Zhao et al. 2005). We provide these data as a
145 potentially useful data resource (see [Supplementary Information](#)).

146 Generating biologically relevant predictors for environmental stress

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

167 Estimating extinction and speciation

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

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

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

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

210 Phylogenetic comparative analysis

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

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

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

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

253 RESULTS

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

255 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ($n = 5,812$
256 species; 58% of all birds; [Figure 1](#)). To do this, we tested the association between speciation/extinction and
257 sexual selection, environmental variability and their interaction using phylogenetic least squares (PGLS)
258 models with λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} as the response variable. These are three different tip-rate metrics
259 of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one of extinction (μ_{BAMM} , see Methods for details). Predictors
260 included one measure of sexual selection (one of two measures of sexual dichromatism or the index of
261 male-biased sexual selection), four measures of environmental variation, range size and 2-way interactions
262 between the measure of sexual selection and each of the environmental measures including range size, with

263 subsequent model simplification using AIC model selection. In all cases the best model had a Δ AICc above
 264 20 against the second model, and an evidence ratio above 100.

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

274 **We investigated which of the three variables comprising the index of male-biased sexual se-
 275 lection was driving the association observed with λ_{DR} .** Our results over 300 trees showed that this
 276 pattern is mainly driven by the sexual size dimorphism component (HPD Interval = 8.53×10^{-1} , 3.11), with
 277 the effects of other components overlapping zero; paternal care (HPD Interval = -1.78×10^{-1} , 7.90×10^{-3})
 278 and mating system (HPD Interval = -7.35×10^{-2} , 4.32×10^{-2}). Importantly, the association between
 279 sexual size dimorphism and speciation rates is also present when using λ_{ND} (HPD Interval = 1.80×10^{-1} ,
 280 6.38×10^{-1}), but not when using λ_{BAMM} (HPD Interval = -1.49, 7.45×10^{-1} , [Figure 3](#)).

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

294 Our analyses also show that the differences in results between sexual dichromatism and male-biased sexual
 295 selection (i.e. association with speciation rates only for the latter) were not due to differences in the size
 296 of the datasets used (5,812 species vs. 2,465, [Figure S17](#)). No interaction terms were present in the top
 297 models (Δ AICc > 4) for any measure of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) or sexual selection (RGB values,
 298 spectrophotometry and the index of male-biased sexual selection; Δ AICc > 4; [Table S5](#), [Table S6](#), [Table S11](#),
 299 [Table S14](#)). Thus we found no evidence that the effect of sexual selection on speciation is dependent on our
 300 measures of environmental variation or range size. Furthermore, we found no evidence that these environmental
 301 factors — seasonal temperature variation, long-term temperature variation, spatial temperature variation,
 302 and Net Primary Productivity (NPP) — predict speciation independently from sexual dichromatism/selection
 303 ([Figure 2](#), [Figure S11](#)).

304 Species with smaller ranges have increased rates of speciation

305 Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation, we found a negative association between range size
 306 and speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This
 307 negative association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.58 \times 10^{-3}$, $p =$
 308 1.48×10^{-3} ; λ_{ND} : $\beta = -1.46 \times 10^{-4}$, $p = 0.03$; [Figure 2a](#), [Figure 1](#)). This association was also evident across
 309 the estimates from models using the 1,000 trees (λ_{DR} : HPD Interval = -8.87×10^{-3} , -6.61×10^{-4} ; λ_{ND} :
 310 HPD Interval = -1.51×10^{-4} , 1.72×10^{-5} ; [Figure 2a](#)). Subset models with reduced sample size and different
 311 measures of sexual selection — but the same measure of range size — showed equivocal evidence that range
 312 size is negatively associated with speciation. Range size is significantly associated with λ_{DR} ([Figure 2b](#)) using
 313 data subset for species with an index of male-biased sexual selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} .
 314 Models using data subset for spectrophotometry-based dichromatism ($n = 581$) gave non-significant estimates
 315 for the effect of range size on all measures of speciation ([Figure S11](#), [Table S12](#), [Table S13](#)). Because the
 316 range size dataset is the same across the three data subsets, we draw our conclusions from the models with
 317 the highest power using near-complete taxon sampling ($n = 5,812$).

318 Phylogenetic path analysis

319 Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
 320 ([Figure 4](#); [Figure S14](#)). There was a modest effect of male-biased sexual selection on sexual dimorphism (β
 321 = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism ($\beta = 0.07$) and strongly
 322 affected range size ($\beta = 0.52$). This suggests an indirect effect of temperature seasonality on λ_{DR} ($\beta_{indirect} =$
 323 -0.02; [Figure 4](#)), given the negative association we identified between λ_{DR} and range size in PGLS models.

324 Extinction rate

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

329 Variability across phylogenetic trees and speciation rate measures

330 Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially
 331 in the BAMM rates (λ_{BAMM} and μ_{BAMM}), where the 95 % HPD interval across PGLS model estimates
 332 from 100 trees was often > 20 times larger than the 95 % confidence interval for estimates from a single
 333 PGLS model using the MCC tree. This contrasts with variation across trees for the other rate estimates
 334 (λ_{DR} and λ_{ND}), where the 95 % HPD interval of model estimates for pgls models using 1,000 trees was near-
 335 equivalent to the 95 % confidence interval calculated for PGLS model estimates of the MCC tree ([Table S9](#)).
 336 **Given the computational requirements of BAMM, the great majority of earlier studies have**
 337 **based their estimates on a single consensus tree. However, our results suggest that BAMM**

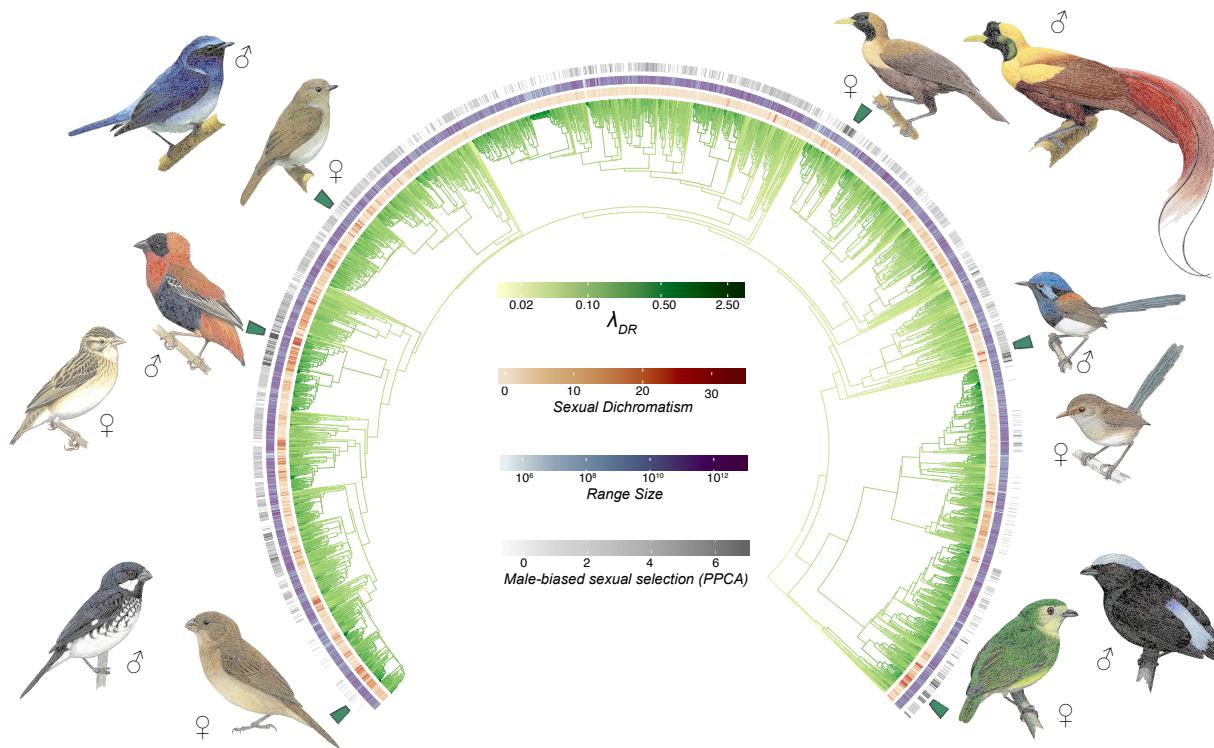


Figure 1: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism, range size available for 5,812 species and an index of male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative association between λ_{DR} and log-range size as well as a significant positive association between λ_{DR} and male-biased sexual selection but no significant association between λ_{DR} and sexual dichromatism based on RGB measures. λ_{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 λ_{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.

338 **estimates between alternative, similarly plausible phylogenies vary substantially.** Mean measures
 339 of speciation rate across 100 trees were positively correlated between measures ($\lambda_{DR} - \lambda_{BAMM}$: $r=0.75$, λ_{DR}
 340 - λ_{ND} : $r=0.65$, $\lambda_{ND} - \lambda_{BAMM}$: $r=0.51$; [Figure S15](#)). Given that the calculation of BAMM rates can be
 341 affected by the settings of the run and the use of different priors, we compared the estimate of our MCC tree
 342 with that of previous published analyses on birds and found a high correlation ($r=0.81$, [Figure S6](#), [Figure S8](#),
 343 Harvey et al. (2017)). Full details of the BAMM results are presented as supplementary materials.

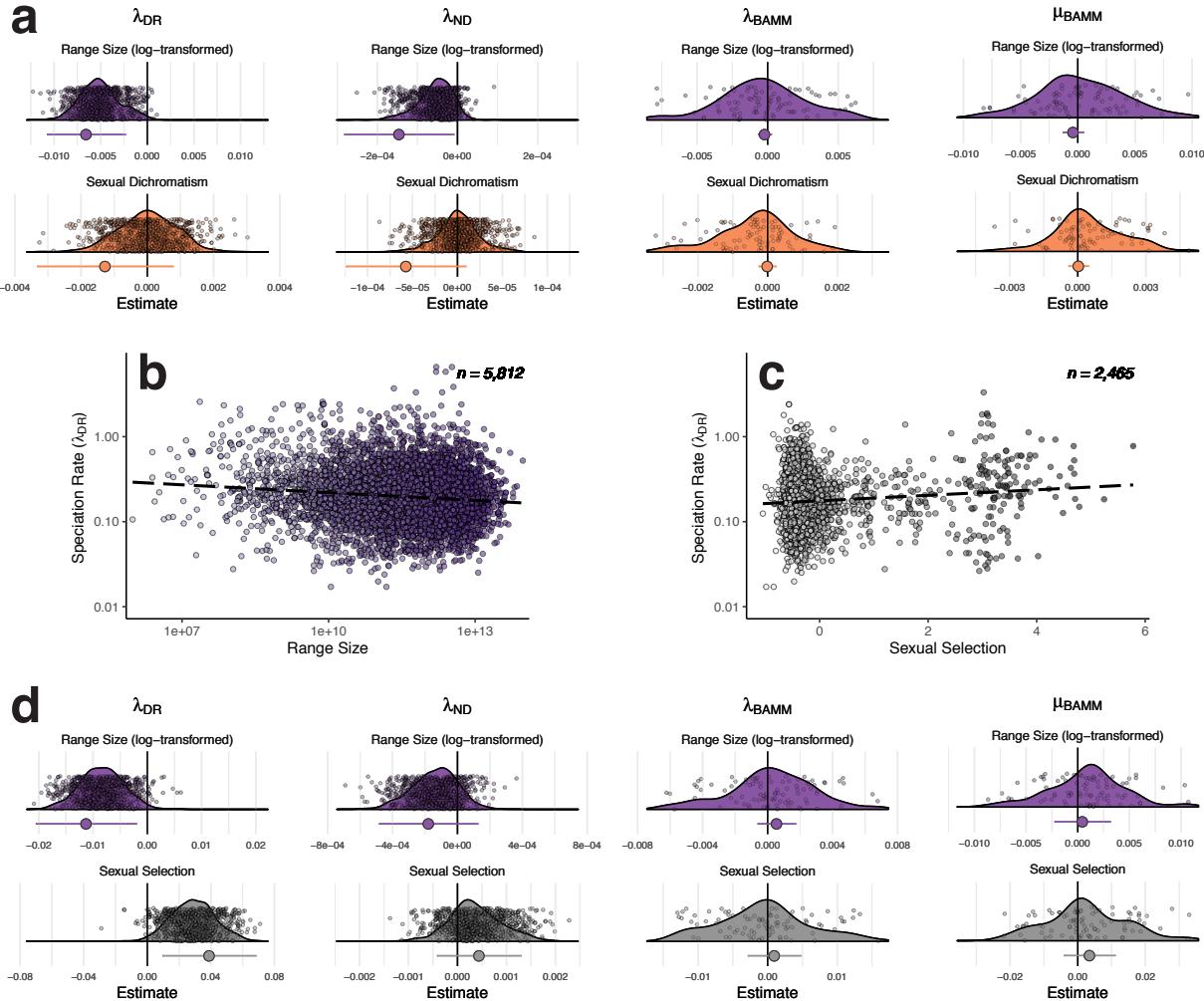


Figure 2: Model estimates (a) showing the effect size (i.e. slope) of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset (RGB values, $n = 5,812$). (b) depicts the scatter plot of speciation rate (λ_{DR}) and log-range size with the model estimate presented as a dashed line. (c) shows the scatter plot of speciation rate (λ_{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 (λ_{DR} , λ_{ND} , λ_{BAMM}) and one measure of extinction (μ_{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 λ_{DR} and λ_{ND}) or 100 randomly sampled trees for λ_{BAMM} and μ_{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.

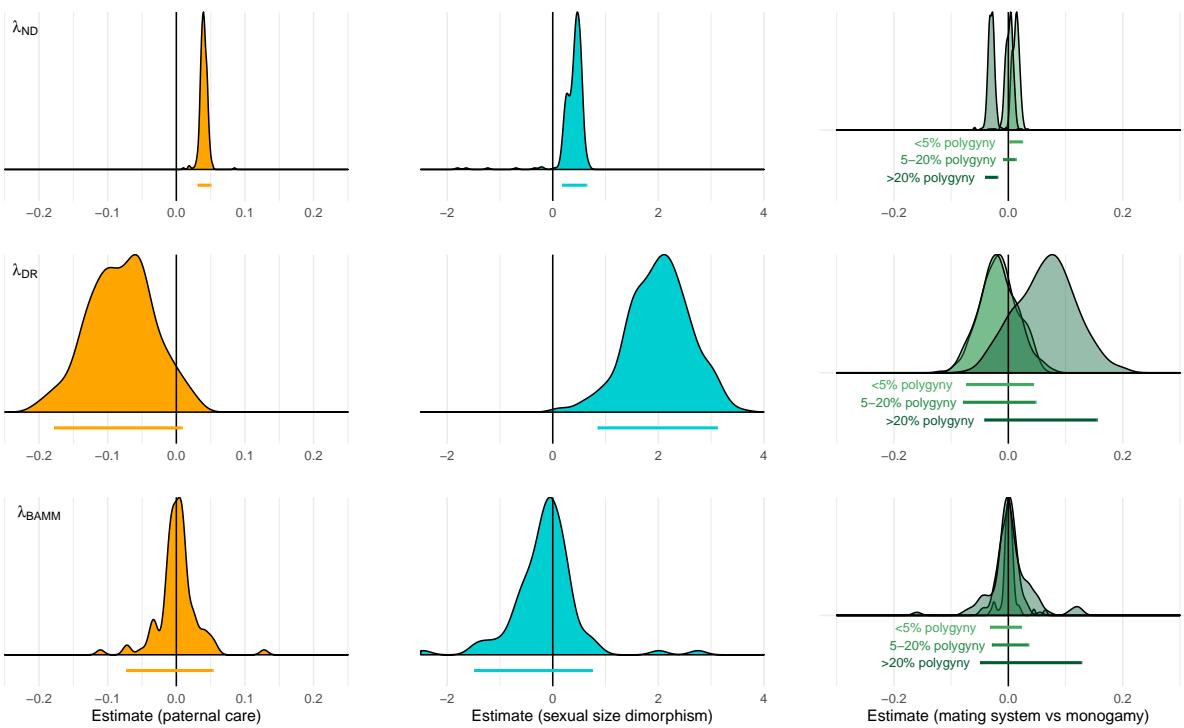


Figure 3: Estimates of the effect of individual sexual selection components included in the PPCA (paternal care, sexual size dimorphism and mating system) on three measures of speciation rate (λ_{DR} , λ_{ND} and λ_{BAMM}). Estimates are presented as density intervals from pgls models on 300 phylogenetic 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).

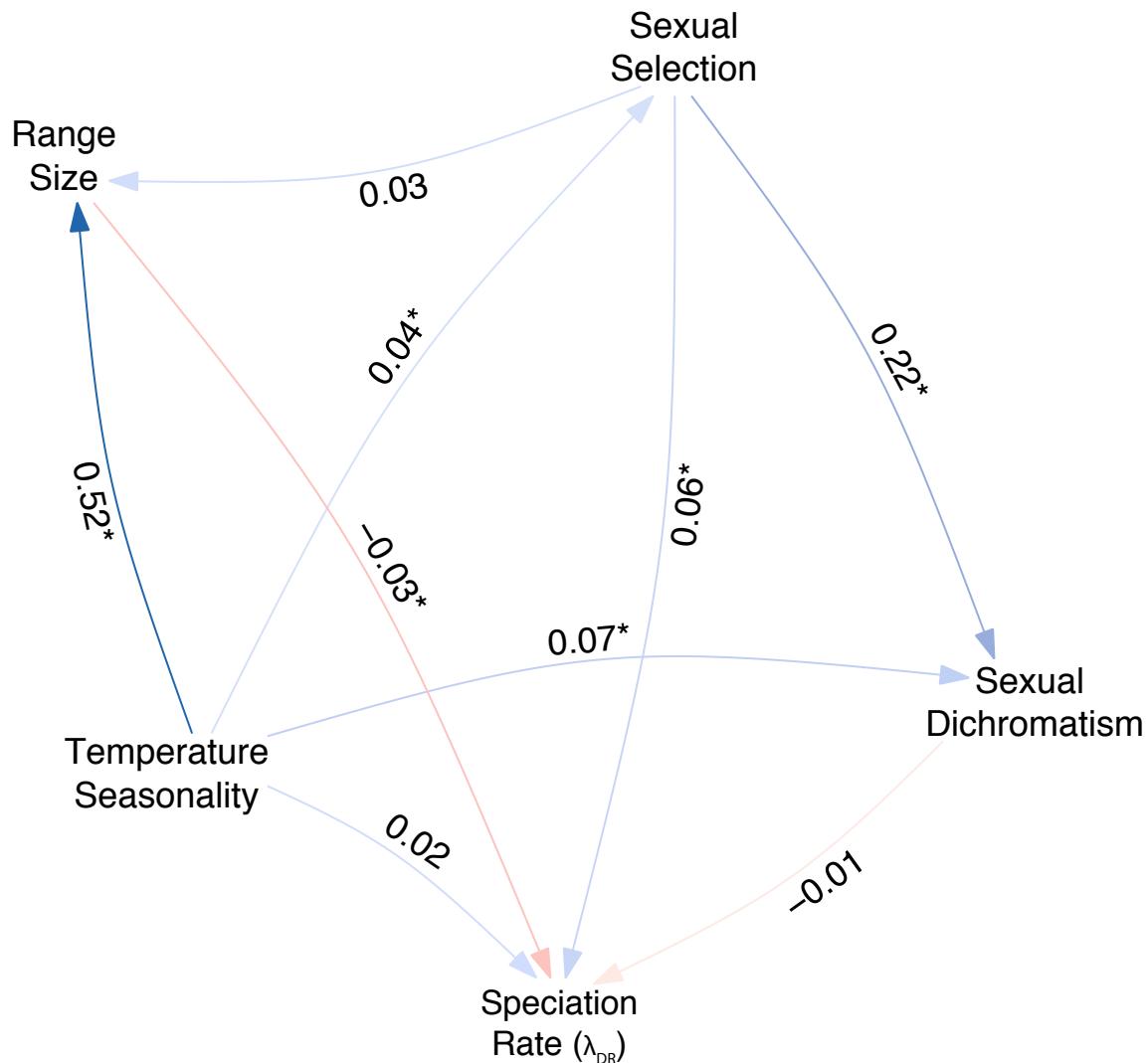


Figure 4: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with the direction of effect corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95% confidence intervals 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 ($n = 2,465$).

344 DISCUSSION

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

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

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

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

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

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

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

and Price 2011; Price and Eaton 2014). However, species undergoing adaptive radiation in new habitats are unlikely to be limited by competition for resources from existing taxa. One further explanation for the negative association between range size and sexual dichromatism/sexual selection is the potential bias of taxonomic classification, whereby over-splitting of species in clades with large ranges leads to increased recent phylogenetic branching as well as smaller ranges.

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

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

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

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