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

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Abstract

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

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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 (Barraclough 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 diversifica-
42 tion 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 raclough 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

58 selection and speciation, with the average effect size in birds stronger than in mammals but weaker than in
59 insects or fish (Kraaijeveld et al. 2011). However, there was large variation in effect size estimates across the
60 20 studies, likely reflecting differences in methodology, such as metrics used to characterise speciation and
61 sexual selection, in addition to true biological differences. More recently, Huang and Rabosky (2014) found no
62 association between sexual dichromatism and speciation ($n = 918$ species) in a study using spectrophotometric
63 measurements of museum specimens (Armenta et al. 2008) and tip-rate estimates from a molecular-only
64 phylogeny (Jetz et al. 2012). Similarly, Cooney et al. (2017) found no effect of sexual dichromatism on
65 diversification across 1,306 pairs of species, using dichromatism scores provided by human observers. More
66 recently, social polygyny (a proxy for sexual selection) was found to have a positive association with speciation
67 rate across 954 species of birds (Iglesias-Carrasco et al. 2019). We summarize the major findings from
68 previous studies testing the association between sexual selection and speciation in birds and other taxa since
69 Kraaijeveld et al. (2011) meta-analysis (Table 1).

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

82 We use multiple approaches for quantifying speciation and extinction rates at the tips of phylogenetic trees,
83 including Bayesian Analysis of Macroevolutionary Mixtures (BAMM; Beaulieu and O’Meara 2015; Rabosky
84 2016; Moore et al. 2016; Rabosky et al. 2017), as well as older but reliable tip-rate statistics, namely
85 diversification rate (λ_{DR}) and node density (λ_{ND}) (Jetz et al. 2012). Our results show that (i) a composite
86 measure of sexual selection, but not sexual dichromatism, significantly predicts speciation rates, (ii) the
87 significant association between the composite measure of sexual selection and speciation rate is largely driven
88 by sexual size dimorphism, (iii) species with smaller ranges have higher speciation rates and (iv) there
89 is no evidence that environmental variables or their interaction with sexual selection have an impact on
90 diversification rates. Therefore, we provide evidence at a very large scale that sexual selection can have
91 positive effects on diversification in the largest radiation of birds. Furthermore, we suggest that the use of
92 sexual dichromatism as the sole proxy for sexual selection should be reconsidered, since it appears to be
93 inconsistently associated with the operation of sexual selection.

94 MATERIALS AND METHODS

95 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ($n = 5,812$
96 species; 58% of all birds). Specifically, we (i) compiled datasets for sexual dichromatism/selection strength

97 and environmental variability, (ii) obtained estimates of speciation and extinction rates across passerines,
98 and (iii) conducted phylogenetic generalized least-squares (PGLS) regressions. Analyses are documented
99 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
103 al. 2015). Briefly, Dale et al. (Dale et al. 2015) obtained sex-specific RGB (red-green-blue) values across
104 six body patches (nape, crown, forehead, throat, upper breast, and lower breast) from *Handbook of the*
105 *Birds of the World* (Del Hoyo et al. 2011). The relative contribution of male and female RGB colour values
106 were averaged across body patches and provide ‘male-like’ and ‘female-like’ plumage scores. Here we use
107 the absolute difference between male and female plumage scores as an estimate of sexual dichromatism.
108 Technically, this measures differences in the ‘degree of male-ness’ between males and females, rather than
109 sex differences in colour *per se* (i.e. dichromatism in the strict sense). For example, the metric would fail to
110 capture dichromatism when both the male and female possess a single, but differently coloured ‘male-like’
111 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](#)
117 [S10](#)).

118 Male-biased sexual selection

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

129 Environmental variables

130 We obtained estimates of species range size using expert range maps (BirdLife International and Handbook of
131 the Birds of the World 2017). The names of 1,230 species in the Birdlife database (Hoyo and Collar 2016) have
132 been recently changed, so we manually matched these taxa with the names used in the sexual dichromatism
133 dataset (Hoyo and Collar 2016). For each species' range, we obtained estimates of climatic conditions by
134 extracting 1,000 random point samples of each bioclimatic variable. We extracted 19 present-day bioclimatic
135 variables (representing a variety of biologically relevant annual trends in temperature and precipitation) with
136 30-second ($\sim 1 \text{ km}^2$) spatial resolution (Fick and Hijmans 2017). From the 1000 values of each bioclimatic
137 variable, we obtained means and standard deviations for each species. Using the same spatial sampling,
138 we extracted means and standard deviations of bioclimatic variables from the paleoclimate during the last
139 interglacial (LIG; 120,000 - 140,000 years ago) (Otto-Bliesner et al. 2006). To estimate variability in the
140 energy available to species, we obtained the mean and standard deviation of net primary productivity (NPP)
141 values between 2000 - 2015 across each species distribution. Estimates of NPP had 30-second resolution
142 and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production
143 products stage 3 (MOD17A3) (Zhao et al. 2005). We provide these data as a potentially useful data resource
144 (see [Supplementary Information](#)).

145 Generating biologically relevant predictors for environmental stress

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

166 Estimating extinction and speciation

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

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

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

207 phylogeny across all birds (Harvey et al. 2017). All analyses were conducted on log-rates.

208 Phylogenetic comparative analysis

209 To test the association between speciation/extinction and sexual selection, environmental variability and their
210 interaction, we used phylogenetic least squares (PGLS) models in the `nlme` package (Pinheiro et al. 2018).
211 Firstly, we conducted model selection to compare models in which λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} were the
212 response variable: these tip-rate estimates all came from the same MCC tree (derived from 2,500 draws of
213 the posterior distribution (Jetz et al. 2012)). For models of λ_{BAMM} and μ_{BAMM} , we used the inverse of
214 the variance associated with each tip rate estimate as weights, to account for the variable precision of the
215 estimates provided by BAMM. For each response variable, we conducted model selection to compare models
216 with different combinations of predictor variables. The most complex model in each set under comparison
217 contained one of the measures of sexual selection (sexual dichromatism or the index of male-biased sexual
218 selection), all of the environmental measures (i.e. log-transformed range size, seasonal temperature variation,
219 spatial temperature variation, long-term temperature variation, and NPP), and all of the 2-way interactions
220 between sexual selection and each of the environmental measures. The simpler models contained all of the
221 same main effects, but had fewer 2-way interaction terms (potentially none). Model selection was done in
222 `MuMIn` using the `dredge` function (Bartoń 2017). Using the terms from the top-ranked model (ranked by
223 AICc), we ran the equivalent model for each of the 1,000 phylogenetic trees used to derive λ_{DR} , λ_{ND} and
224 each of the 100 trees used to derive λ_{BAMM} and μ_{BAMM} . Additionally, we investigated the effect of the
225 individual variables used to derive the index of male-biased sexual selection on speciation rate. For these pgl
226 models we replaced the composite index score with the individual biological variable (sexual size dimorphism,
227 social polygyny and [lack of] paternal care) and ran the equivalent model for 300 phylogenetic trees used to
228 derive λ_{DR} , λ_{ND} and 100 trees used to derive λ_{BAMM} .

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

240 Finally, using the subset of species with an index of male-biased sexual selection, we conducted a phylogenetic
241 path analysis using the `phylopath` R package (Bijl 2018). The phylogenetic path analysis was used to assess
242 causal paths between variables unable to be modelled within the univariate response of PGLS. That is, a
243 phylogenetic path analysis allowed us to model relationships between the predictor variables used in our
244 PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection, and range size to
245 have effects on each other and not just on speciation rate. To minimise path complexity, we used temperature
246 seasonality (BIO4) as the single measure for environmental variability, λ_{DR} as the single measure of speciation,

247 and the tip-rates from the MCC tree. Further details of the path analysis, including our rationale for each
248 path's directions, can be found within the [Supplementary Information](#) along with all other analyses and the
249 relevant R code to reproduce results.

250 RESULTS

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

252 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ($n =$
253 5,812 species; 58% of all birds; [Figure 1](#)). We found a significant positive association between the index of
254 male-biased sexual selection ($n = 2,465$) and λ_{DR} from the maximum clade credibility (MCC) tree ($\beta =$
255 3.89×10^{-2} , $p = 0.01$; [Figure 2b](#)). However, this association was not significant for the other two measures of
256 speciation rate (λ_{ND} : $\beta = 4.38 \times 10^{-4}$, $p = 0.35$; λ_{BAMM} : $\beta = 9.42 \times 10^{-4}$, $p = 0.76$; [Figure 2b](#)). When
257 we took into account phylogenetic uncertainty by running the models using 1,000 trees, the distribution of
258 estimates from PGLS models was similar to the estimate from the MCC tree: among the 1,000 trees there
259 was a positive association between sexual selection and λ_{DR} (highest posterior density (HPD) Interval =
260 4.51×10^{-3} , 5.72×10^{-2}), and the distribution skewed towards a positive association between sexual selection
261 and λ_{ND} (HPD Interval = -5.04×10^{-4} , 1.58×10^{-3}) as well as the 100 models using λ_{BAMM} (HPD Interval
262 = -1.30×10^{-2} , 3.09×10^{-2} ; [Table S15](#)).

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

270 In contrast to male-biased sexual selection, we found no evidence that species with increased sexual dichro-
271 matism have higher or lower rates of speciation. Sexual dichromatism showed no association with λ_{DR}
272 ($\beta = -1.28 \times 10^{-3}$, $p = 0.15$; [Figure 2a](#), [Figure 1](#)), λ_{ND} ($\beta = -5.75 \times 10^{-5}$, $p = 0.08$; [Figure 2a](#)) or
273 λ_{BAMM} ($\beta = -1.43 \times 10^{-5}$, $p = 0.87$; [Figure 2a](#)). PGLS analyses using sexual dichromatism ($n = 581$)
274 measured by spectrophotometry (Armenta et al. 2008) yielded results concordant with the full dataset; i.e. no
275 association between sexual dichromatism and speciation ([Figure S11](#)). Our results from models based on
276 the MCC tree are largely corroborated by model estimates from PGLS analyses of the rates and correlation
277 structures from 1,000 trees (for λ_{DR} , λ_{ND}) and 100 trees for λ_{BAMM} . The HPD intervals show model
278 estimates are distributed around zero when using complete taxon sampling models and RGB measures of
279 sexual dichromatism (λ_{DR} : HPD Interval = -1.63×10^{-3} , 1.66×10^{-3} , λ_{ND} : HPD Interval = -4.26×10^{-5} ,
280 5.50×10^{-5} , [Figure 2a](#), [Table S8](#)). For PGLS models using spectrophotometry-based measures of sexual
281 dichromatism, the estimates from the 100 trees in the λ_{DR} models are positively skewed (HPD Interval =
282 -1.78×10^{-2} , 3.49×10^{-2}) but normally distributed around zero for λ_{ND} and λ_{BAMM} ([Table S12](#)).

283 Our analyses also show that the differences in results between sexual dichromatism and male-biased sexual

284 selection (i.e. association with speciation rates only for the latter) were not due to differences in the size
285 of the datasets used (5,812 species vs. 2,465, [Figure S17](#)). No interaction terms were present in the top
286 models ($\Delta \text{AICc} > 4$) for any measure of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) or sexual selection (RGB values,
287 spectrophotometry and the index of male-biased sexual selection; $\Delta \text{AICc} > 4$; [Table S5](#), [Table S6](#), [Table S11](#),
288 [Table S14](#)). Thus we found no evidence that the effect of sexual selection on speciation is dependent on our
289 measures of environmental variation or range size. Furthermore, we found no evidence that these environmental
290 factors — seasonal temperature variation, long-term temperature variation, spatial temperature variation,
291 and Net Primary Productivity (NPP) — predict speciation independently from sexual dichromatism/selection
292 ([Figure 2](#), [Figure S11](#)).

293 Species with smaller ranges have increased rates of speciation

294 Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation, we found a negative association between range size
295 and speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This
296 negative association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.58 \times 10^{-3}$, $p =$
297 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
298 the estimates from models using the 1,000 trees (λ_{DR} : HPD Interval = -8.87×10^{-3} , -6.61×10^{-4} ; λ_{ND} :
299 HPD Interval = -1.51×10^{-4} , 1.72×10^{-5} ; [Figure 2a](#)). Subset models with reduced sample size and different
300 measures of sexual selection — but the same measure of range size — showed equivocal evidence that range
301 size is negatively associated with speciation. Range size is significantly associated with λ_{DR} ([Figure 2b](#)) using
302 data subset for species with an index of male-biased sexual selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} .
303 Models using data subset for spectrophotometry-based dichromatism ($n = 581$) gave non-significant estimates
304 for the effect of range size on all measures of speciation ([Figure S11](#), [Table S12](#), [Table S13](#)). Because the
305 range size dataset is the same across the three data subsets, we draw our conclusions from the models with
306 the highest power using near-complete taxon sampling ($n = 5,812$).

307 Phylogenetic path analysis

308 Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
309 ([Figure 4](#); [Figure S14](#)). There was a modest effect of male-biased sexual selection on sexual dimorphism (β
310 $= 0.22$). Additionally, temperature seasonality weakly affected sexual dimorphism ($\beta = 0.07$) and strongly
311 affected range size ($\beta = 0.52$). This suggests an indirect effect of temperature seasonality on λ_{DR} ($\beta_{indirect} =$
312 -0.02 ; [Figure 4](#)), given the negative association we identified between λ_{DR} and range size in PGLS models.

313 Extinction rate

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

Variability across phylogenetic trees and speciation rate measures

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

DISCUSSION

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

The difference in findings between the analyses of sexual dichromatism *versus* the index of male-biased sexual selection is noteworthy, because the majority of earlier studies used dichromatism alone as their proxy for sexual selection (e.g., Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014). Given our findings, and the modest correlation between dichromatism and the sexual selection index ($r = 0.34$; Dale et al. 2015), we suggest that sexual dichromatism may not be a robust proxy for sexual selection (Cooney et al. 2018). Although dichromatism almost certainly provides some insight into the operation of sexual selection, it may be too indirect a measure to detect any association with

356 speciation rate, even with large sample size. There are several reasons why the use of sexual dichromatism as
357 a proxy for sexual selection is problematic. Sexual dichromatism can evolve for reasons other than sexual
358 selection, such as when males and females occupy different ecological niches (Wallace 1889; Kottler 1980;
359 Slatkin 1984; Shine 1989) or experience different selective pressures in contexts other than competition for
360 mates (Price and Eaton 2014). For example, in superb fairy-wrens (*Malurus cyaneus*) female colouration has
361 probably evolved in response to spatial variation in predation pressure, increasing dichromatism (Medina et al.
362 2017). In fact, our path analysis detected a weak relationship between environment and sexual dichromatism,
363 where sexual dichromatism was positively predicted by temperature seasonality (a measure of environmental
364 variation).

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

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

392 We also found that the association between sexual selection and speciation appears to be independent of
393 net primary productivity and spatiotemporal variation in the environment. The lack of an effect of these
394 environmental variables on speciation rate has several possible interpretations. Firstly, the effects of sexual
395 selection on adaptation and speciation may depend on the type of environmental variability under which the
396 species is evolving. Specifically, speciation rates might be impacted by genetic constraints on adaptation,
397 that vary across environments. Theory suggests that sexual antagonism (which is often exacerbated in

398 species with strong sexual selection) may be lower in habitats experiencing cyclical environmental variation
399 (e.g. seasonality), relative to those experiencing directional change in the environment (Connallon and Hall
400 2016). Another possibility is that the environmental predictors we chose may not account for the key ecological
401 sources of selection that interact with sexual selection to drive speciation. For example, our study does
402 not include direct measure of food availability or the severity of predation and parasitism, which are both
403 hypothesised to affect sexual selection and speciation (reviewed in Maan and Seehausen 2011). Finally, it
404 is possible that environmental variability genuinely has little effect on speciation rates, at least in the taxa
405 investigated here.

406 We found that species with smaller ranges have elevated speciation rates. This result is similar to a study of
407 329 amphibian genera, which found higher diversification rates in taxa with smaller range size (Greenberg
408 and Mooers 2017). Intuitively, large range size should promote speciation by creating more opportunities
409 for geographic barriers to form (Rosenzweig 1995; Castiglione et al. 2017). However, the opposite pattern
410 is also plausible because birds with limited dispersal or more specialised niches can have more fragmented
411 populations, which would promote vicariant divergence and higher speciation rates (Jablonski and Roy 2003;
412 Birand et al. 2012; Claramunt et al. 2012). Moreover, species that have recently split as a consequence of
413 vicariant divergence might have smaller ranges as a result of the split of the ancestral lineage, leading to a
414 link between smaller ranges and shorter divergence times. It is also possible that high speciation rates cause
415 smaller range sizes, rather than the other way around, for example because repeatedly-speciating lineages
416 tend to fill niches in ways that hinder the geographical expansion of new species (Rosenzweig 1995; Weir
417 and Price 2011; Price and Eaton 2014). However, species undergoing adaptive radiation in new habitats
418 are unlikely to be limited by competition for resources from existing taxa. One further explanation for the
419 negative association between range size and sexual dichromatism/sexual selection is the potential bias of
420 taxonomic classification, whereby over-splitting of species in clades with large ranges leads to increased recent
421 phylogenetic branching as well as smaller ranges.

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

440 One outcome of our analyses was that different measures of speciation rates presented different results.
441 This is not completely surprising, because each of the rates is calculated differently (Title and Rabosky
442 2018). For instance, λ_{DR} is weighted more towards speciation events close to the tips and allows more rate
443 heterogeneity compared to λ_{BAMM} estimates. Rate shifts are unlikely to be detected in smaller clades in
444 BAMM, meaning that it is not uncommon for whole genera to have the same rate. Using the λ_{DR} metric,
445 only sister species are guaranteed to have the same rate. This leads to greater variation in λ_{DR} relative to the
446 λ_{BAMM} estimates, which is suggested to be an advantage when studying diversification patterns (Quintero
447 et al. 2015). Additionally, λ_{BAMM} estimates were more sensitive to phylogenetic uncertainty and were 20
448 times more variable across trees compared to λ_{DR} estimates. We cannot completely reject the idea that the
449 lack of association between λ_{BAMM} and sexual selection could be the result of low statistical power, due to
450 the combination of both low variation across species in the speciation rates and high levels of variation in the
451 estimates across trees.

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

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463 AUTHOR CONTRIBUTIONS

464 All authors contributed to conception, design and approach to analyses; J.G.C. and J.D. compiled the data;
465 J.G.C. and I.M. conducted analyses; J.G.C. wrote the first draft of the manuscript; all authors contributed
466 substantially to further manuscript revisions.

467 DATA ACCESSIBILITY

468 We have sought to make the data and Supplementary Material (including R code) freely accessible to
469 readers. The code and Supplementary Material for this manuscript are available on [GitHub](#) and as an
470 attached HTML document (Supplementary Material) for reviewers. Data is archived in the adjoined
471 GitHub repository and the environmental dataset collated for this manuscript is available on Dryad: <https://doi.org/10.5061/dryad.573n5tb6n>.
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⁴⁷³ **CONFLICTS OF INTEREST**

⁴⁷⁴ The authors declare no conflicts of interests to declare.

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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 (<i>Sturnidae</i>), 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
		Size dimorphism	Yes	Sexual size dimorphism predicts two out of three measures of speciation rates
This study	Across passerines, 5812 species	Plumage dichromatism	No	There was no link between plumage dichromatism (measured from spectral info or RGB values) and any speciation rate

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

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.

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 pgl 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 ($n = 2,465$).