

<sup>1</sup> Sexual selection, environmental variation, range size and speciation  
<sup>2</sup> in passerine birds

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<sup>4</sup> **Abstract**

<sup>5</sup> Sexual selection may influence patterns of diversification. Yet their relationship remains unclear with  
<sup>6</sup> controversy on whether sexual selection leads to a net increase or decrease in speciation rate. Sexual  
<sup>7</sup> selection is predicted to increase speciation rate as it can facilitate adaptation to new environments by  
<sup>8</sup> elevating the average fitness of a population. Additionally, sexual selection may work alongside divergent  
<sup>9</sup> natural selection and swiftly promote reproductive isolation. Here we use sexual dichromatism as a  
<sup>10</sup> proxy for sexual selection across 5,812 species of passerine birds and a multivariate male-bias measure of  
<sup>11</sup> sexual selection (sexual dimorphism, polygyny and paternal care) across 2,465 species to investigate the  
<sup>12</sup> association of sexual selection with speciation and extinction. Importantly, we test whether the effects of  
<sup>13</sup> sexual selection on speciation are dependent upon ecological pressures such as temperature variability  
<sup>14</sup> across time and space, primary productivity and range size. Our results from three distinct measures  
<sup>15</sup> of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) and one measure of extinction ( $\mu_{BAMM}$ ) find that male-bias sexual  
<sup>16</sup> selection but not sexual dichromatism predicts speciation. Additionally, we find that birds with smaller  
<sup>17</sup> ranges have higher speciation rates; however the causality of this finding remains inconclusive.

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## 18 Introduction

19 **Process of speciation:** Selection pressures drive speciation. As populations diverge they accumulate  
20 genetic and phenotypic changes that ultimately erect barriers against gene flow (Presgraves 2010; *but see*  
21 Shaw and Mullen 2011). In this view populations will speciate and adapt more readily to new divergent  
22 environments if the selection pressures and evolvability of the traits under selection are high. Hence, the  
23 rate at which speciation occurs is likely dependent on both the populations adaptive potential/fitness  
24 and the evolvability of phenotypic traits such as morphology or chromatism (Hugall and Stuart-Fox 2012;  
25 Rabosky et al. 2013). Sexual selection is an evolutionary force likely to affect fitness components as well  
26 as the evolvability of morphological and chromatic traits such as ornaments involved in mating displays or  
27 weapons used in male-male competition. It is therefore hypothesised that sexual selection is a key driver of  
28 diversification through shifting the rates of adaptation, speciation and extinction.

29 **Sexual selection and fitness:** Sexual selection is applied by one sex on the other - more often by females  
30 on males (Kokko and Jennions 2008; Fromhage and Jennions 2016; Janicke et al. 2016) and can increase  
31 or decrease the average fitness of a population; often termed population fitness (*reviewed in*, Kokko and  
32 Brooks 2003; Whitlock and Agrawal 2009; Holman and Kokko 2013). Specifically, in line with the 'good genes'  
33 perspective, sexual selection may purge deleterious mutations, (Agrawal 2001; Siller 2001) and fixate beneficial  
34 mutations (Whitlock 2000). Thus, sexual selection is thought to be a key process in mitigating extinction  
35 risk and facilitating adaptation. However, the beneficial aspects of sexual selection are dependent on the  
36 genotypes under sexual selection (e.g. those that increase male mating/fertilisation success) being genetically  
37 positively correlated with traits affecting fitness (e.g. female fecundity or survival). This positive correlation  
38 is unlikely to always be the case; regularly, sexual selection favours traits having negative pleiotropic effects  
39 on female fitness (Pischedda and Chippindale 2006; Bonduriansky and Chenoweth 2009; Pennell and Morrow  
40 2013; Berger et al. 2014). For instance, in species with high levels of sexual selection mating success becomes  
41 more variable and uncertain, thus individuals must heavily invest to increase their chances of successfully  
42 reproducing. Through prioritising mating success a sex may invest in costly weaponry and sexual signals,  
43 while forgoing strategies that would improve offspring fitness (parental care). This is a potentially costly  
44 consequence that affects persistence, adaptation and extinction (Kokko and Brooks 2003).

45 **Sexual selection, heritability and mechanisms of speciation:** Alongside changes to fitness, sexual  
46 selection has been proposed to facilitate ecological diversification and speciation through increased evolvability  
47 of divergent signals/ornaments associated with improved mating success (Lande 1981, 1982). Under this  
48 model of speciation, divergent sexual signals in one sex (usually males) co-evolve with divergent preferences for

49 those signals in the opposite sex, and by itself sexual selection could lead to behavioural reproductive isolation  
50 (Safran et al. 2013). But sexual selection is unlikely to be occurring without the effects of natural selection.  
51 In this situation, adaptation and speciation may be further enforced if female preference in mating signals are  
52 dually favoured by natural selection (Maan and Cummings 2008). The extent to which sexually selected traits  
53 can evolve is dependent on the underlying genetic variation. Under sexual selection a wider phenotypic space  
54 may be available for a population to evolve into than natural selection acting alone as genetic variation can  
55 be maintained under sexual conflict arising from heightened sexual selection (Lorch et al. 2003; Bonduriansky  
56 2011; Radwan et al. 2016). Furthermore, the evolvability and transmission of fitness and sexually selected  
57 traits may vary due to different sex determination systems across taxa. In male homogametic species (ZZ/ZW  
58 or ZZ/ZO) — such as birds — males are anticipated to have increased heritability of male-specific genotypes  
59 on the Z chromosome associated with mating success: such as elaborate ornamentation or plumage coloration  
60 (Hastings 1994; Reeve and Pfennig 2003). We might therefore expect birds with higher opportunities for  
61 sexual selection to have increased evolvability and speciation rates, especially in environments where natural  
62 selection pressures are high and working concordantly to sexual selection.

63 **Environmental interaction:** Importantly, the effects of sexual selection, adaptation and speciation may  
64 depend on environmental conditions. Studies suggest that under stressful/changing environments sexual  
65 selection may have greater fitness benefits than under benign environments. In stressful environments, the  
66 positive correlation between male mating success and female fitness components improves, reducing the  
67 burden of negative pleiotropic effects (Long et al. 2012; Berger et al. 2014; Connallon and Hall 2016;  
68 Martinossi-Allibert et al. 2017). Conversely, under benign environments environmental stability ensures  
69 consistent selection, preferentially removing genetic variation at sexually concordant loci (i.e. loci where  
70 the optimum genotype is equivalent for both sexes). In these cases genetic variation preferentially remains  
71 at sexually antagonistic loci; causing displacement of male and female traits from their optimum. These  
72 predictions would ensue that populations subject to persistent environmental variability would have increased  
73 fitness and adaptive benefits under increased sexual selection; allowing them to adapt to novel environments  
74 (*reviewed in* Candolin and Heuschele 2008). Increased environmental variability in a species ecological and  
75 climatic niche may also work synergistically with natural selection to promote diverging phenotypic traits  
76 (Safran et al. 2013). In certain circumstances sexual selection will reinforce diverging locally adapted  
77 phenotypes through mate choice on phenotypes that advertise quality in a specific ecological context (Maan  
78 and Seehausen 2011). If mate choice operates on both sexes — or there is a correlation in trait values between  
79 a pair — assortative mating is likely to strengthen this positive feedback loop and promote population  
80 divergence (Lande 1981). Sexual selection may also interact with natural selection in opposing directions

81 when environmental conditions modify the sexually selected signal, such as turbid waters that reduce the  
82 signalling strength in stickbacks (Candolin et al. 2007; Wong et al. 2007). In this opposing view, changing  
83 environments may limit the divergence of sexually selected traits and consequently reduce speciation rate.

84 **Previous limitations:** The association between sexual selection and speciation has been investigated using  
85 many macroevolutionary approaches across various taxa. Importantly, macroevolutionary comparative studies  
86 can examine the association between sexual selection and extinction risk in more diverse taxon, over longer  
87 evolutionary time-scales and in more natural environments. A meta-analysis of 64 effect sizes from 20 papers  
88 found a small, significant association between sexual selecetion and speciation (Kraaijeveld et al. 2011).  
89 However, variation in sexual selection proxies used and other methodological choices (species richness vs  
90 rate estimates) led to heterogeneity in effect sizes for the correlation between sexual selection and speciation.  
91 Given that species richness and speciation rate may be negatively correlated (Rabosky et al. 2018) and  
92 the recent development and refinement of methodologies in obtaining tip-rate estimates of speciation and  
93 extinction (Jetz et al. 2012; Rabosky 2014; Rabosky and others 2018) the association between sexual selection  
94 and speciation rate is worth revisiting with methods that address several issues that have previously limited  
95 macroevolutionary comparative studies. Firstly, sexual selection strength in macroevolutionary studies are  
96 often estimated using measures of dimorphism or dichromatism; but these are often partial measures of  
97 sexual selection and may not account for the true variation in sexual selection across taxa, which arguably  
98 decreases the power to detect an association, especially if phylogenetic signal is strong. Secondlly, many  
99 studies use incomplete taxon sampling, with family-level analysis restricted to well sampled avian clades  
100 (Seddon et al. 2008; Huang and Rabosky 2014). Thirdly, until recently studies have rarely incorporated  
101 extensive bioclimatic predictors into large-scale comparative analyses (*sensu* Jetz and Rubenstein 2011; Pigot  
102 et al. 2016). Fourthly, phylogenetic uncertainty in the avian tree (Jetz et al. 2012; *but see* Rubolini et al.  
103 2015) and uncertainty in tip-rate measures of speciation such as the diversification rate statistic ( $\lambda_{DR}$ ) or  
104 node density ( $\lambda_{ND}$ ) (Rabosky and others 2018) as well as speciation and extinction tip-rates from models  
105 using BAMM (Bayesian Analysis of Macroevolutionary Mixtures) (*see*, Beaulieu and O'Meara 2015; Moore et  
106 al. 2016; Rabosky 2016; Rabosky et al. 2017) continue to plague the ability to draw widely accepted findings

107 **I don't know if this is true.**

108 **Our study:** Because of the wealth of data available for passerine birds (Order: Passeriformes) we are able  
109 to conduct a large comparative analysis across nearly all species of passerines. Recently, Huang and Rabosky  
110 (2014) found no association between sexual dichromatism and speciation using tip-rate estimates from a  
111 genetic-only phylogeny (Jetz et al. 2012) and sexual dichromatism data from a limited spectrophotometry  
112 dataset ( $n = 918$ ) (Armenta et al. 2008). Here we assess the relationship between sexual dichromatism,

environmental variability and their interaction with three tip-rate measures of speciation and one measure of extinction ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ;) in 5,812 species of passerines. We assess the effects of sexual dichromatism measures based on RGB values alongside smaller datasets of sexual dichromatism from spectrophotometry measures ( $n = 581$ ) and male-bias sexual selection measures ( $n = 2,465$ ). Using expert range maps and bioclimatic variables we are able to investigate whether the effect of sexual selection on speciation is dependent on range size, seasonal variation in temperature, spatial temperature variation (across a species' range), long-term variation in temperature between now and the last inter-glacial (LIG) as well net primary productivity (NPP).

## Materials and methods

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. Many of the processes undertaken in this study are documented with reproducible code in the electronic supplementary material (ESM).

## Compiling data for sexual selection and environmental stress

### Sexual dichromatism

We used sexual dichromatism as proxy of sexual selection strength. Male and female plumage scores have previously been measured across 5,983 species of passerines (Dale et al. 2015). Briefly, Dale et al. (2015) obtained sex-specific RGB (red, green and blue) values across six body patches (nape, crown, forehead, throat, upper breast and lower breast) from *Handbook of the Birds of the World* (volumes 8–16) (Del Hoyo et al. 2011). The mean values of red, green and blue were calculated and provided male and female plumage scores. Here we use the absolute difference between males and female RGB scores as an estimate of sexual dichromatism. Additionally, we compiled a colour discriminability measure of sexual dichromatism from spectrophotometer measures (Armenta et al. 2008). These measurements include variation in the ultraviolet and bird-visible range and — unlike the RGB measures — are sourced from taxonomic samples (as opposed to colour drawings). However, this spectrophotometry data is not as extensive as the RGB measures; with only 581 passerine species available for this analysis. While there is a correlation between these two measures, there is residual variation ( $r = 0.79$ ; **Figure S9**).

**141 Male-biased sexual selection**

142 Sexual dichromatism has long been associated with levels of sexual selection (Darwin 1871), with sexual  
143 dichromatism often used as a measure of sexual selection in avian taxa (*e.g.*, Barraclough et al. 1995; Owens et  
144 al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014). However, sexual dichromatism  
145 is likely to account for only partial variation in sexual selection across taxa. Here we use an existing dataset  
146 (Dale et al. 2015) of male-bias sexual selection based on the first component of a phylogenetic principle  
147 component analysis (ppca) of three characteristics associated with sexual selection (sexual size dimorphism,  
148 social polygyny and [lack of] paternal care). However, this measure of male-bias sexual selection is present  
149 for only 2,465 species and is weakly correlated with the absolute values for sexual dichromatism using RGB  
150 measures ( $r = 0.34$ ; **Figure S10**).

**151 Environmental variables**

152 Using expert range maps (BirdLife International and Handbook of the Birds of the World 2017) we obtained  
153 estimates of species range size. Using these distributions we were able to obtain estimates for extensive  
154 climatic conditions that each species is exposed to. Because of taxonomic changes to 1,230 species in the  
155 *Birdlife* database (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual  
156 dichromatism dataset (Dale et al. 2015). From 1,000 random point samples in each range we extracted 19  
157 present day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature  
158 and precipitation) with 30 seconds ( $\sim 1 \text{ km}^2$ ) spatial resolution (Fick and Hijmans 2017). From these values  
159 we obtained means and standard deviations for each species. Using the same spatial sampling we extracted  
160 means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial  
161 (LIG; 120,000 - 140,000 years ago) (Otto-Bliesner et al. 2006). Furthermore, to estimate variability in the  
162 energy available to species we obtained the mean and standard deviation of net primary productivity (NPP)  
163 values between 2000 - 2015 across each species distribution. Estimates of NPP had 30 second resolution  
164 and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production  
165 products stage 3 (MOD17A3) (Zhao et al. 2005). Using this data, which we provide as a potentially useful  
166 data resource (see ESM), we generated five predictors of speciation associated with different patterns in  
167 environmental variability (see below).

168 **Estimating extinction and speciation.**

169 Phylogenetic information was obtained from [www.birdtree.org](http://www.birdtree.org) (Jetz et al. 2012). We used a maximum clade  
170 credibility tree (MCC) from 2,500 samples of the posterior distribution that were subset to the passerine bird  
171 order ( $n = 5,965$ ) as the main phylogenetic tree in our comparative analysis. Additionally, a random draw of  
172 100 full trees (including species without genetic data) from the posterior distribution of phylogenetic trees  
173 was used. These trees used a ‘Hackett backbone’ and were constructed using the a pure birth (Yule) model.  
174 We calculated three different tip-rate metrics of speciation and one of extinction across all trees.

175 Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes  
176 and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating  
177 the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES),  
178 also known as diversification rate (DR) (e.g., Jetz et al. 2012; Quintero and Jetz 2018; Rabosky et al. 2018),  
179 is derived from the sum of edge lengths branching from a node, with each more basal node having the sum of  
180 lengths down-weighted. Studies have suggested that DR and ND (henceforth referred to as  $\lambda_{DR}$  and  $\lambda_{ND}$ )  
181 are more reflective estimates of speciation than diversification (Belmaker and Jetz 2015; Rabosky and others  
182 2018). Therefore,  $\lambda_{DR}$  is a measure of speciation rate more heavily weighted to recent speciation events  
183 and  $\lambda_{ND}$  is a measure of speciation across the root to tip path. These tip-rate measures are alternatives to  
184 state-dependent diversification models such as Quantitative State Speciation-Extinction (QuaSSE) models.  
185 Based on previous comparisons  $\lambda_{DR}$  and  $\lambda_{ND}$  are anticipated to achieve high power and low false discovery  
186 rate with large phylogenies when incorporated into Phylogenetic Generalized Least Squares (PGLS) models  
187 (Harvey Michael et al. 2017).

188 Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic  
189 trees (Rabosky 2014). The model uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo)  
190 to generate a probability distribution of evolutionary regimes with variable speciation and extinction rates.  
191 Importantly, these models provide tip-rate estimates of speciation and extinction rate. The parameters of the  
192 100 BAMM runs are detailed in full in the ESM; briefly we used a time-variable model with 100 expected  
193 number of shifts and prior rates set from the initial speciation and extinction values using the **BAMMtools**  
194 R package (Rabosky et al. 2014). Each BAMM model (one MCC and 100 random draws of the posterior)  
195 was run for 100 million generations, and given the computationally intensive nature of BAMM, runs were  
196 conducted across multiple CPU’s. We obtained effective sample sizes for log-likelihood and number of rate  
197 shifts over 200 for each run (Table S3, Table S4). Further details of BAMM parameters and output is available  
198 through ESM, with tip-rate means and variances included in the ESM. Additionally, given the variability in

199 BAMM estimates we also provide some analysis of BAMM shift configurations and tip-rate estimates from  
200 our run on the MCC tree and within a BAMM run on an MCC from a genetic-only phylogeny across all  
201 birds (Harvey et al. 2017). All analyses was conducted on log-rates.

## 202 Statistical analysis

### 203 Generating biologically relevant predictors for environmental variation

204 Using the extracted environmental variables from each species range size we developed biologically meaningful  
205 predictors of environmental variation/stress relating to (i) seasonal climate variation, (ii) spatial climate  
206 variation and (iii) long-term climate variation. To obtain seasonal climate variation we used mean values  
207 of temperature seasonality (BIO4) for each range. To estimate levels of spatial environmental variation  
208 a species may endure we used the first principle component (PC1) from a PCA on standard deviations  
209 from all bioclimatic variables, excluding temperature (BIO4) and precipitation seasonality (BIO15). PC1  
210 was heavily loaded towards bioclimatic variables relating to temperature, thus PC1 reflects the variation  
211 in temperature across a species' range (**Table S1**). Given that species range is a potentially informative  
212 predictor of speciation and extinction we control for the correlation between spatial variation and range size  
213 — where larger ranges have larger variation in PC1 — by taking the residuals of a fitted general additive  
214 model (GAM; **Figure S1**). To obtain long-term variation in climates for each species range we take the first  
215 principal component of the absolute difference in the bioclimatic variables between the LIG and current values.  
216 Similarly to spatial variation, the long-term climate variation is primarily loaded to temperature differences  
217 between the LIG and current climates (**Table S2, Figure S2**). Despite similar theoretical underpinnings  
218 the predictors of environmental variability used in PGLS analyses are not strongly correlated (**Figure S3**).  
219 Details and code to generate these predictors can be found within the ESM.

### 220 Phylogenetic camparative analysis

221 To test the association between speciation/extinction and sexual selection, environmental variability and its  
222 interaction we used phylogenetic least squares (PGLS) models in the `nlme` package (Pinheiro et al. 2018).  
223 We began by estimating the phylogenetic signal — Pagel's  $\lambda$  (Pagel 1999) — using `corPagel` in the `ape`  
224 package (Paradis et al. 2004) on a MCC tree. The estimate of  $\lambda$  was then fixed for model selection, which was  
225 conducted on the same MCC tree derived from 2,500 draws from the posterior distribution (Jetz et al. 2012).  
226 Model selection used  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  and  $\mu_{BAMM}$  tip-rate estimates from the MCC ( $n = 5,812$ ) as the  
227 response variable and only compared interaction terms. That is, we fixed the individual predictors of: sexual

228 dichromatism/selection, log-transformed range size, seasonal temperature variation, spatial temperature  
229 variation, long-term temperature variation and NPP while comparing 32 models with different combinations  
230 of interactions (including none). Model selection was done in MuMIn using the `dredge` function (Bartoń  
231 2017). Using the terms from the top-ranking model (lowest AICc) we ran the equivalent model in each of the  
232 100 phylogenetic trees, using the unique response variables and phylogenetic tree correlation structure in  
233 each model. This method gave us the ability to present model estimates for an MCC alongside 100 random  
234 draws; acknowledging the potential role phylogenetic uncertainty has in tapering conclusions drawn from a  
235 random sample of the data. This method was conducted on models that used data from all available passerine  
236 species ( $n = 5,812$ ). PGLS analyses were also applied to a subset dataset of passerine birds ( $n = 581$ ), where  
237 sexual dichromatism measures were sourced from spectrophotometry measures (Armenta et al. 2008) and  
238 where male-bias sexual selection pPCA was used as a predictor instead of sexual dichromatism ( $n = 2,465$ ).  
239 Finally, using this data subsetted for species with measurements of male-bias sexual selection we conducted a  
240 phylogenetic path analysis using the `phylopath` R package (Bijl 2018). The phylogenetic path analysis was  
241 used to assess causal paths between variables not able to be modelled within the univariate response of PGLS.  
242 To minimise path complexity we use temperature seasonality (BIO4) as the single measure for environmental  
243 variability and use  $\lambda_{DR}$  as the single measure of speciation. Further details of the path analysis including  
244 reasons for path directions can be found within the ESM along with all other analyses and the relevant R  
245 code to reproduce results.

## 246 Results

### 247 Effects of sexual dichromatism/selection on speciation are not dependent upon 248 environmental variability

249 PGLS models with interaction terms between the respective measure of sexual dichromatism/selection and  
250 the five measures of environmental variability (seasonal temperature variation, log-range size, long-term  
251 temperature variation, spatial temperature variation and NPP) were included in global models. However, in  
252 all model selection phases for different measure of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) and different measures of  
253 sexual selection (RGB values, spectrophotometry and male-biased sexual selection) no interaction terms were  
254 significant or present in the top models ( $\delta \text{ AICc} > 4$ ; **Table S5**, **Table S6**, **Table S10**, **Table S13**). Hence  
255 we find no evidence that the effect of sexual selection on speciation or extinction is dependent upon certain  
256 environmental conditions. Furthermore, we find no support for these individual bioclimatic factors (seasonal

257 temperature variation, long-term temperature variation, spatial temperature variation and NPP) acting as a  
258 driver of speciation independently from sexual dichromatism/selection (Figure 1, **Figure S10**).

## 259 No evidence that sexual dichromatism affects speciation

260 We found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation.  
261 Using three response measures of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ), the effect of sexual dichromatism was  
262 not significant in any PGLS model based on tip-rate estimates and correlation structures from a MCC tree.  
263 Specifically, sexual dichromatism showed no association with  $\lambda_{DR}$  ( $\beta = -1.279e-03$ ,  $p = 0.147$ ; Figure 1a,  
264 Figure 2a) or  $\lambda_{ND}$  ( $\beta = -5.745e-05$ ,  $p = 0.078$ ; Figure 1a). Furthermore, speciation rates from BAMM  
265 ( $\lambda_{BAMM}$ ) were also unaffected by sexual dichromatism ( $\beta = -1.430e-05$ ,  $p = 0.872$ ; Figure 1a). PGLS analyses  
266 using subsetted data ( $n = 581$ ), where sexual dichromatism was measured using spectrophotometry distance  
267 measures (Armenta et al. 2008) yielded results concordant to the full data set; that is, no association between  
268 sexual dichromatism and speciation or extinction (**Figure S10**). Our results from MCC models are largely  
269 corroborated by model estimates from PGLS analyses of the rates and correlation structures from 100 random  
270 trees. Model estimates are normally distributed around zero when using complete taxon sampling models  
271 and RGB measures of sexual dichromatism (Figure 1a, See HPD intervals in **Table S8**). For PGLS using  
272 the subsetted dataset where sexual dichromatism was determined with spectrophotmetry (Armenta et al.  
273 2008) the estimates from the 100 trees in the  $\lambda_{DR}$  models are positively skewed (-1.781e-02, 3.488e-02) but  
274 normally distributed around zero for  $\lambda_{ND}$  and  $\lambda_{BAMM}$  (**Table S12**).

## 275 Male-bias sexual selection increases speciation

276 When we conducted PGLS analysis using data subsetted for values of sexual selection estimated from  
277 a phylogenetic PCA of sexual dimorphism, social polygyny and paternal care ( $n = 2,465$ ) there was a  
278 significant positive association between sexual selection and  $\lambda_{DR}$  ( $\beta = 3.887e-02$ ,  $p = 0.012$ ; Figure 1b)  
279 and a non-significant positive association between sexual selection and  $\lambda_{ND}$  ( $\beta = 4.381e-04$ ,  $p = 0.351$ ;  
280 Figure 1b). However, no association was found between sexual selection and  $\lambda_{BAMM}$  ( $\beta = 9.422e-04$ ,  $p$   
281 = 0.764; Figure 1b). For PGLS models on 100 random trees, we find the distribution to be similar to the  
282 estimates when an MCC tree is used. Among the 100 trees we find a positive association between sexual  
283 selection and  $\lambda_{DR}$  (HPD Interval = 9.115e-03, 6.085e-02), and a positive (but less so) association between  
284 sexual selection and  $\lambda_{ND}$  (HPD Interval = -3.104e-04, 1.536e-03; ) as well as  $\lambda_{BAMM}$  (HPD Interval =  
285 -1.297e-02, 3.089e-02). Complete HPD intervals for models using male-bias sexual selection pPCA as a predictor

286 can be found within **Table S15**.

287 **Species with smaller ranges have increased rates of speciation**

288 Based on  $\lambda_{DR}$  and  $\lambda_{ND}$  tip-rate metrics of speciation we find a negative association between range size and  
289 speciation; that is, species with smaller ranges show marginally higher values for  $\lambda_{DR}$  and  $\lambda_{ND}$ . Model  
290 estimates from PGLS models using an MCC tree for determining tip-rates and correlation structures place  
291 this negative association as small but significant ( $\lambda_{DR}$ :  $\beta = -6.578e-03$ ,  $p = 0.001$ ;  $\lambda_{ND}$ :  $\beta = -1.462e-04$ ,  $p$   
292 = 0.034; Figure 1a, Figure 2a). This association was also evident across the estimates from models using  
293 the 100 trees ( $\lambda_{DR}$ : HPD Interval = -8.438e-03, -1.823e-03;  $\lambda_{ND}$ : HPD Interval = -1.899e-04, 9.112e-06;  
294 Figure 1a). Subsetted models with reduced sample size and different measures of sexual selection — but the  
295 same measure of range size — show variable evidence that range size is negatively associated with speciation.  
296 Data subsetted based on the sexual selection pPCA ( $n = 2,465$ ) show that smaller range size significantly  
297 predicted increased  $\lambda_{DR}$  (Figure 1b), yet this negative association was not significant for  $\lambda_{ND}$  and near-zero  
298 for  $\lambda_{BAMM}$ . Alternatively, models using subsetted data ( $n = 581$ ), where sexual dichromatism was measured  
299 using spectrophotometry distance measures (Armenta et al. 2008) gave non-significant estimates for the  
300 effect of range size on all measures of speciation (**Figure S10**, **Table S11**, **Table S2**). Because the range  
301 size dataset is the same across the three data subsets we draw our conclusions from the models with highest  
302 power using near-complete taxon sampling ( $n = 5,812$ ).

303 **Phylogenetic path analysis**

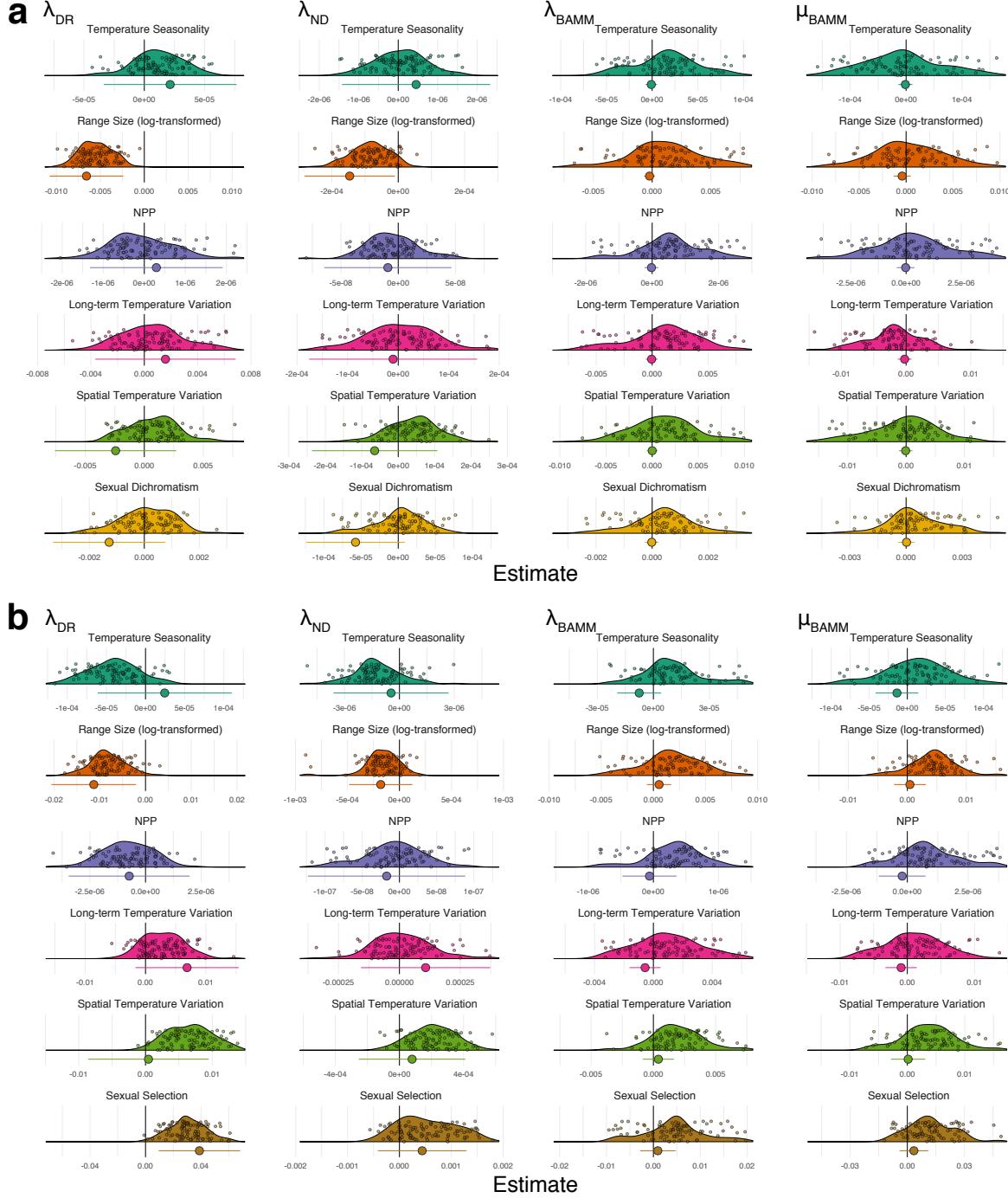
304 Using a phylogenetic path analysis we found there to be multiple significant paths between variables used in  
305 the PGLS (Figure 3; **Figure S13**). Notably, environmental variability (temperature seasonality) directly  
306 affected sexual dichromatism ( $\beta = 0.07$ ) and the path from sexual selection to sexual dichromatism was  
307 relatively weak given the expectations of dichromatism being a well utilised proxy of sexual selection ( $\beta =$   
308 0.22). Additionally, given the large direct effect of temperature seasonality on range size ( $\beta = 0.52$ ) and  
309 our findings from the PGLS that range size is negatively associated with  $\lambda_{DR}$ , there is an indirect effect of  
310 temperature seasonality on  $\lambda_{DR}$  ( $\beta = -0.02$ ; Figure 3).

### 311 Extinction rate

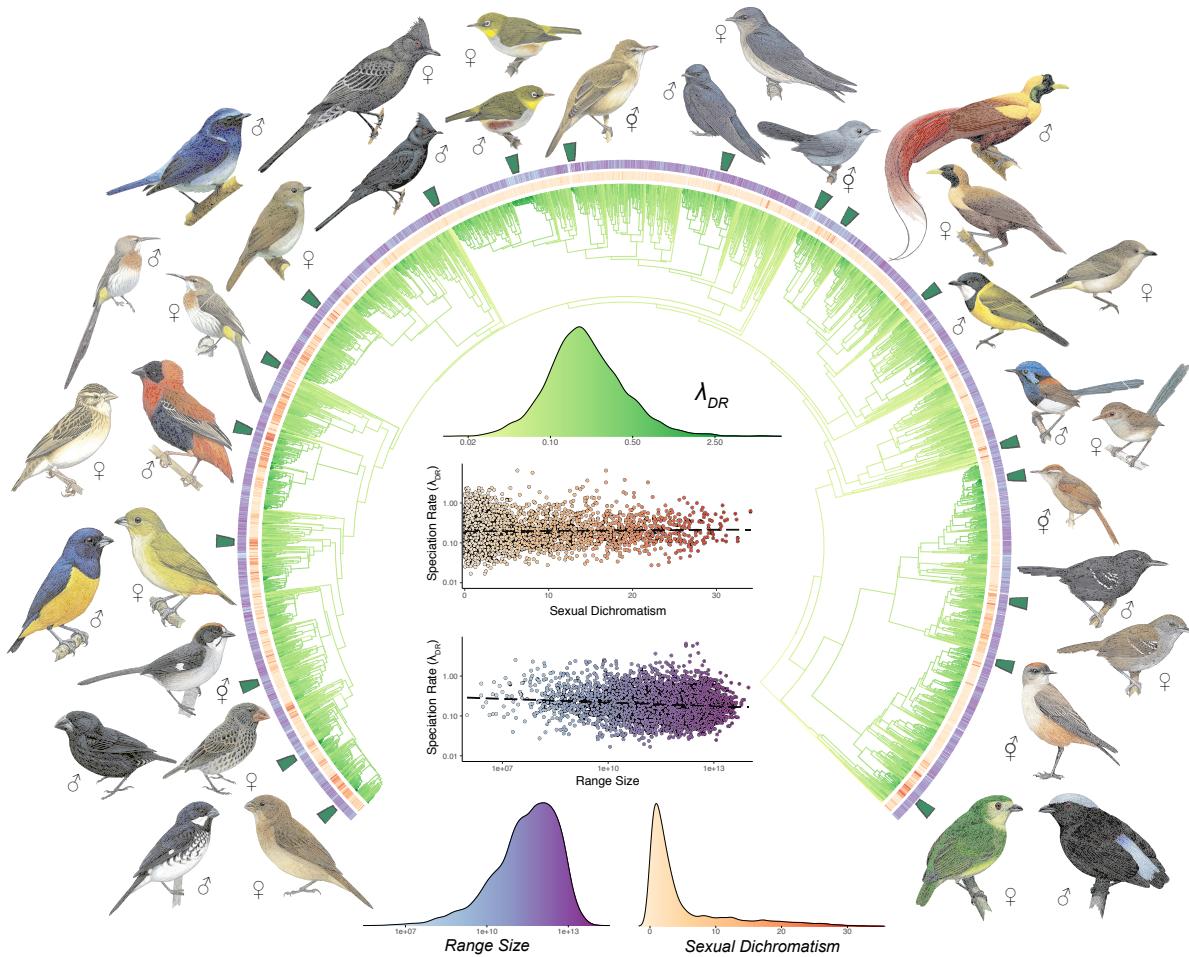
312 We found no evidence that extinction ( $\mu_{BAMM}$ ) was impacted by the extent of sexual dichromatism for  
313 full-taxon sampling ( $\beta = 2.390\text{e-}05$ ,  $p = 0.93$ ; Figure 1a). This null result was consistent for spectrophotometry  
314 measures of sexual dichromatism (**Figure S10**, **Table S11**, **Table S12**) and for the estimates of sexual  
315 selection using the sexual selection ppca (Figure 1, **Table S14**, **Table S15**).

### 316 Variability across trees and methods

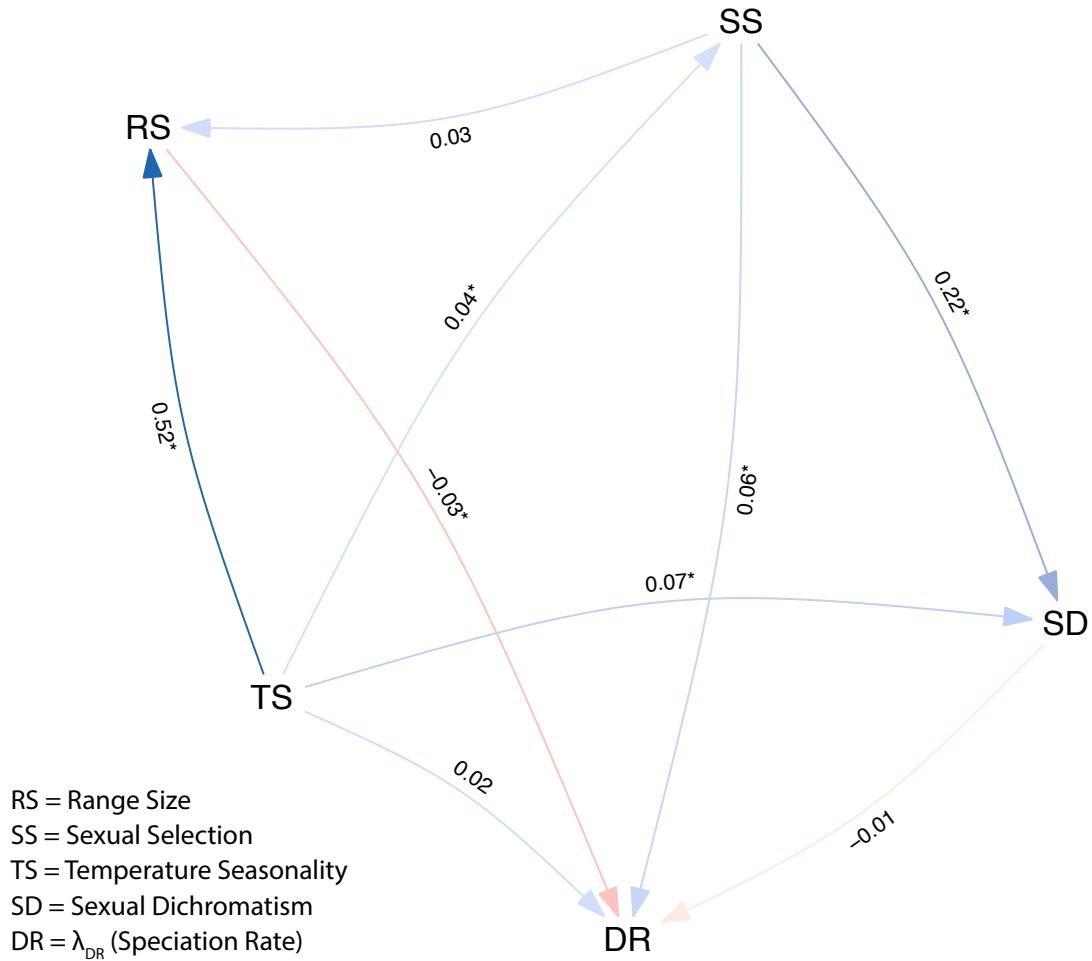
317 We tested our hypothesis that sexual selection is associated with speciation using several methods and across  
318 100 samples of phylogenetic trees drawn from the post burn-in posterior (Jetz et al. 2012). The range of  
319 methods utilised were implemented to overcome uncertainty in the power and precision of various tip-rate  
320 estimates as well as the variation between trees. We found that that the tip-rate estimates across the 100  
321 trees were quite variable for both  $\lambda_{DR}$  and  $\lambda_{BAMM}$  (**Figure S13**). Despite this variation, both methods  
322 provided similar estimates for speciation in each species for the mean values across the 100 trees ( $r = 0.67$ )  
323 and for the tip-rate estimates from the MCC ( $r = 0.68$ ). However in comparison to  $\lambda_{DR}$ , the value of  $\lambda_{BAMM}$   
324 was the *mean* drawn from a posterior distribution ( $n = 1,000$ ) of BAMM generations, thus estimates of  
325  $\lambda_{BAMM}$  (and  $\mu_{BAMM}$ ) have an added level of variation. To account for this variation, weights (using the  
326 inverse of the variance) were used for the PGLS models. From 1000 posterior samples of the MCC BAMM  
327 run the coefficient of variation (CV) for all log-rates of  $\lambda_{BAMM}$  was relatively low (*mean CV* = 21.49, *median*  
328  $CV = 15.76$ ; see **Figures S5 and S7**). Despite the convergence of the BAMM model in all runs — where  
329 effective sample sizes of the number of shifts and log-likelihood were all greater than 200 (**Table S3 and S4**)  
330 — we found that the unique combinations of rate shifts across the large phylogenetic tree ( $n = 5,966$  species)  
331 was high. This means that although the number of rate shifts reached convergence and is more precise  
332 (*median* = 59; **Figure S6**) the locations of the rate shifts (*i.e.* the credible shift set) across the tree is highly  
333 heterogeneous. The variability in the locations for the shift configurations is a likely source of uncertainty in  
334 downstream tip-rates used as the response variable in PGLS models. Notably the model estimate BAMM  
335 produced varied a lot between trees relative to the confidence interval of the MCC tree, with 95 % HPD  
336 interval being approximately 20-fold wider than the MCC 95 % CI for models using BAMM, whereas for  $\lambda_{DR}$   
337 and  $\lambda_{ND}$  the HPD 95 % interval width was equal to or less than the MCC 95 % CI (Figure 1, **Table S9**).



**Figure 1:** Model estimates for (a) PGLS analyses using sexual dichromatism measures ( $n = 5,812$ ) and (b) PGLS analyses using a subsetted male-bias measure of sexual selection ( $n = 2,465$ ). Both datasets were used for analyses with three measures of speciation  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  and one measure of extinction  $\mu_{BAMM}$  as response variables. When using  $\lambda_{DR}$  and  $\lambda_{ND}$  as the response variable, they provide relatively congruent results; with a negative relationship between  $\lambda_{DR/ND}$  and range size as well as a positive relationship between  $\lambda_{DR/ND}$  and sexual selection (b). Alternatively, when using  $\lambda_{BAMM}$  and  $\mu_{BAMM}$  the model estimates are more variable across trees compared to the MCC estimate, which do not significantly differ from zero. The numerical values for the model estimates using the MCC tree and hpd of estimates from 100 random trees can be found within the ESM. Density curves are based on estimates from 100 trees and the circle below with error bars is the estimate and 95 % CIs from the MCC. For this figure we removed outliers from estimates coming from the 100 random trees for BAMM models in order to interpret the MCC 95 % CIs.



**Figure 2:** Speciation rate ( $\lambda_{DR}$ ) across all passerine birds ( $n = 5,965$ ) with estimates of sexual dichromatism and range size available for 5,812 of them. Across these species there was a small but significant negative association between  $\lambda_{DR}$  and log-range size but no significant association between  $\lambda_{DR}$  and sexual dichromatism based on RGB measurements.  $\lambda_{DR}$  are those from the MCC tree and images of birds are from the *Handbook of the Birds of the World*. Clockwise the species are: *Sporophila bouvronides*, *Geospiza magnirostris*, *Atlapetes leucopterus*, *Euphonia rufiventris*, *Euplectes franciscanus*, *Promerops gurneyi*, *Phainopepla nitens*, *Zosterops erythropleurus*, *Acrocephalus australis*, *Progne cryptoleuca*, *Mayrornis schistaceus*, *Paradisaea rubra*, *Pachycephala pectoralis*, *Malurus pulcherrimus*, *Cranioleuca curtata*, *Cercomacra manu*, *Muscisaxicola capistratus*, *Lepidothrix coeruleocapilla*. Edge colours for the terminal branch correspond to  $\lambda_{DR}$  but all precluding branches have been generated for graphical purposes using ancestral character state estimation and should not be interpreted.



**Figure 3:** Path analysis of evolutionary and ecological variables. Arrows represent direct effects with numeric values corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisk 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 male-bias sexual selection measures ( $n = 2,465$ ).

## 338 Discussion

339 We found no evidence that sexual dichromatism alters the rate of speciation in passerine birds independently  
340 or via interactions with environmental variability. This result is consistent across different measures of  
341 speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$  and  $\lambda_{BAMM}$ ) and two measures of dichromatism: a near-complete dataset of 5,812  
342 species using RGB scores and a smaller dataset of 581 species where measurements were obtained from  
343 spectrophotometry (allowing variation in the ultraviolet and bird-visible range to be detected). However,  
344 we did find that when using a male-bias measure of sexual selection — instead of sexual dichromatism —  
345 there was a positive association with speciation: with significance varying across different rate estimates.  
346 Our findings suggest that the components that were used in the pPCA of male-bias sexual selection (sexual  
347 size dimorphism, social polygyny and [lack of] paternal care) are better predictors of speciation than sexual  
348 dichromatism and provide discussion points for the contentious topic of sexual selection proxies. No bioclimatic  
349 measures of environmental variability (temperature seasonality, long-term temperature variation and spatial  
350 temperature variation) predicted speciation, but range size was negatively associated with two measures of  
351 speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ). This finding suggests that species with smaller range sizes have increased speciation  
352 rate. However, small range size may be a cause or effect of speciation rate and potentially even an artifact of  
353 taxonomic classification. Interestingly we found a discrepancy in the model results obtained from tip-rate  
354 statistics ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ) and those using tip-rate estimates from a model based approach ( $\lambda_{BAMM}$ ); whereby  
355 BAMM produced precise null results for associations between predictors and speciation as well as extinction.  
356 Despite the association between sexual selection and sexual dichromatism in passerine birds (Dale et al. 2015)  
357 we find that sexual dichromatism does not predict speciation rate as sexual selection does. The association  
358 between sexual selection and sexual dichromatism in birds is a Darwinian trope (Darwin 1871) that allows it  
359 to be commonly used as a proxy for sexual selection in comparative studies (e.g., Barraclough et al. 1995;  
360 Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014). However, the  
361 presence of high sexual dichromatism in bird species may be also dependent on ecological selection pressures.  
362 Ecological pressures could drive sexual dichromatism in the absence of mate choice if sex-specific niches  
363 provide opportunity for the evolution of sex-limited traits (Kottler 1980; Slatkin 1984; Shine 1989). In  
364 damselflies, differences between the sexes in their exposure to UV radiation drives dichromatism between the  
365 sexes (Cooper 2010; Punzalan and Hosken 2010). Ecological impacts on sexual dichromatism are supported by  
366 our path analysis; which reveals that sexual dichromatism is positively affected by temperature seasonality (a  
367 measure of environmental variation) albeit by a relatively small amount. Given that speciation rate increases  
368 with sexual selection strength but not sexual dichromatism we are led to conclude that sexual dichromatism

369 is a seemingly poor proxy of sexual selection and that the noise associated with the proxy measurement of  
370 sexual selection cancels out the obtained signal; this is despite the high power of our comparative study.  
371 The usefulness of sexual dichromatism as a proxy of sexual selection may be dependent upon the metabolic  
372 pathways that give rise to plumage colouration; with not all plumage colouration reflecting mate quality.  
373 A recent meta-analysis found that converted carotenoids (but not those sourced from diet) predict mate  
374 quality through improvements in parasite resistance and reproductive success (Weaver et al. 2018). Given  
375 the importance of honest signalling in sexual selection and the variability in colour production across birds,  
376 sexual dichromatism in many species may unreliable measure of mate quality for female birds and sexual  
377 selection for researchers.

378 In-line with predictions and a previous meta-analysis (Kraaijeveld et al. 2011) we find male-bias sexual  
379 selection marginally increases speciation rate (at least for  $\lambda_{DR}$ ,  $\lambda_{ND}$ ) yet there is no direct evidence of this  
380 association being dependent on variable or stressful environments; albeit a phylogenetic path analysis shows  
381 an indirect effect of environmental variability (through range size). When evolving under stressful conditions,  
382 sexually antagonistic selection is hypothesised to be weakened relative to selection that is conchordant between  
383 the sexes (Connallon 2015; Connallon and Hall 2016). While these predictions are supported in several lab  
384 (experimental evolution) studies (Long et al. 2012; Punzalan et al. 2013; Berger et al. 2014), other studies  
385 have not found the association (Delcourt et al. 2009; Holman and Jacomb 2017; Martinossi-Allibert et al.  
386 2017). Given that we did not detect an effect of environmental variability (by itself or as an interaction  
387 with sexual selection) we are left with several possible explanations. Firstly, the effects of sexual selection  
388 on adaptation and thus speciation may depend on the type of environmental variability the species is  
389 evolving under. Specifically, sexual antagonism may be more easily purged in environments where directional  
390 environment pressures are maintained; whereas when environmental variability is cyclical (e.g. seasonal or  
391 glacial climate cycles) sexual antagonism can remain indefinitely as a fitness burden (Connallon and Hall  
392 2016). Secondly, the environmental predictors used here may not account for the key ecological forces/natural  
393 selection pressures that interact with sexual selection to drive speciation. Specifically, access to dietary  
394 resources, and the impacts of predation or parasitism are unaccounted for here: arguably these are key  
395 processes affecting sexual selection and speciation (*reviewed in*, Maan and Seehausen 2011). Thirdly, it is  
396 also likely that there is no effect; at least not in the species investigated here.

397 The most convincing finding uncovered in this comparative analysis is that smaller range sizes are associated  
398 with increased speciation rates. But drawing conclusions from this finding is fraught with challenges.  
399 Challenges arise on determining the causality of range size and speciation; as arguably small range size could  
400 either be a cause or effect of speciation. High speciation rate may lead to smaller range sizes as niche filling

401 by recently diverged species will suppress the expansion of newly speciated taxa. Within Himalayan songbirds  
402 range expansions are prevented by the competition for resources by related species (Price et al. 2014);  
403 however this limitation on range expansion is then expected to prevent future speciation events (Rosenzweig  
404 1995; Weir and Price 2011). Thus, if range size is a cause of speciation we might expect it to be smaller  
405 but if it is a predictor of speciation it arguably should be larger; with greater opportunities for geographic  
406 barriers to form in larger ranges (Rosenzweig 1995). Unlike Himalayan songbirds, species undergoing adaptive  
407 radiation into newly formed ecological environments are unlikely to be limited by competition for resources  
408 from pre-existing taxa. Across islands we expect to see a correlation between speciation and small range size,  
409 not because of any inherent properties of the range size, rather that they reflect newly formed islands with  
410 empty niches **This seems like a very established idea but not sure whose it is.** Thus our findings  
411 may be heavily dependent on species whose range size is restricted to a single island within an archipelago  
412 (e.g., *Geospiza* sp.; aka Darwin's finches). Birds with large range sizes are also predicted to have greater  
413 dispersal ability; in these cases individuals may be more able to overcome geographical barriers and maintain  
414 gene flow; thus lowering speciation in these wide-ranging species (Birand et al. 2012; Claramunt et al. 2012).  
415 Several studies have used morphological measures of wing shape, a proxy for dispersal ability (Hand-wing  
416 index/ Kipp's distance), as a predictor of speciation and coexistence (e.g., Kennedy et al. 2016; Pigot et  
417 al. 2016), but these measurements across passerines is not yet extensive **I think? ~ 1000.** One further  
418 explanation for the negative association between range size and sexual dichromatism/sexual selection is the  
419 potential bias of taxonomic classification whereby splitting of species leads to increased recent phylogenetic  
420 branching as well as a more subdivided range **Has this argument been articulated?.** The role of range  
421 size in speciation may be further investigated through ancestral geographic range reconstruction (Quintero et  
422 al. 2015), as ancestral ranges may be beneficial in understanding modes of speciation and the causality of  
423 range size expansions and contractions (Losos and Glor 2003).

424 Here we used BAMM to assess extinction rates across passerines and whether these rates were associated with  
425 sexual dichromatism/selection or various ecological variables. We found no associations in this respect despite  
426 the wealth of theoretical predictions on the effects of sexual selection on fitness. Extinction is notoriously  
427 difficult to obtain accurate estimates for in comparative studies, as it is a process that occurs over millennia,  
428 leaving scant traces. One exception to this comes from fossil ostracods, a group of marine invertebrates. In  
429 these species there is an extensive fossil record of extinct ostracods from the Late Cretaceous epoch (84–66  
430 million years ago) as well as identifiable sexual dimorphism. Recently, Martins et al. (2018) found that species  
431 of ostracods with larger sexual dimorphism (representing larger investment by males in reproductive organs)  
432 had higher extinction rates; suggesting that sexual selection increases extinction risk. Other comparative

433 studies have assessed the relationship between sexual selection and extinction in birds (Doherty et al. (2003);  
434 Mitra et al. (1996); Morrow and Pitcher (2003)) and mammals (Morrow and Fricke 2004; Bro-Jorgensen  
435 2014) without consensus. Yet these methods often rely on extinction threat status from the International  
436 Union for Conservation of Nature (IUCN) Red List (*e.g.*, Morrow and Pitcher 2003; Morrow and Fricke 2004;  
437 Bro-Jorgensen 2014) and may be heavily biased to species under greater anthropogenic threat, culturally  
438 valued or well researched. While estimating extinction risk from the phylogeny may not come with these  
439 biases, they are riddled with others (*reviewed in*, Pyron and Burbrink 2016). BAMM has been subject to  
440 controversy in its ability to model rate shifts and extinction rates (*see*, Beaulieu and O'Meara 2015; Moore  
441 et al. 2016; Rabosky 2016; Rabosky et al. 2017), and while several tip-rate estimates exist for speciation  
442 (*e.g.*,  $\lambda_{DR}$  and  $\lambda_{ND}$ ) extinction estimates are not as easily obtained. Here we anticipated extinction rates  
443 would be underestimated because we used a phylogeny constructed with a birth-only (Yule) model (Jetz  
444 et al. 2012). Given these underestimates of  $\mu_{BAMM}$  it is highly likely we failed to detect true associations  
445 between sexual dichromatism/selection and extinction. The power of BAMM as a model based-approach in  
446 estimating  $\lambda$  and  $\mu$  is dependent size of the rate regimes. BAMM often produces homogeneous  $\lambda_{BAMM}$  and  
447  $\mu_{BAMM}$  for clades with few rate shifts, whereas  $\lambda_{DR}$  produces higher heterogeneity in tip-rates; arguably  
448 this could reflect increased power or sampling error (Rabosky et al. 2017; Rabosky and others 2018). Thus  
449 we are somewhat uncertain in the validity of conclusions from  $\mu_{BAMM}$  estimates as well as  $\lambda_{BAMM}$  and  $\lambda_{DR}$   
450 given their discrepancy.

451 Improvements in estimating tip-rates of speciation in the last few years has allowed us to revisit the association  
452 between sexual selection and speciation. With high power and alongside extensive ecological predictors we  
453 find that male-bias measures of sexual selection better predict speciation than sexual dichromatism. If sexual  
454 selection promotes speciation through improvements in fitness and adaptation the implications are manifold  
455 with sexual selection a potentially valuable utility in conservation (*reviewed in*, Holman and Kokko 2013)  
456 and captive breeding programs for threatened species (*reviewed in*, Charge et al. 2014). Additionally, our  
457 finding that high speciation rate is associated with smaller range size has pronounced significance to the  
458 future survival of these rapidly speciating species in a world with increased habitat loss and anthropogenic  
459 stress. Range size is the best predictor of extinction risk (Harris and Pimm 2008) and the association found  
460 here ensues that many newly speciated clades may be at greater risk of extinction due to anthropogenic  
461 effects if not evolutionary or ecological effects.

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