

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

3 Justin G. Cally\*§, Devi Stuart-Fox§, Luke Holman§ and Iliana Medina§

\**justin.g.cally@gmail.com*

4 **Abstract**

5 Sexual selection is thought to shape phylogenetic diversity by affecting speciation or extinction rates.  
6 However, the net effect of sexual selection on diversification is hard to predict *a priori*, because many of  
7 the hypothesised effects on speciation or extinction have opposing signs and uncertain magnitudes. Here,  
8 we test whether the strength of sexual selection predicts variation in speciation and extinction rates across  
9 passerine birds (up to 5,812 species, covering most genera). We tested for associations between speciation  
10 or extinction and two measures of sexual selection (sexual dichromatism and a multivariate measure  
11 of male-biased sexual selection), accounting for range size and measures of environmental variability.  
12 Male-biased sexual selection, but not sexual dichromatism, predicted speciation rates ( $\lambda_{DR}$ ) in passersines.  
13 This relationship was independent of range size or environmental variability, though species with smaller  
14 ranges had higher speciation rates. There was no association between sexual selection and extinction rate  
15 ( $\mu_{BAMM}$ ). Our findings show that sexual dichromatism is a poor proxy for sexual selection at least a  
16 broad-scale and support the view that sexual selection has shaped diversification in songbirds.

---

§School of BioSciences, The University of Melbourne, Parkville, VIC, 3052, Australia

## 17 INTRODUCTION

18 Sexual selection is a fundamental evolutionary process; yet there is long-standing debate about how it shapes  
19 patterns of species diversity<sup>1–5</sup>. Sexual selection can promote speciation because it operates on traits that  
20 can create reproductive isolation when they diverge between lineages, such as signals and preferences involved  
21 in mate selection<sup>1,2,6</sup>, sperm-egg interactions<sup>7</sup>, or genital morphology<sup>8</sup>. Sexual selection could also promote  
22 speciation or prevent extinction by purging deleterious mutations<sup>9</sup>, fixing beneficial ones<sup>10</sup>, and accelerating  
23 adaptation in different environments<sup>11–13</sup>. Conversely, sexual selection might hinder speciation or make  
24 extinction more likely by favouring traits that improve mating success but reduce population fitness<sup>14–17</sup>.  
25 For example, species with costly sexual signals may be less resilient to environmental change<sup>18</sup>. Extinction  
26 risk may also be exacerbated by sexual selection causing maladaptation ('gender load') in female traits that  
27 are genetically correlated with sexually-selected male traits<sup>19–23</sup>. Although numerous studies have examined  
28 the relationship between sexual selection and speciation or extinction rates<sup>4,24–28</sup>, the availability of more  
29 complete phenotypic, ecological and phylogenetic data<sup>29</sup>, together with significant advances in phylogenetic  
30 methods<sup>30,31</sup>, present new opportunities to test whether and how sexual selection drives diversification.

31 The relationship between sexual selection and diversification may depend on the environment. Theoretical  
32 work predicts that sexual selection should have a more positive effect on adaptation and population fitness  
33 in variable environments relative to stable ones<sup>32,33</sup>. In stable environments, consistent selection depletes  
34 genetic variation at sexually concordant loci (i.e. loci where the same allele is fittest for both sexes). In these  
35 environments, genetic variation remains disproportionately at sexually antagonistic loci, leading to stronger  
36 gender load and reduced net benefits of sexual selection<sup>33</sup>. By contrast, in spatially or temporally variable  
37 environments, sexual selection can enhance local adaptation. For example, in Darwin's finches (*Geospiza*  
38 *fortis*) divergent beak morphology is an adaptation to local food availability that has been maintained through  
39 assortative mating<sup>34</sup>. Despite the potential interaction between sexual selection and environmental variability  
40 in diversification, comparative tests are currently lacking.

41 Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification<sup>4,24,25,27,28</sup>  
42 because their biology and phylogenetic relationships are comparatively well-known. A 2011 meta-analysis  
43 covering 20 primary studies of birds and other taxa found a small but significant positive association between  
44 sexual selection and speciation, with the average effect size in birds stronger than in mammals but weaker  
45 than in insects or fish<sup>26</sup>. However, there was large variation in effect size estimates across the 20 studies, likely  
46 reflecting differences in methodology, such as metrics used to characterise speciation and sexual selection,  
47 in addition to true biological differences. More recently, Huang & Rabosky<sup>28</sup> found no association between  
48 sexual dichromatism and speciation ( $n = 918$  species) in a study using spectrophotometric measurements of  
49 museum specimens<sup>35</sup> and tip-rate estimates from a molecular-only phylogeny<sup>29</sup>. Similarly, Cooney et al.<sup>36</sup>  
50 found no effect of sexual dichromatism on diversification across 1,306 pairs of species, using dichromatism  
51 scores provided by human observers. However, another study using the prevalence of polygyny (as opposed  
52 to sexual dichromatism) as a proxy of sexual selection found a positive association with speciation rate across  
53 954 species of birds<sup>37</sup>.

54 Here, we investigate the association between sexual selection and diversification in birds while building upon  
55 previous approaches in multiple ways. We use two measures of the strength of sexual selection: sexual  
56 dichromatism<sup>38</sup>, as well as an index of male-biased sexual selection<sup>38</sup>, which captures (co)variation in sexual

size dimorphism, social polygyny and paternal care. We use these two measures because sexual dichromatism does not always signal the presence of strong sexual selection and *vice versa*<sup>38</sup>. For example, male and female dunnocks (*Prunella modularis*) are similarly coloured yet sexual selection appears to be strong<sup>39</sup>. Furthermore, a recent comparative study found a negative relationship between dichromatism and another sexually-selected trait (song) across species, suggesting that a multi-trait focus would improve estimates of sexual selection intensity<sup>5</sup>. Additionally, our analysis includes multiple ecological and environmental variables, allowing us to adjust for potential confounds, to identify environmental factors driving diversification, and to test whether environmental factors interact with sexual selection as theory predicts<sup>33</sup>. We use multiple approaches for quantifying speciation and extinction rates at the tips of phylogenetic trees, including BAMM (Bayesian Analysis of Macroevolutionary Mixtures)<sup>40–43</sup>, as well as older but reliable tip-rate statistics, namely diversification rate ( $\lambda_{DR}$ ) and node density ( $\lambda_{ND}$ )<sup>29</sup>.

## RESULTS

We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ( $n = 5,812$  species; 58% of all birds). We calculated three different tip-rate metrics of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) and one of extinction ( $\mu_{BAMM}$ ) for a maximum clade credibility (MCC) tree and, to account for phylogenetic uncertainty, 1,000 trees for  $\lambda_{DR}$  and  $\lambda_{ND}$  and 100 trees for  $\lambda_{BAMM}$ <sup>30</sup>.  $\lambda_{DR}$  is a measure of speciation rate more heavily weighted to recent speciation events while  $\lambda_{ND}$  measures speciation across the root-to-tip path. Alternatively,  $\lambda_{BAMM}$  uses a Bayesian approach to assess the probability of evolutionary rate-shift configurations, from which it generates tip-rate speciation and extinction estimates.

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we fitted phylogenetic least squares (PGLS) models with  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  or  $\mu_{BAMM}$  as the response variable. Predictors included one measure of sexual selection (one of two measures of sexual dichromatism or the index of male-biased sexual selection), five environmental measures, and 2-way interactions between the measure of sexual selection and each of the environmental measures, with subsequent model simplification using AIC model selection.

The two measures of sexual dichromatism were from previously published data, one based on RGB (red-green-blue) values from images in *Handbook of the Birds of the World*<sup>44</sup> ( $n = 5,983$ ), and the other based on spectrophotometry and avian colour space ( $n = 581$ )<sup>35</sup>. The index of male-biased sexual selection is associated with greater sexual size dimorphism, social polygyny and lack of paternal care ( $n = 2,465$ ).

The five environmental variables were (*i*) the log-transformed range size; (*ii*) the average Net Primary Productivity (NPP) in each species' range; (*iii*) mean temperature seasonality (BIO4) for each range; (*iv*) variation in temperature across a species' range and (*v*) long-term climate variation, which primarily reflects temperature differences between the last interglacial and current climates. We included an estimate of climate variability during recent evolutionary history as it may be a better indicator of environmental effects on speciation than present-day environmental variability.

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

93 We found a significant positive association between the index of male-biased sexual selection ( $n = 2,465$ ) and  
 94  $\lambda_{DR}$  for the MCC tree ( $\beta = 3.887\text{e-}02$ ,  $p = 0.012$ ; [Figure 1b](#)). However, this association was not significant  
 95 for the other two measures of speciation rate ( $\lambda_{ND}$ :  $\beta = 4.383\text{e-}04$ ,  $p = 0.351$ ;  $\lambda_{BAMM}$ :  $\beta = 9.423\text{e-}04$ ,  $p =$   
 96  $0.764$ ; [Figure 1b](#)). The distribution of estimates from PGLS models on 1,000 trees was similar to the estimate  
 97 from the MCC tree: among the 1,000 trees there was a positive association between sexual selection and  $\lambda_{DR}$   
 98 (highest posterior density (HPD) Interval =  $4.513\text{e-}03$ ,  $5.718\text{e-}02$ ), and the distribution skewed towards a  
 99 positive association between sexual selection and  $\lambda_{ND}$  (HPD Interval =  $-5.044\text{e-}04$ ,  $1.585\text{e-}03$ ; ) as well as the  
 100 100 models using  $\lambda_{BAMM}$  (HPD Interval =  $-1.295\text{e-}02$ ,  $3.088\text{e-}02$ ; [Table S15](#)).

101 In contrast to male-biased sexual selection, we found no evidence that species with increased sexual dichro-  
 102 matism have higher or lower rates of speciation. Sexual dichromatism showed no association with  $\lambda_{DR}$  ( $\beta$   
 103 =  $-1.279\text{e-}03$ ,  $p = 0.147$ ; [Figure 1a](#), [Figure 2](#)),  $\lambda_{ND}$  ( $\beta = -5.745\text{e-}05$ ,  $p = 0.078$ ; [Figure 1a](#)) or  $\lambda_{BAMM}$  ( $\beta$   
 104 =  $-1.429\text{e-}05$ ,  $p = 0.872$ ; [Figure 1a](#)). PGLS analyses using sexual dichromatism ( $n = 581$ ) measured by  
 105 spectrophotometry<sup>35</sup> yielded results concordant with the full dataset; i.e. no association between sexual  
 106 dichromatism and speciation ([Figure S11](#)). Our results from models based on the MCC tree are largely  
 107 corroborated by model estimates from PGLS analyses of the rates and correlation structures from 1,000 trees  
 108 (for  $\lambda_{DR}$ ,  $\lambda_{ND}$ ) and 100 trees for  $\lambda_{BAMM}$ . The HPD intervals show model estimates are distributed around  
 109 zero when using complete taxon sampling models and RGB measures of sexual dichromatism ( $\lambda_{DR}$ : HPD  
 110 Interval =  $-1.635\text{e-}03$ ,  $1.658\text{e-}03$ ,  $\lambda_{ND}$ : HPD Interval =  $-4.256\text{e-}05$ ,  $5.499\text{e-}05$ , [Figure 1a](#), [Table S8](#)). For PGLS  
 111 models using spectrophotometry-based measures of sexual dichromatism, the estimates from the 100 trees  
 112 in the  $\lambda_{DR}$  models are positively skewed (HPD Interval =  $-1.780\text{e-}02$ ,  $3.489\text{e-}02$ ) but normally distributed  
 113 around zero for  $\lambda_{ND}$  and  $\lambda_{BAMM}$  ([Table S12](#)).

114 No interaction terms were present in the top models ( $\Delta \text{AICc} > 4$ ) for any measure of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  
 115  $\lambda_{BAMM}$ ) or sexual selection (RGB values, spectrophotometry and the index of male-biased sexual selection;  
 116  $\Delta \text{AICc} > 4$ ; [Table S5](#), [Table S6](#), [Table S10](#), [Table S13](#)). Thus we found no evidence that the effect of sexual  
 117 selection on speciation is dependent on our measures of environmental variation. Furthermore, we found no  
 118 evidence that these environmental factors (seasonal temperature variation, long-term temperature variation,  
 119 spatial temperature variation, and NPP) predict speciation independently from sexual dichromatism/selection  
 120 ([Figure 1](#), [Figure S11](#)).

121 Species with smaller ranges have increased rates of speciation

122 Based on  $\lambda_{DR}$  and  $\lambda_{ND}$  tip-rate metrics of speciation, we found a negative association between range size  
 123 and speciation; that is, species with smaller ranges show marginally higher values for  $\lambda_{DR}$  and  $\lambda_{ND}$ . This  
 124 negative association was small but significant for models using the MCC tree ( $\lambda_{DR}$ :  $\beta = -6.579\text{e-}03$ ,  $p =$   
 125  $0.001$ ;  $\lambda_{ND}$ :  $\beta = -1.462\text{e-}04$ ,  $p = 0.034$ ; [Figure 1a](#), [Figure 2](#)). This association was also evident across the  
 126 estimates from models using the 1,000 trees ( $\lambda_{DR}$ : HPD Interval =  $-8.871\text{e-}03$ ,  $-6.610\text{e-}04$ ;  $\lambda_{ND}$ : HPD Interval  
 127 =  $-1.514\text{e-}04$ ,  $1.724\text{e-}05$ ; [Figure 1a](#)). Subset models with reduced sample size and different measures of sexual  
 128 selection — but the same measure of range size — showed equivocal evidence that range size is negatively  
 129 associated with speciation. Range size significantly predicted  $\lambda_{DR}$  ([Figure 1b](#)) using data subset for species  
 130 with an index of male-biased sexual selection ( $n = 2,465$ ) but not  $\lambda_{ND}$  or  $\lambda_{BAMM}$ . Models using data subset

for spectrophotometry-based dichromatism ( $n = 581$ ) gave non-significant estimates for the effect of range size on all measures of speciation (Figure S11, Table S11, Table S12). Because the range size dataset is the same across the three data subsets we draw our conclusions from the models with the highest power using near-complete taxon sampling ( $n = 5,812$ ).

### Phylogenetic path analysis

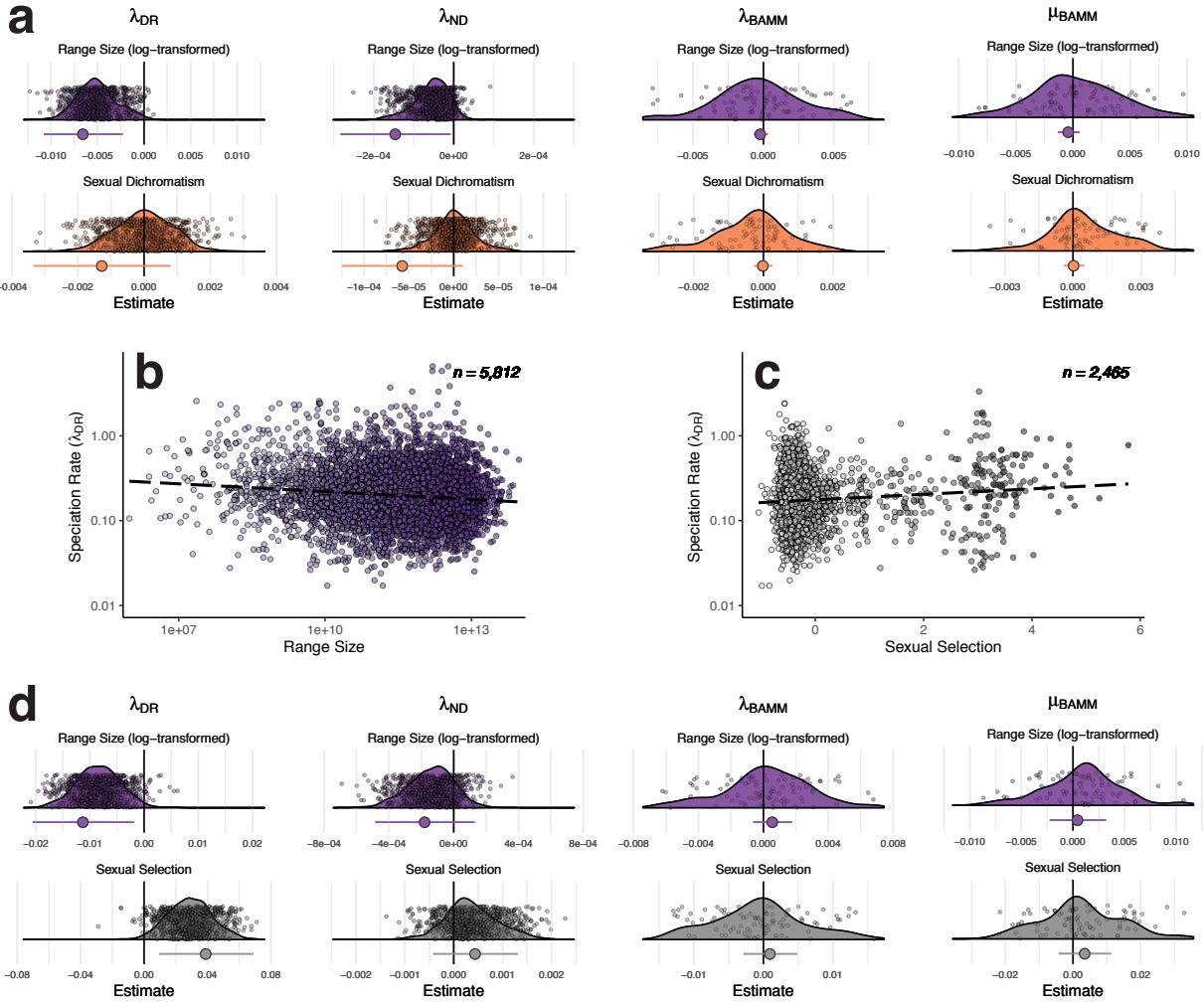
Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS (Figure 3; Figure S14). There was a modest effect of male-biased sexual selection on sexual dimorphism ( $\beta = 0.22$ ). Additionally, temperature seasonality weakly affected sexual dimorphism ( $\beta = 0.07$ ) and strongly affected range size ( $\beta = 0.52$ ). This suggests an indirect effect of temperature seasonality on  $\lambda_{DR}$  ( $\beta_{indirect} = -0.02$ ; Figure 3), given the negative association we identified between  $\lambda_{DR}$  and range size in PGLS models.

### Extinction rate

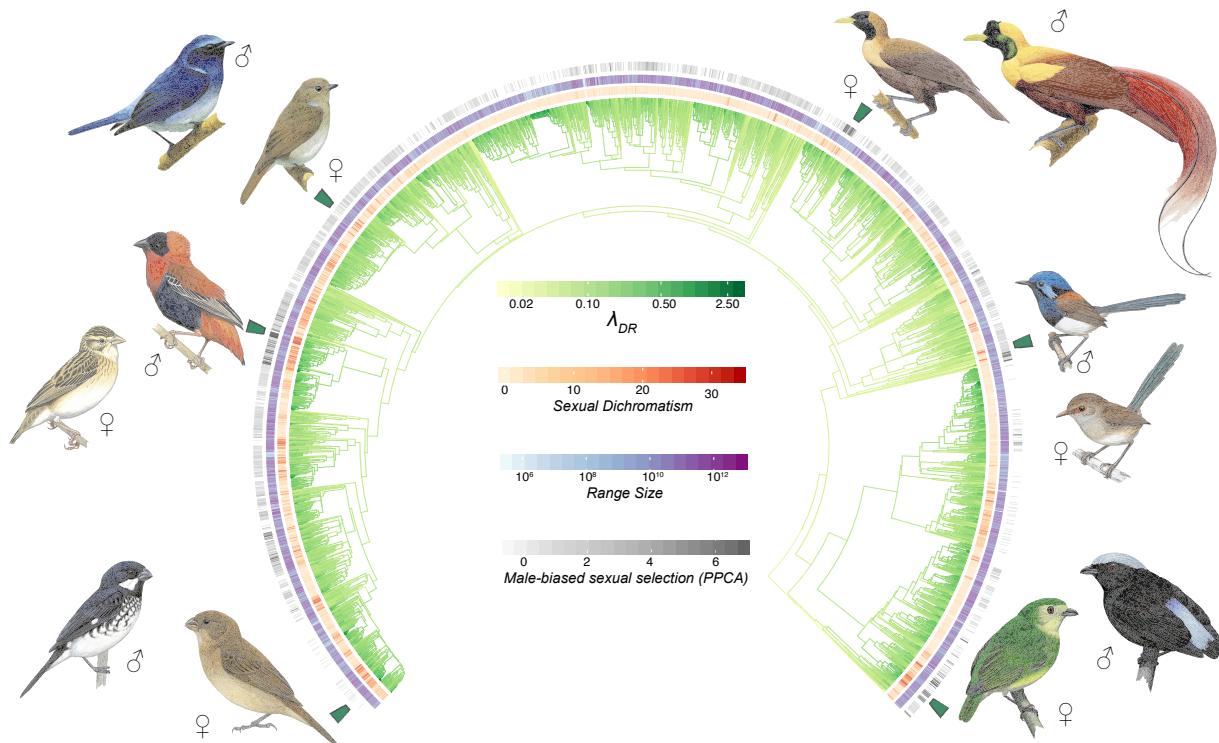
We found no evidence that extinction ( $\mu_{BAMM}$ ) was impacted by the extent of sexual dichromatism for full-taxon sampling ( $\beta = 2.385e-05$ ,  $p = 0.93$ ; Figure 1a), nor spectrophotometry-based measures of sexual dichromatism (Figure S11, Table S11, Table S12) or male-biased sexual selection (Figure 1b, Table S14, Table S15).

### Variability across phylogenetic trees and speciation rate measures

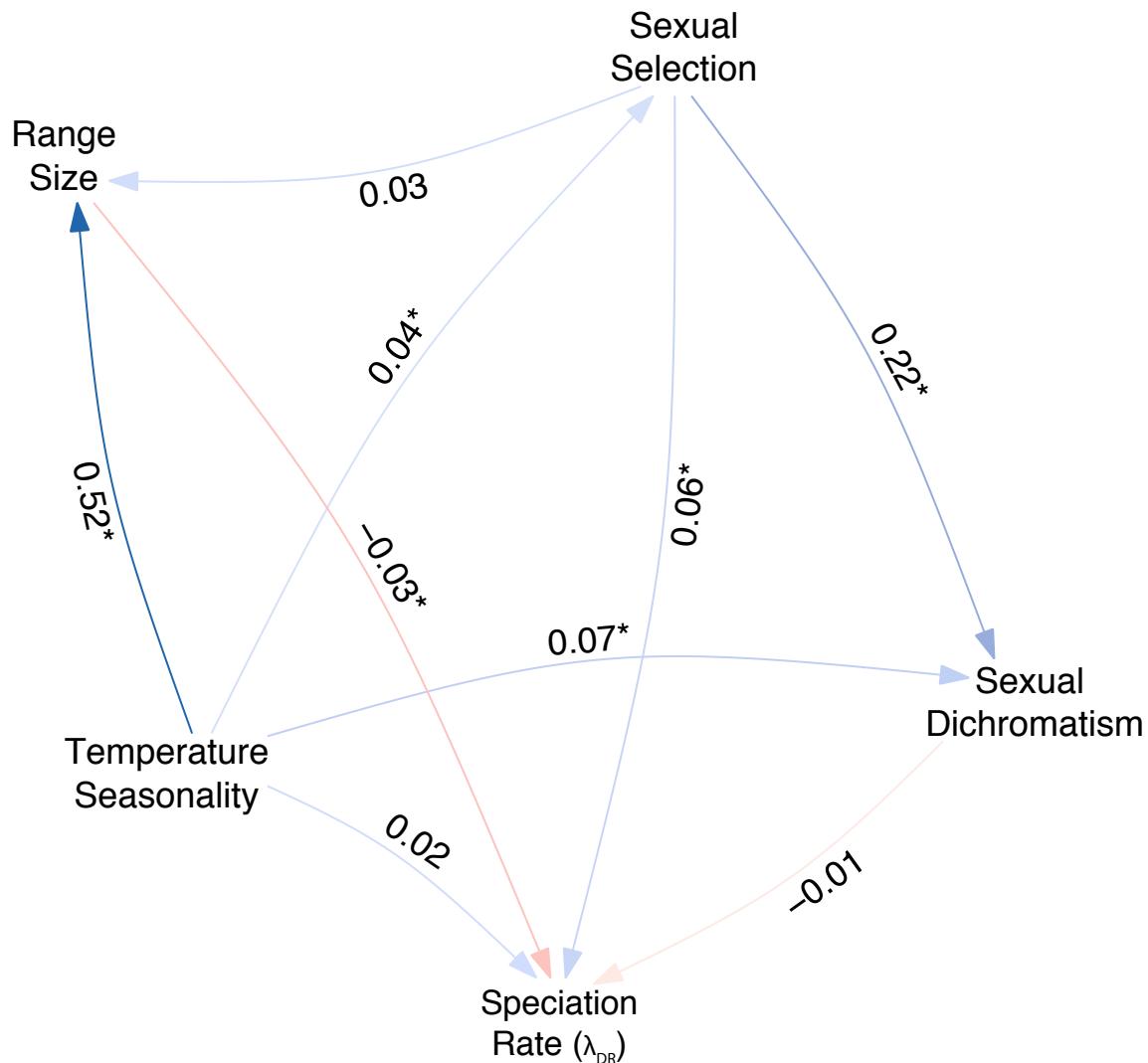
Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially in the BAMM rates ( $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ), where the 95 % HPD interval across PGLS model estimates from 100 trees was often  $> 20$  times larger than the 95 % confidence interval for estimates from a single PGLS model using the MCC tree. This contrasts with variation across trees for the other rate estimates ( $\lambda_{DR}$  and  $\lambda_{ND}$ ), 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). Given the computational requirements of BAMM, the great majority of earlier studies have based their estimates on a single consensus tree, and so the inconsistency of the BAMM estimates between different phylogenies with similar statistical support is notable. 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). Given that the calculation of BAMM rates can be affected by the settings of the run and the use of different priors, we compared the estimate of our MCC tree with that of previous published analyses on birds, and found a high correlation ( $r=0.81$ , Figure S8). Full details of the BAMM results are presented as supplementary materials.



**Figure 1:** Model estimates (a) for the effect of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset (RGB values,  $n = 5,812$ ). (b) depicts the scatter plot of speciation rate ( $\lambda_{DR}$ ) and log-range size with the model estimate presented as a dashed line. (c) shows the scatter plot of speciation rate ( $\lambda_{DR}$ ) and male-biased sexual selection ( $n = 2,465$ ). Similar to (a), (d) presents model estimates for PGLS analyses using a restricted dataset with measures of an index of male-biased sexual selection ( $n = 2,465$ ) and shows the effect of log-range size and male-biased sexual selection on speciation and extinction rates. Both datasets were used for analyses with three measures of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) and one measure of extinction ( $\mu_{BAMM}$ ) as response variables. The numerical values for the model estimates using the MCC tree and HPD intervals of estimates from 1,000 randomly sampled trees (for  $\lambda_{DR}$  and  $\lambda_{ND}$ ) or 100 randomly sampled trees for  $\lambda_{BAMM}$  and  $\mu_{BAMM}$  can be found in the ESM. 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 2:** Speciation rate ( $\lambda_{DR}$ ) across all passerine birds ( $n = 5,965$ ) with estimates of sexual dichromatism, range size available for 5,812 species and an index of male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative association between  $\lambda_{DR}$  and log-range size as well as a significant positive association between  $\lambda_{DR}$  and male-biased sexual selection but no significant association between  $\lambda_{DR}$  and sexual dichromatism based on RGB measures.  $\lambda_{DR}$  are those from the MCC tree and images of birds are from the *Handbook of the Birds of the World*. Clockwise the six species are: *Sporophila bouvronides*, *Euplectes franciscanus*, *Phainopepla nitens*, *Paradisaea rubra*, *Malurus pulcherrimus*, *Lepidothrix coeruleocapilla*. Edge colours for the terminal branch correspond to  $\lambda_{DR}$  but all precluding branches have been generated for graphical purposes using ancestral character state estimation and should not be interpreted.



**Figure 3:** 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 ( $n = 2,465$ ).

## 161 DISCUSSION

162 We found evidence that the composite index of male-biased sexual selection, but not measures of sexual  
163 dichromatism, is correlated with the rate of speciation in passerine birds. The absence of a detectable  
164 correlation between sexual dichromatism and speciation rate was consistent across different measures of  
165 speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$  and  $\lambda_{BAMM}$ ) and both measures of dichromatism (spectral and RGB), and it cannot  
166 be explained by a difference in statistical power since the sample size for the dichromatism analyses was much  
167 larger. These findings reaffirm the conclusions of previous, smaller studies in which sexual dichromatism  
168 was measured using spectrophotometry<sup>28</sup> or human observers<sup>36</sup>. The correlation between speciation rate  
169 and the index of male-biased sexual selection (which encapsulates variation in sexual size dimorphism, social  
170 polygyny, and paternal care) was statistically significant for  $\lambda_{DR}$ , but not for  $\lambda_{ND}$  and  $\lambda_{BAMM}$ . Interestingly,  
171 we also found a consistent negative relationship between range size and speciation rate, at least when this  
172 rate was quantified using  $\lambda_{DR}$  and  $\lambda_{ND}$ . None of the bioclimatic measures of environmental variability that  
173 we investigated (i.e., temperature seasonality, long-term temperature variation, and spatial temperature  
174 variation) significantly predicted speciation rate.

175 The difference in findings between the analyses of sexual dichromatism *versus* the index of sexual selection  
176 is noteworthy, because the majority of earlier studies used dichromatism alone as their proxy for sexual  
177 selection<sup>24,25,27,28,45</sup>. Given our findings, and the modest correlation between dichromatism and the sexual  
178 selection index<sup>38</sup>, we suggest that sexual dichromatism may not be a robust proxy for sexual selection.  
179 Although dichromatism clearly reflects sexual selection to some extent, it may be too indirect a measure to  
180 detect any association with speciation rate, even with large sample size. There are several reasons why the use  
181 of sexual dichromatism as a proxy for sexual selection is problematic. Firstly, sexual dichromatism can evolve  
182 for reasons other than sexual selection, such as when males and females occupy different ecological niches<sup>46–49</sup>  
183 or experience different selective pressures in contexts other than competition for mates<sup>50</sup>. For example,  
184 in superb fairy-wrens (*Malurus cyaneus*) female colouration has probably evolved in response to spatial  
185 variation in predation pressure, increasing dichromatism<sup>51</sup>. Ecological selection on sexual dichromatism was  
186 implicated by our path analysis, which found that sexual dichromatism is positively affected by temperature  
187 seasonality (a measure of environmental variation), albeit weakly. Secondly, colour is only one of the traits  
188 subject to sexual selection<sup>13,52</sup>. For instance, sexual selection may promote investments in other mating  
189 signals (e.g. song) that trade-off against plumage colour, leading to variable investment in different sexually  
190 selected signals across species<sup>5</sup>. Lastly, not all plumage colouration honestly reflects mate quality. A recent  
191 meta-analysis found that converted carotenoids (but not carotenoids sourced from the diet) predict mate  
192 quality through improvements in parasite resistance and reproductive success<sup>53</sup>. Given the importance of  
193 honest signaling in sexual selection and the variability in colour production mechanisms across birds, sexual  
194 dichromatism in many species may be an unreliable measure of mate quality for female birds and sexual  
195 selection for researchers.

196 In-line with some theoretical predictions and previous studies<sup>26</sup> we found that male-biased sexual selection  
197 increases speciation rate, at least when speciation is measured by  $\lambda_{DR}$ . Additionally, we found that this  
198 association appears to be independent of net primary productivity and spatiotemporal variation in the  
199 environment. The lack of an effect of these environmental variables on speciation rate has several possible  
200 interpretations. Firstly, the effects of sexual selection on adaptation and speciation may depend on the type of  
201 environmental variability under which the species is evolving. Specifically, speciation rates might be impacted

202 by genetic constraints on adaptation, that vary across environments. Theory suggests that sexual antagonism  
203 (which is often exacerbated in species with strong sexual selection) may be lower in habitats experiencing  
204 cyclical environmental variation (e.g. seasonality), relative to those experiencing directional change in the  
205 environment<sup>33</sup>. Another possibility is that the environmental predictors we chose may not account for the  
206 key ecological sources of selection that interact with sexual selection to drive speciation. For example, our  
207 study does not include direct measure of food availability or the severity of predation and parasitism, which  
208 are both hypothesised to affect sexual selection and speciation<sup>54</sup>. Finally, it is possible that environmental  
209 variability genuinely has little effect on speciation rates, at least in the taxa investigated here.

210 The most robust finding in our study is the finding that species with smaller ranges have elevated speciation  
211 rates. This result is similar to a study of 329 amphibian genera, which found higher diversification rates  
212 in taxa with smaller range size<sup>55</sup>. Intuitively, large range size should promote speciation by creating more  
213 opportunities for geographic barriers to form<sup>56,57</sup>. However, the opposite pattern is also plausible because  
214 birds with limited dispersal or more specialised niches can have more fragmented populations, which would  
215 promote vicariant divergence and higher speciation rates<sup>58–60</sup>. It is also possible that high speciation rates  
216 cause smaller range sizes, rather than the other way around, for example because repeatedly-speciating  
217 lineages tend to fill niches in ways that hinder the geographical expansion of new species<sup>50,56,61</sup>. However,  
218 species undergoing adaptive radiation in new habitats are unlikely to be limited by competition for resources  
219 from existing taxa. One further explanation for the negative association between range size and sexual  
220 dichromatism/sexual selection is the potential bias of taxonomic classification, whereby over-splitting of  
221 species in clades with large ranges leads to increased recent phylogenetic branching as well as smaller ranges.

222 In addition to speciation, sexual selection is hypothesised to affect extinction. Using the model-based  
223 approach of BAMM, we found no association between the estimated extinction rate and sexual dichromatism,  
224 male-biased sexual selection, or our measures of environmental variability. However, these extinction results  
225 should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from  
226 phylogenies, principally because different combinations of speciation and extinction rates can give rise to  
227 similar patterns of diversity<sup>41</sup>. Phylogenetic methods such as BAMM allow for speciation and extinction rates  
228 to be estimated using moderately-sized phylogenies, although the ability of BAMM to model evolutionary rate  
229 shifts and extinction rates is debated<sup>40–43</sup>. Additionally, while several tip-rate estimates exist for speciation  
230 rate (e.g.,  $\lambda_{DR}$  and  $\lambda_{ND}$ ), tip-rate estimates of extinction rate are difficult to obtain without complex Bayesian  
231 models which are sensitive to sampling bias<sup>62</sup>. Although extinction rates can be inferred from alternative  
232 sources, such as the fossil record<sup>63</sup>, direct observation extinction, or IUCN red list status<sup>55</sup>, each approach  
233 has its limitations. Across the passerine bird phylogeny, we found that BAMM often produced homogeneous  
234 speciation and extinction rates for smaller clades showing few rate shifts, which might reduce our power  
235 to detect small differences in extinction rates among closely-related taxa<sup>43,64</sup>. Thus, this methodological  
236 constraint likely decreases our ability to accurately measure the correlation between metrics of sexual selection  
237 and the probability of extinction.

238 One outcome of our analyses was that different measures of speciation rates presented different results. This is  
239 not completely surprising, because each of the rates is calculated differently<sup>64</sup>. For instance,  $\lambda_{DR}$  is weighted  
240 more towards speciation events close to the tips and allows more rate heterogeneity compared to BAMM  
241 estimates. This leads to greater variation in  $\lambda_{DR}$  relative to the BAMM estimates, potentially explaining the  
242 difference in results. The BAMM estimates were also more sensitive to phylogenetic uncertainty.

243 To summarise, we have shown that male-biased sexual selection, but not sexual dichromatism, predicts

<sup>244</sup> speciation in passerines, that the magnitude of this effect is modest, and that this relationship is not markedly  
<sup>245</sup> affected by environmental variability. These findings imply that sexual dechromatism is not a reliable proxy for  
<sup>246</sup> sexual selection, and that alternative measures of sexual selection are more directly related to diversification.  
<sup>247</sup> Our results also add indirect support to the hypothesis that sexual selection promotes adaptation, which  
<sup>248</sup> has implications for conservation<sup>16</sup> and captive breeding programs for threatened species<sup>65</sup>. Furthermore, our  
<sup>249</sup> finding that high speciation rate is associated with smaller range size highlights the threat to the persistence  
<sup>250</sup> of rapidly-speciating lineages in a world with increased habitat loss and anthropogenic stress. This concern  
<sup>251</sup> arises as the best predictor of extinction risk is range size<sup>66</sup> and the association found here implies that many  
<sup>252</sup> newly-speciated clades have small range sizes and could thus be at greater risk of extinction.

## 253 MATERIALS AND METHODS

254 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ( $n = 5,812$   
255 species; 58% of all birds). Specifically, we (i) compiled datasets for sexual dichromatism/selection strength  
256 and environmental variability, (ii) obtained estimates of speciation and extinction rates across passerines,  
257 and (iii) conducted phylogenetic generalized least-squares (PGLS) regressions. Analyses are documented  
258 with reproducible code in the [Electronic Supplementary Material \(ESM\)](#).

### 259 Compiling data for sexual selection and environmental stress

#### 260 Sexual dichromatism

261 We used a previously-published measure of sexual dichromatism for 5,983 species of passerines<sup>38</sup>. Briefly, Dale  
262 et al.<sup>38</sup> obtained sex-specific RGB (red-green-blue) values across six body patches (nape, crown, forehead,  
263 throat, upper breast, and lower breast) from *Handbook of the Birds of the World*<sup>44</sup>. The relative contribution  
264 of male and female RGB colour values were averaged across body patches and provide ‘male-like’ and  
265 ‘female-like’ plumage scores. Here we use the absolute difference between male and female plumage scores as  
266 an estimate of sexual dichromatism. Additionally, we used another measure of dichromatism corresponding to  
267 colour distance in avian colour space derived from spectral data<sup>35</sup>. These measurements include variation in  
268 the ultraviolet and bird-visible range and — unlike the RGB measures — are sourced from museum specimens  
269 as opposed to illustrations. The spectrophotometry data covers only 581 passerine species (10-fold fewer  
270 than the RGB data), although there was a substantial correlation between the two dichromatism measures  
271 ( $r = 0.79$ ; [Figure S10](#)).

#### 272 Male-biased sexual selection

273 Because sexual dichromatism is presumably imperfectly correlated with variation in the strength of sexual  
274 selection across taxa, we sourced an additional measure of sexual selection<sup>38</sup>, referred to here as the ‘index  
275 of male-biased sexual selection’. This index is the first principal component from a phylogenetic principal  
276 component analysis (PPCA) of three characteristics positively associated with sexual selection (sexual size  
277 dimorphism, social polygyny and [lack of] paternal care). This measure of male-biased sexual selection  
278 is available for only 2,465 species, and shows a moderate correlation with the RGB measure of sexual  
279 dichromatism ( $r = 0.34$ ; [Figure S12](#)).

#### 280 Environmental variables

281 We obtained estimates of species range size using expert range maps<sup>67</sup>. Because of taxonomic changes  
282 to 1,230 species in the Birdlife database<sup>68</sup> we manually matched these taxa with the names used in the  
283 sexual dichromatism dataset<sup>38</sup>. From these distributions, we obtained estimates of climatic conditions that  
284 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19  
285 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature

and precipitation) with 30-second ( $\sim 1 \text{ km}^2$ ) spatial resolution<sup>69</sup>. From these values, we obtained means and standard deviations for each species. Using the same spatial sampling, we extracted means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial (LIG; 120,000 - 140,000 years ago)<sup>70</sup>. To estimate variability in the energy available to species, we obtained the mean and standard deviation of net primary productivity (NPP) values between 2000 - 2015 across each species distribution. Estimates of NPP had 30-second resolution and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production products stage 3 (MOD17A3)<sup>71</sup>. Using these data, which we provide as a potentially useful data resource (see [ESM](#)), we generated five predictors of speciation associated with different patterns in environmental variability (see below).

## Generating biologically relevant predictors for environmental stress

Given that stressful environments are expected to interact with sexual selection and have a positive effect on adaptation<sup>13</sup>, we used the extracted environmental variables from each species range size to create predictors of environmental variation/stress. Firstly we used (i) the average NPP in each species' range and (v) the log-transformed range size as potentially informative predictors of speciation rates. We also used three environmental predictors derived from bioclimatic data. These predictors relate to seasonal climate variation, spatial climate variation and long-term climate variation. To obtain seasonal climate variation we used (iii) mean values of temperature seasonality (BIO4) for each range. (iv) To estimate levels of spatial environmental variation a species may endure we used the first principle component (PC1) from a PCA on standard deviations from all bioclimatic variables, excluding temperature and precipitation seasonality (BIO4 and BIO15). PC1 was heavily loaded towards bioclimatic variables relating to temperature, thus PC1 reflects the variation in temperature across a species' range ([Table S1](#)). Species range is a potentially informative predictor of speciation and extinction, so we controlled for the correlation between environmental spatial variation and range size — where larger ranges have larger variation in PC1 — by using the residuals of a fitted general additive model (GAM; [Figure S1](#)) as a predictor. To obtain long-term variation in climates for each species range we take (v) the first principal component of the absolute difference in the bioclimatic variables between the LIG and current values. Similarly to spatial variation, the long-term climate variation is primarily loaded to temperature differences between the LIG and current climates ([Table S2](#), [Figure S2](#)). The five predictors of environmental variability are not strongly correlated ([Figure S3](#)). Details and R code to generate these predictors can be found within the [ESM](#).

## Estimating extinction and speciation

Phylogenetic information was obtained from [www.birdtree.org](http://www.birdtree.org)<sup>29</sup>. We used a maximum clade credibility (MCC) tree from 2,500 samples of the posterior distribution ( $n = 5,965$ ) as the main phylogenetic hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using tip-rate measures (1,000 trees) and BAMM (100 trees)<sup>30</sup>. These trees used a 'Hackett backbone'<sup>72</sup> and were constructed using a pure birth (Yule) model. We calculated three different tip-rate metrics of speciation and one of extinction across all trees.

Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes

and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES), also known as diversification rate (DR)<sup>29,73,74</sup>, is derived from the sum of edge lengths branching from a node, with each edge towards the root having the length down-weighted. Studies have suggested that DR and ND (henceforth referred to as  $\lambda_{DR}$  and  $\lambda_{ND}$ ) are more reflective estimates of speciation than diversification; this is because  $\lambda_{DR}$  and  $\lambda_{ND}$  cannot account for whole-clade extinctions and thus under-estimate extinction rate, which makes the composite measure of diversification more dependent on speciation<sup>64,75</sup>. Therefore,  $\lambda_{DR}$  is a measure of speciation rate more heavily weighted to recent speciation events while  $\lambda_{ND}$  measures speciation across the root-to-tip path. These tip-rate measures are alternatives to state-dependent diversification models such as Quantitative State Speciation-Extinction (QuaSSE); but, based on previous simulation studies,  $\lambda_{DR}$  and  $\lambda_{ND}$  are robust and intuitive measures that provide high power and low false discovery rate with large phylogenies when incorporated into Phylogenetic Generalized Least Squares (PGLS) models<sup>31</sup>.

Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic trees<sup>30</sup>. This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo) to generate probability distributions of evolutionary rate-shift configurations with variable speciation and extinction rates. Importantly, these models provide tip-rate estimates of speciation and extinction rate. The parameters of the 100 BAMM runs are detailed in full in the [ESM](#); briefly, we used a time-variable model with 100 expected number of shifts and prior rates set from the initial speciation and extinction values using the **BAMMtools** R package<sup>76</sup>. Each BAMM model (one MCC tree and 100 random draws of the posterior) was run for 100 million generations, and given the computationally intensive nature of BAMM, runs were conducted across multiple CPUs. Each run of BAMM reached convergence with effective sample size (ESS) of MCMC (Markov Chain Monte Carlo) samples surpassing 200 (an arbitrary value, above which posterior distributions can often be accurately inferred) for the key model parameters of log-likelihood and number of rate shifts ([Table S3](#), [Table S4](#)). Further details of BAMM parameters and output are available in the [ESM](#), with tip-rate means and variances provided. Additionally, given the variability in BAMM estimates, we also provide analysis of BAMM shift configurations and tip-rate estimates from our run on the MCC tree and within a BAMM run on the MCC tree from a genetic-only phylogeny across all birds<sup>77</sup>. All analyses were conducted on log-rates.

## Phylogenetic comparative analysis

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we used phylogenetic least squares (PGLS) models in the **nlme** package<sup>78</sup>. Firstly, we conducted model selection to compare models in which  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  or  $\mu_{BAMM}$  were the response variable: these tip-rate estimates all came from the same MCC tree (derived from 2,500 draws of the posterior distribution<sup>29</sup>). For models of  $\lambda_{BAMM}$  and  $\mu_{BAMM}$  we used the inverse of the variance associated with each tip rate estimate as weights, to account for the variable precision of the estimates provided by BAMM. The most complicated model in each set under comparison contained one of the measures of sexual selection (sexual dichromatism or the index of male-biased sexual selection), all of the environmental measures (i.e. log-transformed range size, seasonal temperature variation, spatial temperature variation, long-term temperature variation, and NPP), and all of the 2-way interactions between sexual selection and each of the environmental measures. The simpler models contained all of the same main effects, but had fewer 2-way interaction terms (potentially none). Model selection was done in **MuMIn** using the **dredge** function<sup>79</sup>. Using the terms from the top-ranked

364 model (ranked by AICc), we ran the equivalent model for each of the 1,000 phylogenetic trees used to derive  
365  $\lambda_{DR}$ ,  $\lambda_{ND}$  and each of the 100 trees used to derive  $\lambda_{BAMM}$  and  $\mu_{BAMM}$ . In each model we used the unique  
366 response variables and phylogenetic tree correlation structure. Specifically, for models using tip-rate metrics  
367 ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ) we estimated the phylogenetic signal — Pagel's  $\lambda^{80}$  — using the `corPagel` function in the `ape`  
368 package<sup>81</sup> independently for each of the 1,000 trees/models. Alternatively, for models using speciation and  
369 extinction estimates derived using BAMM ( $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ) we found  $\lambda$  was consistently estimated at 1  
370 and hence assumed Brownian motion (using the `corBrownian` function) to estimate the correlation structure.  
371 This method enabled us to present model estimates for an MCC tree alongside 1,000/100 trees from the  
372 posterior distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three  
373 datasets corresponding to each measure of sexual selection: dichromatism derived from RGB values of images  
374 ( $n = 5,812$ ); dichromatism from spectrophotometry ( $n = 581$ ) and the index of male-biased sexual selection  
375 ( $n = 2,465$ ).  
  
376 Finally, using the subset of species with an index of male-biased sexual selection, we conducted a phylogenetic  
377 path analysis using the `phylopath` R package<sup>82</sup>. The phylogenetic path analysis was used to assess causal paths  
378 between variables not able to be modelled within the univariate response of PGLS. That is, a phylogenetic  
379 path analysis allowed us to model relationships between the predictor variables used in our PGLS analysis as  
380 we anticipate environmental variability, sexual dichromatism/selection, and range size to have effects on each  
381 other and not just on speciation rate. To minimise path complexity we used temperature seasonality (BIO4)  
382 as the single measure for environmental variability,  $\lambda_{DR}$  as the single measure of speciation and the tip-rates  
383 from the MCC tree. Further details of the path analysis, including our rationale for each path's directions,  
384 can be found within the [ESM](#) along with all other analyses and the relevant R code to reproduce results.

## 385 ACKNOWLEDGEMENTS

386 We would like to acknowledge Adnan Moussalli for his assistance in conducting BAMM runs across 100  
387 phylogenetic trees.

## 388 REFERENCES

- 389 1. Lande, R. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences* **78**, 3721–3725 (1981).
- 390 2. Lande, R. Rapid origin of sexual isolation and character divergence in a cline. *Evolution* **36**, 213–223 (1982).
- 391 3. West-Eberhard, M. J. Sexual selection, social competition, and speciation. *Quarterly Review of Biology* **58**, 155–183 (1983).
- 392 4. Seddon, N., Merrill, R. M. & Tobias, J. A. Sexually selected traits predict patterns of species richness in a diverse clade of suboscine birds. *American Naturalist* **171**, 620–631 (2008).
- 393 5. Cooney, C. R., MacGregor, H. E. A., Seddon, N. & Tobias, J. A. Multi-modal signal evolution in birds: Re-examining a standard proxy for sexual selection. *Proceedings of the Royal Society of London B: Biological Sciences* **285**, (2018).
- 394 6. Safran, R. J., Scordato, E. S., Symes, L. B., Rodri'guez, R. L. & Mendelson, T. C. Contributions of natural and sexual selection to the evolution of premating reproductive isolation: A research agenda. *Trends in Ecology & Evolution* **28**, 643–650 (2013).
- 395 7. Swanson, W. J. & Vacquier, V. D. Concerted evolution in an egg receptor for a rapidly evolving abalone sperm protein. *Science* **281**, 710–712 (1998).
- 396 8. Sloan, N. S. & Simmons, L. W. The evolution of female genitalia. *Journal of Evolutionary Biology* **in press**, (2019).
- 397 9. Whitlock, M. C. & Agrawal, A. F. Purging the genome with sexual selection: Reducing mutation load through selection on males. *Evolution* **63**, 569–582 (2009).
- 398 10. Whitlock, M. C. Fixation of new alleles and the extinction of small populations: Drift load, beneficial alleles, and sexual selection. *Evolution* **54**, 1855–1861 (2000).
- 399 11. Lorch, P. D., Proulx, S., Rowe, L. & Day, T. Condition-dependent sexual selection can accelerate adaptation. *Evolutionary Ecology Research* **5**, 867–881 (2003).
- 400 12. Candolin, U. & Heuschele, J. Is sexual selection beneficial during adaptation to environmental change? *Trends in Ecology & Evolution* **23**, 446–452 (2008).
- 401 13. Cally, J. G., Stuart-Fox, D. & Holman, L. Meta-analytic evidence that sexual selection improves population fitness. *Nature communications* **10**, 2017 (2019).
- 402 14. Rankin, D. J., Dieckmann, U. & Kokko, H. Sexual conflict and the tragedy of the commons. *American Naturalist* **177**, 780–791 (2011).
- 403 15. Kokko, H. & Jennions, M. D. Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology* **21**, 919–948 (2008).
- 404 16. Holman, L. & Kokko, H. The consequences of polyandry for population viability, extinction risk and conservation. *Philosophical Transactions of the Royal Society B-Biological Sciences* **368**, (2013).

- 423 17. Fromhage, L. & Jennions, M. D. Coevolution of parental investment and sexually selected traits drives  
424 sex-role divergence. *Nature Communications* **7**, 12517 (2016).
- 425 18. Kokko, H. & Brooks, R. Sexy to die for? Sexual selection and the risk of extinction. *Annales Zoologici  
426 Fennici* **40**, 207–219 (2003).
- 427 19. Pischedda, A. & Chippindale, A. K. Intralocus sexual conflict diminishes the benefits of sexual selection.  
428 *PLOS Biology* **4**, e356 (2006).
- 429 20. Harano, T., Okada, K., Nakayama, S., Miyatake, T. & Hosken, D. J. Intralocus sexual conflict unresolved  
430 by sex-limited trait expression. *Current Biology* **20**, 2036–2039 (2010).
- 431 21. Berger, D. *et al.* Intralocus sexual conflict and environmental stress. *Evolution* **68**, 2184–2196 (2014).
- 432 22. Bonduriansky, R. & Chenoweth, S. F. Intralocus sexual conflict. *Trends in Ecology & Evolution* **24**,  
433 280–8 (2009).
- 434 23. Pennell, T. M. & Morrow, E. H. Two sexes, one genome: The evolutionary dynamics of intralocus sexual  
435 conflict. *Ecology and Evolution* **3**, 1819–1834 (2013).
- 436 24. Barraclough, T. G., Harvey, P. H. & Nee, S. Sexual selection and taxonomic diversity in passerine birds.  
437 *Proceedings of the Royal Society B-Biological Sciences* **259**, 211–215 (1995).
- 438 25. Morrow, E. H., Pitcher, T. E. & Arnqvist, G. No evidence that sexual selection is an 'engine of speciation'  
439 in birds. *Ecology Letters* **6**, 228–234 (2003).
- 440 26. Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Maan, M. E. Sexual selection and speciation: The  
441 comparative evidence revisited. *Biological Reviews* **86**, 367–377 (2011).
- 442 27. Seddon, N. *et al.* Sexual selection accelerates signal evolution during speciation in birds. *Proceedings of  
443 the Royal Society B: Biological Sciences* **280**, (2013).
- 444 28. Huang, H. T. & Rabosky, D. L. Sexual selection and diversification: Reexamining the correlation between  
445 dichromatism and speciation rate in birds. *American Naturalist* **184**, E101–E114 (2014).
- 446 29. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in  
447 space and time. *Nature* **491**, 444–448 (2012).
- 448 30. Rabosky, D. L. Automatic detection of key innovations, rate shifts, and diversity-dependence on  
449 phylogenetic trees. *PLOS ONE* **9**, e89543 (2014).
- 450 31. Harvey Michael, G., Rabosky Daniel, L. & Cooper, N. Continuous traits and speciation rates: Alternatives  
451 to state-dependent diversification models. *Methods in Ecology and Evolution* **9**, 984–993 (2017).
- 452 32. Long, T. A. F., Agrawal, A. F. & Rowe, L. The effect of sexual selection on offspring fitness depends on  
453 the nature of genetic variation. *Current Biology* **22**, 204–208 (2012).
- 454 33. Connallon, T. & Hall, M. D. Genetic correlations and sex-specific adaptation in changing environments.  
455 **70**, 2198 (2016).
- 456 34. Huber, S. K., De Leon, L. F., Hendry, A. P., Bermingham, E. & Podos, J. Reproductive isolation  
457 of sympatric morphs in a population of darwin's finches. *Proceedings of the Royal Society of London B:  
458 Biological Sciences* **274**, 1709–1714 (2007).

- 459 35. Armenta, J. K., Dunn, P. O. & Whittingham, L. A. Quantifying avian sexual dichromatism: A comparison  
460 of methods. *Journal of Experimental Biology* **211**, 2423 (2008).
- 461 36. Cooney, C. R., Tobias, J. A., Weir, J. T., Botero, C. A. & Seddon, N. Sexual selection, speciation and  
462 constraints on geographical range overlap in birds. *Ecology Letters* **20**, 863–871 (2017).
- 463 37. Iglesias-Carrasco, M., Jennions, M. D., Ho, S. Y. W. & Duchêne, D. A. Sexual selection, body mass and  
464 molecular evolution interact to predict diversification in birds. *Proceedings of the Royal Society B: Biological  
465 Sciences* **286**, 20190172 (2019).
- 466 38. Dale, J., Dey, C. J., Delhey, K., Kempenaers, B. & Valcu, M. The effects of life history and sexual  
467 selection on male and female plumage colouration. *Nature* **527**, 367–370 (2015).
- 468 39. Davies, N. & Houston, A. Reproductive success of dunnocks, *Prunella modularis*, in a variable mating  
469 system. II. Conflicts of interest among breeding adults. *Journal of Animal Ecology* **55**, 139–154 (1986).
- 470 40. Beaulieu, J. M. & O'Meara, B. C. Extinction can be estimated from moderately sized molecular  
471 phylogenies. *Evolution* **69**, 1036–1043 (2015).
- 472 41. Rabosky, D. L. Challenges in the estimation of extinction from molecular phylogenies: A response to  
473 Beaulieu and O'Meara. *Evolution* **70**, 218–228 (2016).
- 474 42. Moore, B. R., Hohna, S., May, M. R., Rannala, B. & Huelsenbeck, J. P. Critically evaluating the theory  
475 and performance of bayesian analysis of macroevolutionary mixtures. *Proceedings of the National Academy  
476 of Sciences* **113**, 9569–9574 (2016).
- 477 43. Rabosky, D. L., Mitchell, J. S. & Chang, J. Is BAMM flawed? Theoretical and practical concerns in the  
478 analysis of multi-rate diversification models. *Systematic biology* **66**, 477–498 (2017).
- 479 44. Del Hoyo, J., Elliott, A. & Christie, D. *Handbook of the birds of the world.* **8-16**, (Lynx Edicions  
480 2003-2011, 2011).
- 481 45. Owens, I. P. F., Bennett, P. M. & Harvey, P. H. Species richness among birds: Body size, life history,  
482 sexual selection or ecology? *Proceedings of the Royal Society B-Biological Sciences* **266**, 933–939 (1999).
- 483 46. Wallace, A. R. Colours and ornaments characteristic of sex. in *Darwinism, an exponent of the theory of  
484 natural selection, with some of its applications* (Macmillan; Company, 1889).
- 485 47. Kottler, M. J. Darwin, Wallace, and the origin of sexual dimorphism. *Proceedings of the American  
486 Philosophical Society* **124**, 203–226 (1980).
- 487 48. Slatkin, M. Ecological causes of sexual dimorphism. *Evolution* **38**, 622–630 (1984).
- 488 49. Shine, R. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *The  
489 Quarterly Review of Biology* **64**, 419–461 (1989).
- 490 50. Price, J. J. & Eaton, M. D. Reconstructing the evolution of sexual dichromatism: Current color diversity  
491 does not reflect past rates of male and female change. *Evolution* **68**, 2026–2037 (2014).
- 492 51. Medina, I. *et al.* Habitat structure is linked to the evolution of plumage colour in female, but not male,  
493 fairy-wrens. *BMC evolutionary biology* **17**, 35 (2017).

- 494 52. Miles, M. C. & Fuxjager, M. J. Synergistic selection regimens drive the evolution of display complexity in  
495 birds of paradise. *Journal of Animal Ecology* **87**, 1149–1159 (2018).
- 496 53. Weaver, R. J., Santos, E. S., Tucker, A. M., Wilson, A. E. & Hill, G. E. Carotenoid metabolism strengthens  
497 the link between feather coloration and individual quality. *Nature Communications* **9**, 73 (2018).
- 498 54. Maan, M. E. & Seehausen, O. Ecology, sexual selection and speciation. *Ecology Letters* **14**, 591–602  
499 (2011).
- 500 55. Greenberg, D. A. & Mooers, A. Ø. Linking speciation to extinction: Diversification raises contemporary  
501 extinction risk in amphibians. *Evolution Letters* **1**, 40–48 (2017).
- 502 56. Rosenzweig, M. L. *Species diversity in space and time*. (Cambridge University Press, 1995).
- 503 57. Castiglione, S. *et al.* Diversification rates and the evolution of species range size frequency distribution.  
504 *Frontiers in Ecology and Evolution* **5**, 147 (2017).
- 505 58. Birand, A., Vose, A. & Gavrilets, S. Patterns of species ranges, speciation, and extinction. *American  
506 Naturalist* **179**, 1–21 (2012).
- 507 59. Claramunt, S., Derryberry, E. P., Remsen, J. V. & Brumfield, R. T. High dispersal ability inhibits  
508 speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*  
509 **279**, 1567 (2012).
- 510 60. Jablonski, D. & Roy, K. Geographical range and speciation in fossil and living molluscs. *Proceedings of  
511 the Royal Society of London. Series B: Biological Sciences* **270**, 401–406 (2003).
- 512 61. Weir, J. T. & Price, T. D. Limits to speciation inferred from times to secondary sympatry and ages of  
513 hybridizing species along a latitudinal gradient. *American Naturalist* **177**, 462–469 (2011).
- 514 62. Davis, M. P., Midford, P. E. & Maddison, W. Exploring power and parameter estimation of the BiSSE  
515 method for analyzing species diversification. *BMC Evolutionary Biology* **13**, 38 (2013).
- 516 63. Martins, M. J. F., Puckett, T. M., Lockwood, R., Swaddle, J. P. & Hunt, G. High male sexual investment  
517 as a driver of extinction in fossil ostracods. *Nature* **556**, 366 (2018).
- 518 64. Title, P. O. & Rabosky, D. L. Diversification rates and phylogenies: What are we estimating, and how  
519 good are the estimates? *bioRxiv* 369124 (2018).
- 520 65. Charge, R., Teplitsky, C., Sorci, G. & Low, M. Can sexual selection theory inform genetic management of  
521 captive populations? A review. *Evolutionary Applications* **7**, 1120–1133 (2014).
- 522 66. Harris, G. & Pimm, S. L. Range size and extinction risk in forest birds. *Conservation Biology* **22**, 163–171  
523 (2008).
- 524 67. BirdLife International and Handbook of the Birds of the World. *Bird species distribution maps of the  
525 world*. (<http://datazone.birdlife.org/species/requestdis>, 2017).
- 526 68. Hoyo, J. del & Collar, N. J. *HBW and birdlife international illustrated checklist of the birds of the world*.  
527 **1**, (Lynx Edicions; BirdLife International, 2016).
- 528 69. Fick, S. E. & Hijmans, R. J. WorldClim 2: New 1-km spatial resolution climate surfaces for global land  
529 areas. *International Journal of Climatology* **37**, 4302–4315 (2017).

- 530 70. Otto-Bliesner, B. L. *et al.* Simulating arctic climate warmth and icefield retreat in the last interglaciation.  
531 *Science* **311**, 1751–1753 (2006).
- 532 71. Zhao, M., Heinsch, F. A., Nemani, R. R. & Running, S. W. Improvements of the modis terrestrial gross  
533 and net primary production global data set. *Remote Sensing of Environment* **95**, 164–176 (2005).
- 534 72. Hackett, S. J. *et al.* A phylogenomic study of birds reveals their evolutionary history. *Science* **320**,  
535 1763–1768 (2008).
- 536 73. Quintero, I. & Jetz, W. Global elevational diversity and diversification of birds. *Nature* **555**, 246 (2018).
- 537 74. Rabosky, D. L. *et al.* An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392  
538 (2018).
- 539 75. Belmaker, J. & Jetz, W. Relative roles of ecological and energetic constraints, diversification rates and  
540 region history on global species richness gradients. *Ecology Letters* **18**, 563–571 (2015).
- 541 76. Rabosky, D. *et al.* BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic  
542 trees. *Methods in Ecology and Evolution* **5**, 701–707 (2014).
- 543 77. Harvey, M. G. *et al.* Positive association between population genetic differentiation and speciation rates  
544 in new world birds. *Proceedings of the National Academy of Sciences* **114**, 6328–6333 (2017).
- 545 78. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. *nlme: Linear and nonlinear mixed effects*  
546 *models*. (2018).
- 547 79. Bartoń, K. *MuMin: Multi-model inference*. (2017).
- 548 80. Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401**, 877 (1999).
- 549 81. Paradis, E., Claude, J. & Strimmer, K. APE: Analyses of phylogenetics and evolution in R language.  
550 *Bioinformatics* **20**, 289–290 (2004).
- 551 82. Bijl, W. van der. *Phylopath*: Easy phylogenetic path analysis in R. *PeerJ* **6**, e4718 (2018).