

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

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4           Abstract

5           Sexual selection is thought to shape phylogenetic diversity by affecting speciation or extinction rates.  
6           However, the net effect of sexual selection on diversification is hard to predict *a priori*, because many  
7           of the hypothesised effects on speciation or extinction have opposing signs and uncertain magnitudes.  
8           Here, we test whether the strength of sexual selection predicts variation in speciation and extinction  
9           rates across passerine birds (up to 5,812 species, covering most genera). We tested for associations  
10          between two measures of sexual selection (sexual dichromatism, plus an index that captures variance in  
11          sexual size dimorphism, polygyny, and male parental care), several environmental variables, and multiple  
12          measures of speciation and extinction rates. Our results show that male-biased sexual selection, but  
13          not sexual dichromatism, predicts speciation rates ( $\lambda_{DR}$ ) in passerines, and found no evidence that  
14          this relationship varies with the environment. We also found a strong negative relationship between  
15          range size and speciation rate. There was no correlation between sexual selection and extinction rate  
16          XXXXXX. Our findings support the view that sexual selection is a potent evolutionary force that has  
17          shaped diversification in songbirds.

18           **Keywords:** Speciation rate, Comparative analysis, Plumage dichromatism, Range size, Extinction rate.

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## 19 INTRODUCTION

20 Sexual selection results from competition between same-sex individuals for mates, their gametes, or associated  
21 resources, and in most species it predominantly operates on males (Kokko and Jennions 2008; Fromhage  
22 and Jennions 2016; Janicke et al. 2016). There is long-standing interest in the relationship between sexual  
23 selection and the processes of speciation, extinction, and phylogenetic diversification (e.g. Lande 1981, 1982;  
24 West-Eberhard 1983; Seddon et al. 2008; Cooney et al. 2018). Recent empirical and methodological advances,  
25 such as growing evidence that sexual selection can profoundly affect many traits (e.g. life history, body mass,  
26 and immunocompetence; Cally et al. 2019), larger and more accurate phylogenies (Jetz et al. 2012), and  
27 new phylogenetic methods (**REFERENCES**), present new opportunities to test whether and how sexual  
28 selection drives diversification.

29 Several hypotheses predict a positive relationship across species between the strength of sexual selection  
30 and the rate of speciation and/or extinction. For example, sexual selection is involved in reinforcement, a  
31 speciation-promoting process in which members of different phylogenetic lineages evolve to avoid unproductive  
32 inter-lineage mating/fertilisation (**REF**). Additionally, sexual selection often operates on traits that can  
33 create reproductive isolation when they diverge between lineages, such as signals and preferences involved in  
34 mate selection (Lande 1981, 1982; Safran et al. 2013), sperm-egg interactions (Swanson and Vacquier 1998),  
35 or genital morphology (Sloan and Simmons 2019). Furthermore, sexual selection has been hypothesised to  
36 increase diversification by maintaining trait combinations that would be selected out under pure natural  
37 selection (Bonduriansky 2011; Radwan et al. 2016), and by helping to prevent extinction by purging  
38 deleterious mutations (Whitlock and Agrawal 2009), fixing beneficial ones (Whitlock 2000), and accelerating  
39 adaptation in environments (Lorch et al. 2003; Candolin and Heuschele 2008; Cally et al. 2019). Also, sexual  
40 selection sometimes favours individuals with rare phenotypes (Holman et al. 2013), providing a source of  
41 diversifying selection that might increase the rate at which isolated populations diverge genetically.

42 Conversely, there are multiple ways in which sexual selection might hinder speciation or make extinction more  
43 likely. Firstly, sexual selection might promote extinction by favouring traits that improve mating success  
44 but reduce population fitness. For example, species with expensive sexual signals may be less resilient to  
45 environmental change (Kokko and Brooks 2003), and sexual selection often creates a ‘tragedy of the commons’  
46 by selecting for traits that increase the reproductive success of individuals while reducing population-wide  
47 productivity (e.g. infanticide, harassment, and reduced parental care by mate-seeking males; Rankin et al.  
48 2011; Kokko and Jennions 2008; Holman and Kokko 2013; Fromhage and Jennions 2016). Sexual selection  
49 might also promote extinction by causing maladaptation (‘gender load’) in female traits that are genetically  
50 correlated with sexually-selected male traits (Pischedda and Chippindale 2006; Bonduriansky and Chenoweth  
51 2009; Harano et al. 2010; Pennell and Morrow 2013; Berger et al. 2014). Secondly, sexual selection might  
52 promote evolutionary stasis by ensuring that individuals with novel trait values have low mating success.

53 Importantly, the relationship between sexual selection and diversification might be contingent on the  
54 environment. Theoretical work predicts that sexual selection should have a more positive effect on adaptation  
55 and population fitness in variable environments relative to stable ones (e.g. Long et al. 2012; Connallon and  
56 Hall 2016), though the empirical evidence for this theory is mixed and largely limited to insects (Cally et  
57 al. 2019). The mechanism underpinning this prediction is that the environment and the selective history of  
58 the population should influence the relative amounts of genetic variation at sexually concordant loci (*i.e.*

59 loci where the same allele is fittest for both sexes) and sexually antagonistic loci (where different alleles are  
60 favoured in each sex). In stable environments, variation is thought to be preferentially depleted at sexually  
61 concordant loci, leading to stronger gender load and reduced net benefits of sexual selection (e.g. Connallon  
62 and Hall 2016), and potentially to a more negative relationship between sexual selection and diversification  
63 rates across species. Conversely, sexual selection might be especially important at promoting local adaptation  
64 when the environment displays variability at the relevant spatial and temporal scales (e.g. Boughman 2002;  
65 Lorch et al. 2003; Kokko and Heubel 2008; Maan and Seehausen 2011)

66 Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification (e.g.  
67 Barraclough et al. 1995; Morrow et al. 2003; Seddon et al. 2008, 2013; Huang and Rabosky 2014). Birds are  
68 well-suited for this purpose due to their diverse and well-characterised mating systems and sexually-selected  
69 traits, and because their phylogenetic relationships are comparatively well-known. A 2011 meta-analysis  
70 covering 20 primary studies of birds and other taxa found a small but significant positive association between  
71 sexual selection and speciation, with the average effect size in birds stronger than in mammals but weaker than  
72 in insects or fish (Kraaijeveld et al. 2011). However, there was large variation in effect size estimates across  
73 the 20 studies, likely reflecting differences in methodology, such as metrics used to characterise speciation and  
74 sexual selection, in addition to true biological differences. More recently, Huang and Rabosky (2014) found no  
75 association between sexual dichromatism and speciation ( $n = 918$  species) in a study using spectrophotometric  
76 measurements of museum specimens (Armenta et al. 2008) and tip-rate estimates from a molecular-only  
77 phylogeny (Jetz et al. 2012). Similarly, Cooney et al. (2017) found no effect of sexual dichromatism on  
78 diversification across 1,306 pairs of species, using dichromatism scores provided by human observers.

79 Here, we investigate the association between sexual selection and diversification in birds while building upon  
80 previous approaches in multiple ways. We use two measures of the strength of sexual selection: sexual  
81 dichromatism ( $n = 5,812$  species; estimated from illustrations by Dale et al. 2015), as well as an index of  
82 male-biased sexual selection ( $n = 2,465$  species; derived via principal components analysis by Dale et al. 2015),  
83 which captures (co)variation in sexual size dimorphism, social polygyny and paternal care. Most **OR ALL??**  
84 earlier macroevolutionary studies of this topic only quantified sexual selection using dichromatism, which  
85 is problematic since dichromatism does not always signal the presence of strong sexual selection and *vice*  
86 *versa* (Dale et al. 2015). For example, male and female dunnocks (*Prunella modularis*) are similarly coloured  
87 yet sexual selection appears to be strong (Davies and Houston 1986). Furthermore, a recent comparative  
88 study found a negative relationship between dichromatism and another sexually-selected trait (song) across  
89 species, suggesting that a multi-trait focus would improve estimates of sexual selection intensity (Cooney et al.  
90 2018). Additionally, our analysis includes multiple ecological and environmental variables on diversification,  
91 allowing us to adjust for potential confounds, to identify environmental factors driving diversification, and  
92 to test whether environmental factors interact with sexual selection as theory predicts (Connallon and Hall  
93 2016). We use multiple approaches for quantifying speciation and extinction rates at the tips of phylogenetic  
94 trees, including BAMM (Bayesian Analysis of Macroevolutionary Mixtures; *see*, Beaulieu and O'Meara 2015;  
95 Rabosky 2016; Moore et al. 2016; Rabosky et al. 2017), as well as older but reliable tip-rate statistics, such  
96 as diversification rate ( $\lambda_{DR}$ ) and node density ( $\lambda_{ND}$ ). Finally, we incorporate phylogenetic uncertainty into  
97 our analyses, improving over earlier work which assumed the statistically best-fitting phylogeny is correct.

## 98 RESULTS

### 99 Variability across phylogenetic trees and speciation rate measures

100 [Is it possible to move this later in the Results? It's possibly not ideal to start by highlighting  
101 the dependence of our conclusions on the methods we choose, and not mentioning our main  
102 non-null finding regarding the SS index. Having said that I can see a case for leaving it here  
103 too. - Luke]

104 We first estimated speciation rates across the phylogeny, using the maximum clade credibility (MCC) tree, as  
105 well as 100 or 1000 trees sampled from the posterior distribution of trees in Jetz et al. (2012). Estimates  
106 of speciation rates varied between phylogenetic trees, especially for rates calculated by BAMM ( $\lambda_{BAMM}$ )  
107 and  $\mu_{BAMM}$ ), where the 95% highest posterior density (HPD) interval across 100 trees was >20-fold larger  
108 than the **95% confidence interval [SHOULD THIS BE HPD TOO?]** calculated for the MCC tree.  
109 Conversely, for our estimates of diversification rate ( $\lambda_{DR}$ ) and node density ( $\lambda_{ND}$ ), the 95% HPD interval  
110 across 1,000 trees was near-identical to the 95% confidence interval calculated for the MCC tree (Table S9).  
111 Given the computational requirements of BAMM, the great majority of earlier studies have based their  
112 estimates on a single consensus tree, and so the inconsistency of the BAMM estimates between different  
113 phylogenies with similar statistical support is notable. Mean measures of speciation rate across 100 trees  
114 were positively correlated between measures (DR - BAMM:  $r=0.75$ , DR - ND:  $r=0.65$ , ND- BAMM:  $r=0.51$ ;  
115 Figure S15). Given that the calculation of BAMM rates can be affected by the settings of the run and the  
116 use of different priors, we compared the estimate of our MCC tree with that of previous published analyses  
117 on birds, and found a high correlation ( $r=0.81$ , Figure S8). Full details of the BAMM results are presented  
118 as supplementary materials.

119 No evidence that the relationship between sexual selection and speciation  
120 depends on environmental variability

121 [I think this part should go after the next 2 sections, as it's a more confusing being about  
122 interactions, and we should preserve the order of ideas from the Abstract and Intro. - Luke]

123 We next fit Phylogenetic Generalized Least Squares (PGLS) models with **2-way [CORRECT?]** interaction  
124 terms between each measure of sexual dichromatism/selection and the five measures of environmental variability  
125 (seasonal temperature variation, log-range size, long-term temperature variation, spatial temperature variation,  
126 and NPP) and compared them using AICc model selection. However, no interaction terms were present in  
127 the top models ( $\delta$  AICc  $> 4$ ) for any measure of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) or sexual selection (RGB  
128 values, spectrophotometry and male-biased sexual selection;  $\delta$  AICc  $> 4$ ; Table S5, Table S6, Table S10,  
129 Table S13). Thus we found no evidence that the effect of sexual selection on speciation is dependent on our  
130 measures of environmental variation. Furthermore, we found no evidence that these environmental factors  
131 (seasonal temperature variation, long-term temperature variation, spatial temperature variation, and NPP)  
132 predict speciation independently from sexual dichromatism/selection (Figure 1, Figure S11).

133

134 No evidence that sexual dichromatism affects speciation

135 We found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation.  
136 Using three different measures of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$ ) as the response variable, the effect of  
137 sexual dichromatism was not significant in any PGLS model based on tip-rate estimates and correlation  
138 structures from the MCC tree. Specifically, sexual dichromatism showed no association with  $\lambda_{DR}$  ( $\beta =$   
139  $-1.279e-03$ ,  $p = 0.147$ ; [Figure 1a](#), [Figure 2a](#)) or  $\lambda_{ND}$  ( $\beta = -5.745e-05$ ,  $p = 0.078$ ; [Figure 1a](#)). Furthermore,  
140 speciation rates from BAMM ( $\lambda_{BAMM}$ ) were also unaffected by sexual dichromatism ( $\beta = -1.429e-05$ ,  $p =$   
141  $0.872$ ; [Figure 1a](#)). PGLS analyses using sexual dichromatism ( $n = 581$ ) measured by spectrophotometry  
142 (Armenta et al. 2008) yielded results concordant with the full dataset; *i.e.* no association between sexual  
143 dichromatism and speciation ([Figure S11](#)). Our results from models based on the MCC tree are largely  
144 corroborated by model estimates from PGLS analyses of the rates and correlation structures from 1,000 trees  
145 (for  $\lambda_{DR}$ ,  $\lambda_{ND}$ ) and 100 trees for  $\lambda_{BAMM}$ . The HPD intervals show model estimates are distributed around  
146 zero when using complete taxon sampling models and RGB measures of sexual dichromatism ([Figure 1a](#),  
147 [Table S8](#)). For PGLS models using spectrophotometry-based measures of sexual dichromatism, the estimates  
148 from the 100 trees in the  $\lambda_{DR}$  models are positively skewed (HPD Interval =  $-1.780e-02$ ,  $3.489e-02$ ) but  
149 normally distributed around zero for  $\lambda_{ND}$  and  $\lambda_{BAMM}$  ([Table S12](#)).

150 Male-biased sexual selection increases speciation rate

151 We found a significant positive association between male-biased sexual selection ( $n = 2,465$ ) and  $\lambda_{DR}$  for  
152 the MCC tree ( $\beta = 3.887e-02$ ,  $p = 0.012$ ; [Figure 1b](#)). However, this association was not significant for the  
153 other two measures of speciation rate ( $\lambda_{ND}$ :  $\beta = 4.383e-04$ ,  $p = 0.351$ ;  $\lambda_{BAMM}$ :  $\beta = 9.423e-04$ ,  $p = 0.764$ ;  
154 [Figure 1b](#)). The distribution of estimates from PGLS models on 1,000 trees was similar to the estimate from  
155 the MCC tree: among the 1,000 trees there was a positive association between sexual selection and  $\lambda_{DR}$   
156 (HPD Interval =  $4.513e-03$ ,  $5.718e-02$ ), and a smaller positive association between sexual selection and  $\lambda_{ND}$   
157 (HPD Interval =  $-5.044e-04$ ,  $1.585e-03$ ; ) as well as the 100 models using  $\lambda_{BAMM}$  (HPD Interval =  $-1.295e-02$ ,  
158  $3.088e-02$ ). Complete HPD intervals for models using male-bias sexual selection PPCA as a predictor can be  
159 found within [Table S15](#).

160 Species with smaller ranges have increased rates of speciation

161 Based on  $\lambda_{DR}$  and  $\lambda_{ND}$  tip-rate metrics of speciation, we found a negative association between range size and  
162 speciation; that is, species with smaller ranges show marginally higher values for  $\lambda_{DR}$  and  $\lambda_{ND}$ . This negative  
163 association was small but significant for models using the MCC tree ( $\lambda_{DR}$ :  $\beta = -6.579e-03$ ,  $p = 0.001$ ;  $\lambda_{ND}$ :  
164  $\beta = -1.462e-04$ ,  $p = 0.034$ ; [Figure 1a](#), [Figure 2](#)). This association was also evident across the estimates from  
165 models using the 1,000 trees ( $\lambda_{DR}$ : HPD Interval =  $-8.871e-03$ ,  $-6.610e-04$ ;  $\lambda_{ND}$ : HPD Interval =  $-1.514e-04$ ,  
166  $1.724e-05$ ; [Figure 1a](#)). Subset models with reduced sample size and different measures of sexual selection —  
167 but the same measure of range size — showed equivocal evidence that range size is negatively associated  
168 with speciation. Range size significantly predicted  $\lambda_{DR}$  ([Figure 1b](#)) using data subset for male-biased sexual  
169 selection ( $n = 2,465$ ) but not  $\lambda_{ND}$  or  $\lambda_{BAMM}$ . Models using data subset for spectrophotometry-based  
170 dichromatism ( $n = 581$ ) gave non-significant estimates for the effect of range size on all measures of speciation

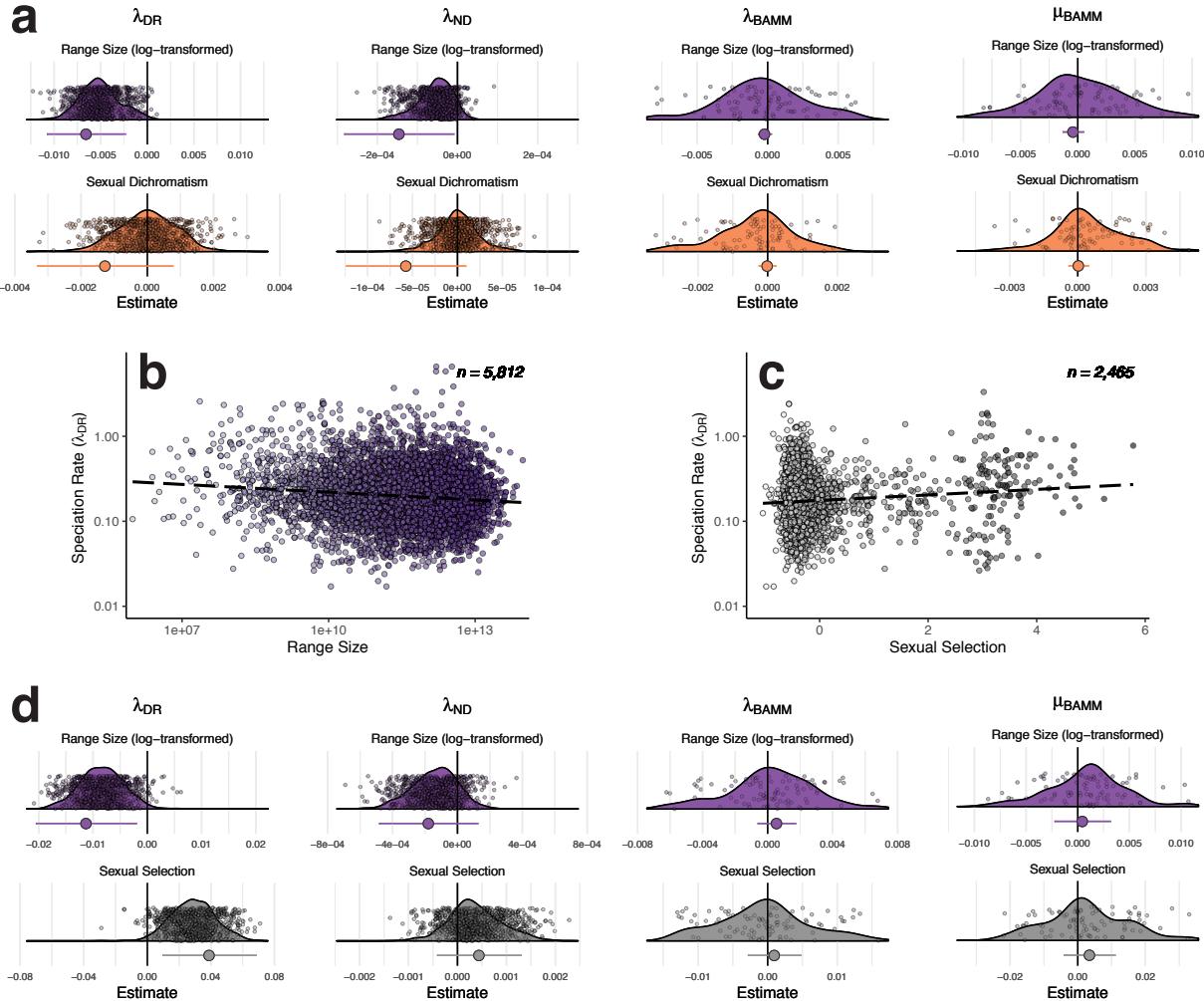
<sup>171</sup> (Figure S11, Table S11, Table S12). Because the range size dataset is the same across the three data subsets  
<sup>172</sup> we draw our conclusions from the models with the highest power using near-complete taxon sampling ( $n =$   
<sup>173</sup> 5,812).

<sup>174</sup> Phylogenetic path analysis

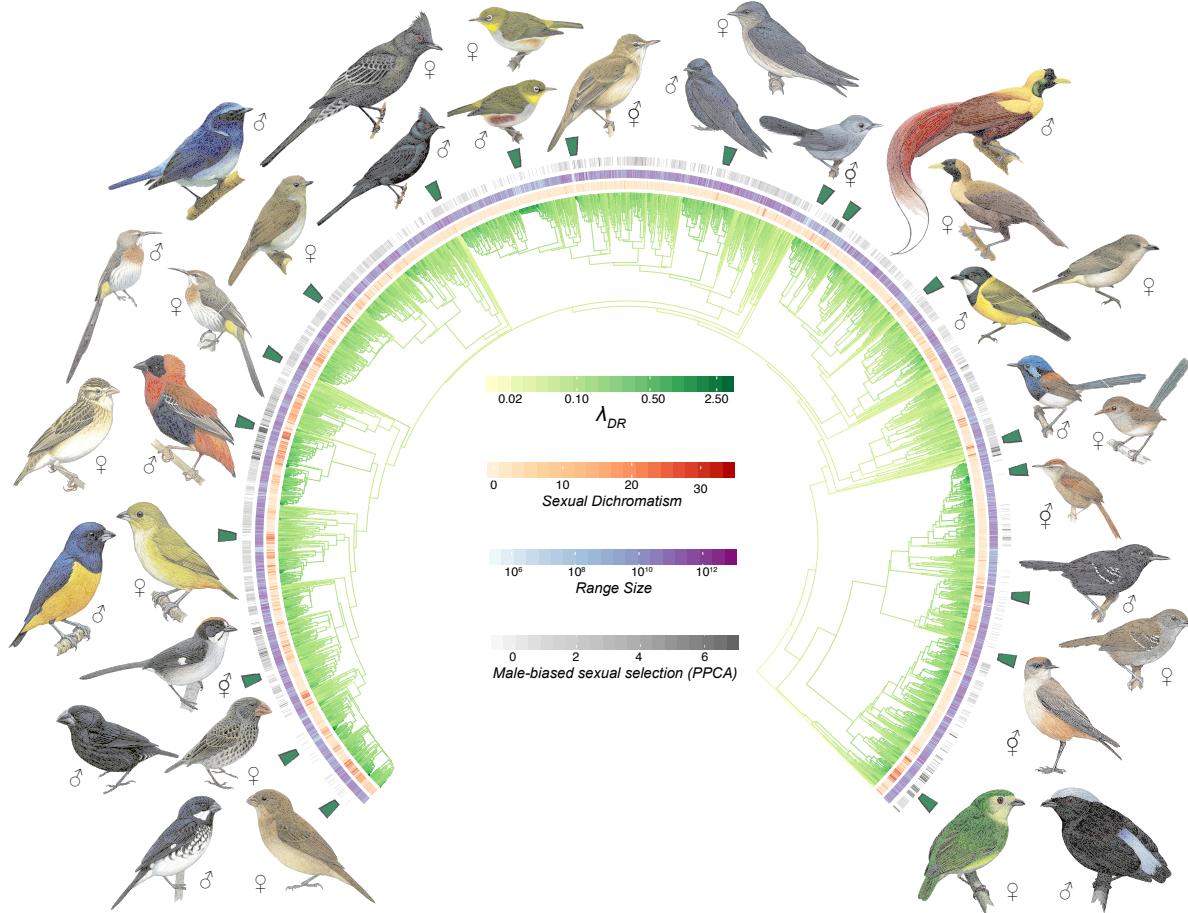
<sup>175</sup> Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS  
<sup>176</sup> (Figure 3; Figure S14). There was a modest effect of male-biased sexual selection on sexual dimorphism ( $\beta$   
<sup>177</sup> = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism ( $\beta = 0.07$ ) and strongly  
<sup>178</sup> affected range size ( $\beta = 0.52$ ). This suggests an indirect effect of temperature seasonality on  $\lambda_{DR}$  ( $\beta_{indirect} =$   
<sup>179</sup> -0.02; Figure 3), given the negative association we identified between  $\lambda_{DR}$  and range size in PGLS models.

<sup>180</sup> Extinction rate

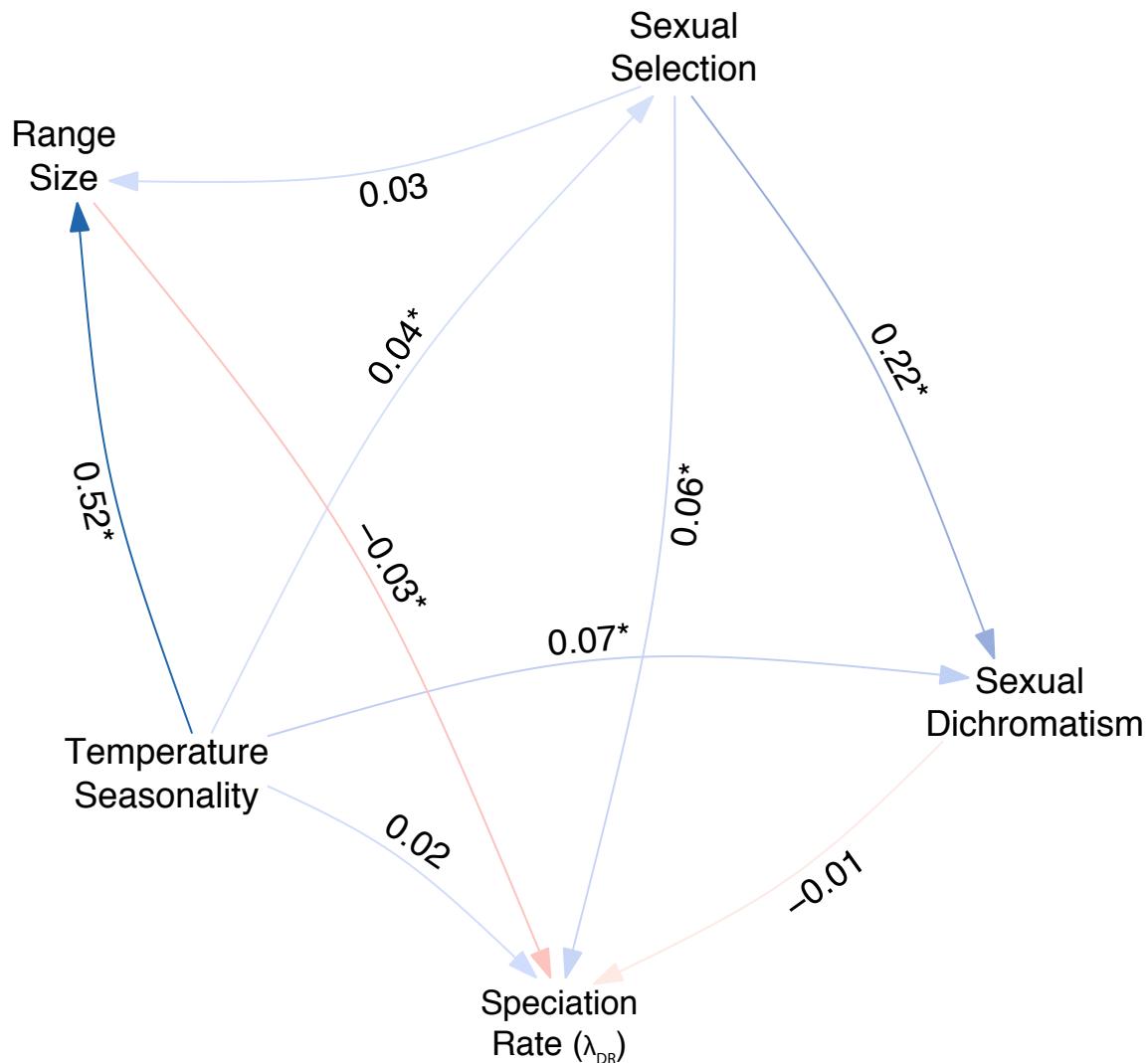
<sup>181</sup> We found no evidence that extinction ( $\mu_{BAMM}$ ) was impacted by the extent of sexual dichromatism for  
<sup>182</sup> full-taxon sampling ( $\beta = 2.385\text{e-}05$ ,  $p = 0.93$ ; Figure 1a), nor spectrophotometry-based measures of sexual  
<sup>183</sup> dichromatism (Figure S11, Table S11, Table S12) or male-biased sexual selection (Figure 1b, Table S14, Table  
<sup>184</sup> S15).



**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 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 random trees (for  $\lambda_{DR}$  and  $\lambda_{ND}$ ) or 100 random 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 random 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 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 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 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 male-biased sexual selection measures ( $n = 2,465$ ).

## 185 DISCUSSION

186 We found evidence that the composite index of male-biased sexual selection, but not measures of sexual  
187 dichromatism, is correlated with the rate of speciation in passerine birds. The absence of a detectable  
188 correlation between sexual dichromatism and speciation rate was consistent across different measures of  
189 speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$  and  $\lambda_{BAMM}$ ) and both measures of dichromatism (spectral and RGB), and it cannot  
190 be explained by a difference in statistical power since the sample size for the dichromatism analyses was much  
191 larger. These findings reaffirm the conclusions of previous, smaller studies in which sexual dichromatism was  
192 measured using spectrophotometry (Huang and Rabosky 2014) or human observers (Cooney et al. 2017).  
193 The correlation between speciation rate and the index of male-biased sexual selection (which encapsulates  
194 variation in sexual size dimorphism, social polygyny, and paternal care) was statistically significant for  
195  $\lambda_{DR}$ , but not for  $\lambda_{ND}$  and  $\lambda_{BAMM}$ , although the estimated direction and magnitude of the correlation was  
196 broadly similar across all three measures. Interestingly, we also found a consistent negative relationship  
197 between range size and speciation rate, at least when this rate was quantified using  $\lambda_{DR}$  and  $\lambda_{ND}$ . None  
198 of the bioclimatic measures of environmental variability that we investigated (*i.e.*, temperature seasonality,  
199 long-term temperature variation, and spatial temperature variation) significantly predicted speciation rate.  
  
200 The difference in findings between the analyses of sexual dichromatism *versus* the index of sexual selection  
201 is noteworthy, because the majority of earlier studies used dichromatism alone as their proxy for sexual  
202 selection (*e.g.*, Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang  
203 and Rabosky 2014). Given our findings, and the modest correlation between dichromatism and the sexual  
204 selection index ( $r = 0.34$ ; Dale et al. 2015), we hypothesise that sexual dichromatism may not be a robust  
205 proxy for sexual selection. Although dichromatism clearly reflects sexual selection to some extent, it is  
206 possibly that it is too indirect a measure to detect any association with speciation rate, even with a high  
207 sample size. There are several reasons why the use of sexual dichromatism as a proxy for sexual selection is  
208 problematic. Firstly, sexual dichromatism can evolve for reasons other than sexual selection, such as when  
209 males and females occupy different ecological niches (Wallace 1889; Kottler 1980; Slatkin 1984; Shine 1989) or  
210 experience different selective pressures in contexts other than competition for mates (Price and Eaton 2014).  
211 For example, in superb fairy-wrens (*Malurus cyaneus*) female colouration has probably evolved in response to  
212 spatial variation in predation pressure, increasing dichromatism (Medina et al. 2017). Ecological selection on  
213 sexual dichromatism was implicated by our path analysis, which found that sexual dichromatism is positively  
214 affected by temperature seasonality (a measure of environmental variation), albeit weakly. Secondly, colour is  
215 only one of the traits subject to sexual selection (Miles and Fuxjager 2018; Cally et al. 2019). For instance,  
216 sexual selection may promote investments in other mating signals (*e.g.* song) that trade-off against plumage  
217 colour, leading to variable investment in different sexually selected signals across species (Cooney et al.  
218 2018). Lastly, not all plumage colouration honestly reflects mate quality. A recent meta-analysis found that  
219 converted carotenoids (but not carotenoids sourced from the diet) predict mate quality through improvements  
220 in parasite resistance and reproductive success (Weaver et al. 2018). Thus, bright colours may signal direct  
221 benefits or ‘good genes’ in some species but not others, and some of the colours used to calculate dichromatism  
222 might be more functionally relevant than others.  
  
223 In-line with some theoretical predictions and previous studies (Kraaijeveld et al. 2011) we found that male-  
224 biased sexual selection increases speciation rate, at least when speciation is measured by  $\lambda_{DR}$ . Additionally,  
225 we found that this association appears to be independent of net primary productivity and spatiotemporal

226 variation in the environment. The lack of an effect of these environmental variables on speciation rate  
227 has several possible interpretations. Firstly, the effects of sexual selection on adaptation and speciation  
228 may depend on the type of environmental variability under which the species is evolving. Specifically,  
229 speciation rates might be impacted by genetic constraints on adaptation, that vary across environments.  
230 Theory suggests that sexual antagonism (which is often exacerbated in species with strong sexual selection)  
231 may be lower in habitats experiencing cyclical environmental variation (*e.g.* seasonality), relative to those  
232 experiencing directional change in the environment (Connallon and Hall 2016). Another possibility is that the  
233 environmental predictors we chose may not account for the key ecological sources of selection that interact  
234 with sexual selection to drive speciation. For example, our study does not include direct measure of food  
235 availability or the severity of predation and parasitism, which are both hypothesised to affect sexual selection  
236 and speciation (*reviewed in* Maan and Seehausen 2011). Finally, it is possible that environmental variability  
237 genuinely has little effect on speciation rates, at least in the taxa investigated here.

238 The most robust finding in our study is the finding that species with smaller ranges have elevated speciation  
239 rates. This result is similar to a study of 329 amphibian genera, which found higher diversification rates  
240 in taxa with smaller range size (Greenberg and Mooers 2017). Intuitively, large range size should promote  
241 speciation by creating more opportunities for geographic barriers to form (Rosenzweig 1995; Castiglione  
242 et al. 2017). However, the opposite pattern is also plausible because birds with limited dispersal or more  
243 specialised niches can have more fragmented populations, which would promote vicariant divergence and  
244 higher speciation rates (Jablonski and Roy 2003; Birand et al. 2012; Claramunt et al. 2012). **Please**  
245 **check this sentence, I didn't understand the original but I tried to re-draft for clarity** It is also  
246 possible that high speciation rates cause smaller range sizes, rather than the other way around, for example  
247 because repeatedly-speciating lineages tend to fill niches in ways that hinder the geographical expansion of  
248 new species (Rosenzweig 1995; Weir and Price 2011; Price and Eaton 2014). However, species undergoing  
249 adaptive radiation in new habitats are unlikely to be limited by competition for resources from existing  
250 taxa. Across islands, we expect to see a correlation between speciation and small range size because small  
251 islands often reflect newly formed environments with empty niches. **As a jerk reviewer, I would say**  
252 **“can’t you re-run it without the island radiations??”** Thus, our findings might be driven by island  
253 radiations (*e.g.* “Darwin’s finches”, *Geospiza* spp.). One further explanation for the negative association  
254 between range size and sexual dichromatism/sexual selection is the potential bias of taxonomic classification,  
255 whereby over-splitting of species in clades with large ranges leads to increased recent phylogenetic branching  
256 as well as smaller ranges.

257 In addition to speciation, sexual selection is hypothesised to affect extinction. Using the model-based  
258 approach of BAMM, we found no association between the estiamted extinction rate and sexual dichromatism,  
259 male-biased sexual selection, or our measures of environmental variability. However, these extinction results  
260 should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from  
261 phylogenies, principally because different combinations of speciation and extinction rates can give rise to  
262 similar patterns of diversity (see Rabosky 2016). Phylogenetic methods such as BAMM allow for speciation  
263 and extinction rates to be estimated using moderately-sized phylogenies, although the ability of BAMM to  
264 model evolutionary rate shifts and extinction rates is debated (*see*, Beaulieu and O’Meara 2015; Rabosky  
265 2016; Moore et al. 2016; Rabosky et al. 2017). Additionally, while several tip-rate estimates exist for  
266 speciation rate (*e.g.*,  $\lambda_{DR}$  and  $\lambda_{ND}$ ), tip-rate estimates of extinction rate are difficult to obtain without  
267 complex Bayesian models which are sensitive to sampling bias (Davis et al. 2013). Although extinction rates

268 can be inferred from alternative sources, such as the fossil record (Martins et al. 2018), direct observation  
269 extinction, or IUCN red list status (Greenberg and Mooers 2017), each approach has its limitations. Across  
270 the passerine bird phylogeny, we found that BAMM often produced homogeneous speciation and extinction  
271 rates for smaller clades showing few rate shifts, which might reduce our power to detect small differences  
272 in extinction rates among closely-related taxa (Rabosky et al. 2017; Title and Rabosky 2018). Thus, this  
273 methodological constraint likely decreases our ability to accurately measure the correlation between metrics  
274 of sexual selection and the probability of extinction.

275 One outcome of our analyses was that different measures of speciation rates presented different results.  
276 This is not completely surprising, because each of the rates is calculated differently (see Title and Rabosky  
277 (2018)). For instance,  $\lambda_{DR}$  is weighted more towards speciation events close to the tips and allows more rate  
278 heterogeneity compared to BAMM estimates. This leads to greater variation in  $\lambda_{DR}$  relative to the BAMM  
279 estimates, potentially explaining the difference in results. The BAMM estimates were also more sensitive to  
280 phylogenetic uncertainty.

281 To summarise, we have shown that male-biased sexual selection, but not sexual dichromatism, predicts  
282 speciation in passernines, and that this relationship is not markedly affected by environmental variability.  
283 These findings imply that sexual dechromatism is not a reliable proxy for sexual selection, and that alternative  
284 measures of sexual selection are more directly related to diversification. Our results also add indirect support  
285 to the hypothesis that sexual selection promotes adaptation, which has implications for conservation (Holman  
286 and Kokko 2013) and captive breeding programs for threatened species (Charge et al. 2014). Furthermore, our  
287 finding that high speciation rate is associated with smaller range size highlights the threat to the persistence  
288 of rapidly-speciating lineages in a world with increased habitat loss and anthropogenic stress. This concern  
289 arises as the best predictor of extinction risk is range size (Harris and Pimm 2008) and the association found  
290 here implies that many newly-speciated clades have small range sizes and could thus be at greater risk of  
291 extinction.

## 292 MATERIALS AND METHODS

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

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

#### 299 Sexual dichromatism

300 We used a previously-published measure of sexual dichromatism for 5,983 species of passerines (Dale et al.  
301 2015). Briefly, Dale et al. (2015) obtained sex-specific RGB (red-green-blue) values across six body patches  
302 (nape, crown, forehead, throat, upper breast, and lower breast) from *Handbook of the Birds of the World* (Del  
303 Hoyo et al. 2011). The relative contribution of male and female RGB colour values were averaged across  
304 body patches and provide ‘male-like’ and ‘female-like’ plumage scores. Here we use the absolute difference  
305 between male and female plumage scores as an estimate of sexual dichromatism. Additionally, we used  
306 another measure of dichromatism corresponding to colour distance in avian colour space derived from spectral  
307 data (Armenta et al. 2008). These measurements include variation in the ultraviolet and bird-visible range  
308 and — unlike the RGB measures — are sourced from museum specimens as opposed to illustrations. The  
309 spectrophotometry data covers only 581 passerine species (10-fold fewer than the RGB data), although there  
310 was a substantial correlation between the two dichromatism measures ( $r = 0.79$ ; [Figure S10](#)).

#### 311 Male-biased sexual selection

312 Because sexual dichromatism is presumably imperfectly correlated with variation in the strength of sexual  
313 selection across taxa, we sourced an additional measure of sexual selection, also from Dale et al. (2015),  
314 referred to here as the ‘index of male-biased sexual selection’. This index is the first principal component  
315 from a phylogenetic principal component analysis (PPCA) of three characteristics positively associated  
316 with sexual selection (sexual size dimorphism, social polygyny and [lack of] paternal care). This measure of  
317 male-biased sexual selection is available for only 2,465 species, and shows a moderate correlation with the  
318 RGB measure of sexual dichromatism ( $r = 0.34$ ; [Figure S12](#)).

#### 319 Environmental variables

320 We obtained estimates of species range size using expert range maps (BirdLife International and Handbook  
321 of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the *Birdlife* database  
322 (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual dichromatism  
323 dataset (Dale et al. 2015). From these distributions, we obtained estimates of climatic conditions that  
324 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19

325 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature  
326 and precipitation) with 30-second ( $\sim 1 \text{ km}^2$ ) spatial resolution (Fick and Hijmans 2017). From these values,  
327 we obtained means and standard deviations for each species. Using the same spatial sampling, we extracted  
328 means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial  
329 (LIG; 120,000 - 140,000 years ago; Otto-Bliesner et al. 2006). We include estimates of climate variability  
330 during recent evolutionary history as they may be a better indicators of environmental effects on speciation  
331 than present-day environmental variability. Furthermore, to estimate variability in the energy available to  
332 species, we obtained the mean and standard deviation of net primary productivity (NPP) values between  
333 2000 - 2015 across each species distribution. Estimates of NPP had 30-second resolution and were obtained  
334 through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production products stage 3  
335 (MOD17A3; Zhao et al. 2005). Using these data, which we provide as a potentially useful data resource  
336 (see [ESM](#)), we generated five predictors of speciation associated with different patterns in environmental  
337 variability (see below).

338 Generating biologically relevant predictors for environmental stress

339 Given that stressful environments are expected to interact with sexual selection and have a positive effect on  
340 adaptation (Cally et al. 2019), we used the extracted environmental variables from each species range size to  
341 create predictors of environmental variation/stress. Firstly we used (*i*) the average NPP in each species' range  
342 and (*v*) the log-transformed range size as potentially informative predictors of speciation rates. We also used  
343 three environmental predictors derived from bioclimatic data. These predictors relate to seasonal climate  
344 variation, spatial climate variation and long-term climate variation. To obtain seasonal climate variation we  
345 used (*iii*) mean values of temperature seasonality (BIO4) for each range. (*iV*) To estimate levels of spatial  
346 environmental variation a species may endure we used the first principle component (PC1) from a PCA  
347 on standard deviations from all bioclimatic variables, excluding temperature and precipitation seasonality  
348 (BIO 4 and BIO15). PC1 was heavily loaded towards bioclimatic variables relating to temperature, thus  
349 PC1 reflects the variation in temperature across a species' range ([Table S1](#)). Species range is a potentially  
350 informative predictor of speciation and extinction, so we controlled for the correlation between environmental  
351 spatial variation and range size — where larger ranges have larger variation in PC1 — by using the residuals  
352 of a fitted general additive model (GAM; [Figure S1](#)) as a predictor. To obtain long-term variation in climates  
353 for each species range we take (*v*) the first principal component of the absolute difference in the bioclimatic  
354 variables between the LIG and current values. Similar to spatial variation, the long-term climate variation is  
355 primarily loaded to temperature differences between the LIG and current climates ([Table S2](#), [Figure S2](#)).  
356 The five predictors of environmental variability are not strongly correlated ([Figure S3](#)). Details and R code to  
357 generate these predictors can be found within the [ESM](#).

358 Estimating extinction and speciation

359 Phylogenetic information was obtained from [www.birdtree.org](http://www.birdtree.org) (Jetz et al. 2012). We used a maximum clade  
360 credibility (MCC) tree from 2,500 samples of the posterior distribution ( $n = 5,965$ ) as the main phylogenetic  
361 hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without  
362 genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using

363 tip-rate measures (1000 trees) and BAMM (100 trees)(Rabosky 2014). These trees used a ‘Hackett backbone’  
 364 (Hackett et al. 2008) and were constructed using a pure birth (Yule) model. We calculated three different  
 365 tip-rate metrics of speciation and one of extinction across all trees.

366 Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes  
 367 and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating  
 368 the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES),  
 369 also known as diversification rate (DR) (*e.g.*, Jetz et al. 2012; Quintero and Jetz 2018; Rabosky et al. 2018),  
 370 is derived from the sum of edge lengths branching from a node, with each edge towards the root having  
 371 the length down-weighted. Studies have suggested that DR and ND (henceforth referred to as  $\lambda_{DR}$  and  
 372  $\lambda_{ND}$ ) are more reflective estimates of speciation than diversification; this is because  $\lambda_{DR}$  and  $\lambda_{ND}$  cannot  
 373 account for whole-clade extinctions and thus under-estimate extinction rate, which makes the composite  
 374 measure of diversification more dependent on speciation (Belmaker and Jetz 2015; Title and Rabosky 2018).  
 375 Therefore,  $\lambda_{DR}$  is a measure of speciation rate more heavily weighted to recent speciation events while  $\lambda_{ND}$   
 376 measures speciation across the root-to-tip path. These tip-rate measures are alternatives to state-dependent  
 377 diversification models such as Quantitative State Speciation-Extinction (QuaSSE); but, based on previous  
 378 simulation studies,  $\lambda_{DR}$  and  $\lambda_{ND}$  are robust and intuitive measures that provide high power and low false  
 379 discovery rate with large phylogenies when incorporated into Phylogenetic Generalized Least Squares (PGLS)  
 380 models (Harvey Michael et al. 2017).

381 Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic  
 382 trees (Rabosky 2014). This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo)  
 383 to generate probability distributions of evolutionary rate-shift configurations with variable speciation and  
 384 extinction rates. Importantly, these models provide tip-rate estimates of speciation and extinction rate. The  
 385 parameters of the 100 BAMM runs are detailed in full in the [ESM](#); briefly, we used a time-variable model with  
 386 100 expected number of shifts and prior rates set from the initial speciation and extinction values using the  
 387 `BAMMtools` R package (Rabosky et al. 2014). Each BAMM model (one MCC tree and 100 random draws of  
 388 the posterior) was run for 100 million generations, and given the computationally intensive nature of BAMM,  
 389 runs were conducted across multiple CPUs. Each run of BAMM reached convergence with effective sample  
 390 size (ESS) of MCMC (Markov Chain Monte Carlo) samples surpassing 200 (an arbitrary value, above which  
 391 posterior distributions can often be accurately inferred) for the key model parameters of log-likelihood and  
 392 number of rate shifts ([Table S3](#), [Table S4](#)). Further details of BAMM parameters and output are available in  
 393 the [ESM](#), with tip-rate means and variances provided. Additionally, given the variability in BAMM estimates,  
 394 we also provide analysis of BAMM shift configurations and tip-rate estimates from our run on the MCC  
 395 tree and within a BAMM run on the MCC tree from a genetic-only phylogeny across all birds (Harvey et al.  
 396 2017). All analyses were conducted on log-rates.

## 397 Phylogenetic comparative analysis

398 To test the association between speciation/extinction and sexual selection, environmental variability and  
 399 their interaction, we used phylogenetic least squares (PGLS) models in the `nlme` package (Pinheiro et al.  
 400 2018). Firstly, we conducted model selection to compare models in which  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  or  $\mu_{BAMM}$   
 401 were the response variable: these tip-rate estimates all came from the same MCC tree (derived from 2,500  
 402 draws of the posterior distribution in Jetz et al. (2012)). For models of  $\lambda_{BAMM}$  and  $\mu_{BAMM}$  we used the

403 inverse of the variance associated with each tip rate estimate as weights, to account for the variable precision  
404 of the estimates provided by BAMM. The most complicated model in each set under comparison contained  
405 one of the measures of sexual selection (sexual dichromatism or the index of male-biased sexual selection),  
406 all of the environmental measures (*i.e.* log-transformed range size, seasonal temperature variation, spatial  
407 temperature variation, long-term temperature variation, and NPP), and all of the 2-way interactions between  
408 sexual selection and each of the environmental measures. The simpler models contained all of the same main  
409 effects, but had fewer 2-way interaction terms (potentially none). Model selection was done in MuMIn using  
410 the `dredge` function (Bartoń 2017). Using the terms from the top-ranked model (ranked by AICc), we ran the  
411 equivalent model for each of the 1,000 phylogenetic trees used to derive  $\lambda_{DR}$ ,  $\lambda_{ND}$  and each of the 100 trees  
412 used to derive  $\lambda_{BAMM}$  and  $\mu_{BAMM}$ . In each model we used the unique response variables and phylogenetic  
413 tree correlation structure. Specifically, for models using tip-rate metrics ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ) we estimated the  
414 phylogenetic signal — Pagel's  $\lambda$  (Pagel 1999) — using the `corPage1` function in the `ape` package (Paradis et  
415 al. 2004) independently for each of the 1,000 trees/models. Alternatively, for models using speciation and  
416 extinction estimates derived using BAMM ( $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ) we found  $\lambda$  was consistently estimated at 1  
417 and hence assumed Brownian motion (using the `corBrownian` function) to estimate the correlation structure.  
418 This method enabled us to present model estimates for an MCC tree alongside 1,000/100 trees from the  
419 posterior distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three  
420 datasets corresponding to each measure of sexual selection: dichromatism derived from RGB values of images  
421 ( $n = 5,812$ ); dichromatism from spectrophotometry ( $n = 581$ ) and the multivariate measure of male-biased  
422 sexual selection ( $n = 2,465$ ).  
423 Finally, using the subset of species with measurements of male-biased sexual selection, we conducted a  
424 phylogenetic path analysis using the `phylopath` R package (Bijl 2018). The phylogenetic path analysis was  
425 used to assess causal paths *between* variables not able to be modelled within the univariate response of  
426 PGLS. That is, a phylogenetic path analysis allowed us to model relationships between the predictor variables  
427 used in our PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection, and  
428 range size to have effects on each other and not just on speciation rate. To minimise path complexity we  
429 used temperature seasonality (BIO4) as the single measure for environmental variability,  $\lambda_{DR}$  as the single  
430 measure of speciation and the tip-rates from the MCC tree. Further details of the path analysis, including  
431 our rationale for each path's directions, can be found within the ESM along with all other analyses and the  
432 relevant R code to reproduce results.

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