

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

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

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

4           Abstract

5           Sexual selection can shape phylogenetic diversity by affecting speciation or extinction rates. The predicted  
6           effects on diversity are often contradictory; for example, sexual selection might promote speciation by  
7           creating reproductive isolation, or hinder it by selecting for traits that facilitate gene flow. Here, we  
8           investigate the relationship between sexual selection and diversification in passerine birds. Multiple studies  
9           use sexual dichromatism as a proxy for sexual selection, however, this relationship can be weak in many  
10          clades. Thus, we use two measures of sexual selection — sexual dichromatism and a multivariate measure  
11          of male-biased sexual selection — to test the link between sexual selection and diversification. We also  
12          test whether the effect of sexual selection on diversification is contingent on ecological variables. Our  
13          results show that male-biased sexual selection, but not sexual dichromatism, can explain speciation rates  
14          ( $\lambda_{DR}$ ) in passerines. We also find that birds with smaller ranges have higher speciation rates, but there  
15          is no interaction between environmental variables and sexual selection. Our findings show that sexual  
16          dichromatism is a poor proxy for sexual selection at least a a broad-scale, and support the view that  
17          sexual selection is an evolutionary force shaping patterns of diversity amongst songbirds.

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

---

§School of BioSciences, The University of Melbourne, Victoria, Australia.

## 19 INTRODUCTION

20 Sexual selection results from competition between same-sex individuals for mates, their gametes, or associated  
21 resources, and is typically stronger in males than females (Kokko and Jennions 2008; Fromhage and Jennions  
22 2016; Janicke et al. 2016). There is long-standing interest in the relationship between sexual selection and the  
23 processes of speciation, extinction, and diversification (e.g. Lande 1981, 1982). Experimental work suggests  
24 that sexual selection shapes the evolution of many different traits — not only the obvious ones such as  
25 courtship songs or antlers (Cally et al. 2019) — while some evolutionary comparative analyses have found  
26 that variation in sexual selection between clades predicts phylogenetic diversity. For instance, in antbirds  
27 (Thamnophilidae), genera with complex songs and pronounced sexual dichromatism are more species-rich  
28 (Seddon et al. 2008). ADD ONE MORE EXAMPLE IF POSSIBLE

29 Several hypotheses predict a positive relationship across clades between the strength of sexual selection  
30 and the diversification rate (or the amount of extant phylogenetic diversity). For example, sexual selection  
31 is the mechanism underlying reinforcement, a speciation-promoting process in which members of different  
32 phylogenetic lineages evolve to avoid unproductive inter-lineage mating/fertilisation (**REFERENCES**).  
33 Additionally, sexual selection often operates on traits that can create reproductive isolation when they differ  
34 between lineages, such as sexual signals and preferences, sperm-egg interactions, or genitalia (**Safran\_2013?**,  
35 **MORE - Lande (1981); Lande (1982) ?**). Furthermore, sexual selection is hypothesised to increase  
36 diversification by maintaining trait combinations that would be disadvantageous under pure natural selection  
37 (**REFS - Bonduriansky\_2011 & Radwan\_2016? NB I think the journal name might be wrong**  
38 **for Radwan\_2016, it's probably JEB**), and by helping to prevent extinction by purging deleterious  
39 mutations (Agrawal 2001; Siller 2001), fixing beneficial ones (Whitlock 2000), and accelerating the rate at  
40 which populations can adapt to novel environments (Lorch et al. 2003; Candolin and Heuschele 2008; Cally  
41 et al. 2019). Also, sexual selection is sometimes diversifying (as opposed to directional or stabilising), for  
42 example when individuals with rare phenotypes have elevated mating success (**REFS? - Holman et al**  
43 **BMC Evol Biol 2009 about Crozier's paradox is one, and likely has some refs in it**): diversifying  
44 selection promotes speciation by increasing the rate at which isolated populations become genetically distinct.  
45 Conversely, there are multiple ways in which sexual selection is hypothesised to reduce the diversification  
46 rate. Firstly, sexual selection can make extinction more likely by favouring traits that improve mating  
47 success but reduce population fitness. For example, species with expensive sexual signals may be less resilient  
48 to environmental change (Kokko and Brooks 2003), and sexual selection often creates a ‘tragedy of the  
49 commons’ by selecting for traits that increase the mating success of individuals while reducing population-wide  
50 productivity (e.g. infanticide, harassment, and reduced parental care in mate-seeking males; Rankin et al.  
51 2011; Holman and Kokko 2013). Sexual selection might also promote extinction by causing maladaptation  
52 (‘gender load’) in female traits that are genetically correlated with sexually-selected male traits (Pischedda and  
53 Chippindale 2006; Bonduriansky and Chenoweth 2009; Pennell and Morrow 2013; Berger et al. 2014) **Add**  
54 **paper with Mikatake, Hosken and other. Current Biology, about selection on a male trait in**  
55 **beetles constraining female trait evolution even tho the male trait is male-only.** Secondly, sexual  
56 selection might decrease the speciation rate by ensuring that individuals with novel trait values have low  
57 reproductive success.  
58 Importantly, the relationship between sexual selection and diversification may depend on the environment.

59 Some theoretical and empirical results suggest that sexual selection has a more positive effect on adaptation  
60 and population fitness in variable relative to stable environments (Long et al. 2012; Berger et al. 2014;  
61 Connallon and Hall 2016; Martinossi-Allibert et al. 2017; Cally et al. 2019). The hypothesised mechanism  
62 is that stable environments lead to the erosion of genetic variation at sexually concordant loci (*i.e.* loci  
63 where the fittest allele is the same in both sexes), while sexually antagonistic loci remain comparatively  
64 genetically variable, reducing the genetic correlation between male and female fitness. In turn, this means  
65 that the most attractive members of the more competitive sex (typically males) produce less fit offspring  
66 of the demographically important sex (usually female), such that sexual selection is less likely to favour  
67 female-detrimental, extinction-promoting alleles in variable environments. Furthermore, sexual selection  
68 might be especially helpful in preventing extinction in variable environments, because (in the words of Charles  
69 Darwin), “sexual selection will give its aid to ordinary selection, by assuring to the most vigorous and best  
70 adapted males the greatest number of offspring” (DARWIN REF; see also Agrawal (2001); Siller (2001);  
71 Boughman (2002); Maan and Seehausen (2011); ALSO KOKKO + HEUBEL 2008 model about GxE).

72 Birds have been a popular focus for macroevolutionary studies of sexual selection and diversification (*e.g.*,  
73 Barraclough et al. 1995; Morrow et al. 2003; Seddon et al. 2008, 2013; Huang and Rabosky 2014). Birds are  
74 well-suited for this questions as their phylogenetic relationships are comparatively well-known, and they have  
75 diverse mating systems and conspicuous sexually-selected traits such as song and colourful plumage. A 2011  
76 meta-analysis, covering 20 studies of birds and other taxa, found a small but significant positive association  
77 between sexual selection and speciation, with the average effect size in birds stronger than in mammals but  
78 weaker than in insects and fish (Kraaijeveld et al. 2011). However, the meta-analysis found large variation in  
79 effect sizes between studies, likely because of differences in the metrics used as estimates of speciation and  
80 the strength of sexual selection. More recently, Huang and Rabosky (2014) found no association between  
81 sexual dichromatism and speciation ( $n = 918$  species) in a study using spectrophotometric measurements of  
82 museum specimens (Armenta et al. 2008) and tip-rate estimates from a molecular-only phylogeny (Jetz et al.  
83 2012). Similarly, Cooney et al. (2017) found no effect of sexual dichromatism on diversification across 1,306  
84 pairs of species, using dichromatism scores from human observers.

85 Here, we investigate the association between sexual selection and diversification in birds while extending  
86 previous work in multiple ways. Firstly, multiple macroevolutionary studies estimate the strength of sexual  
87 selection using proxies such as sexual size dimorphism or dichromatism, but sexual selection in birds can  
88 involve many other traits, such as song, or the use of ornaments like long tail feathers, bows, crests and  
89 displays (*e.g.*, Uy and Borgia 2000; Pryke et al. 2001). In fact, it was recently highlighted that song divergence  
90 is inversely correlated with sexual dichromatism in passerines, suggesting that a focus on one signalling  
91 modality may cause the mismeasurement sexual selection (Cooney et al. 2018). Our study compares the  
92 role of sexual dichromatism and other sexual selection proxies in the **generation of species (Really?**  
93 **Isn't the composite of speciation and extinction?)**. Additionally, we test the relative effect of some  
94 ecological and environmental variables (**I say “ecological” because of range size**) on diversification,  
95 and how environment and sexual selection could interact to drive speciation processes (Long et al. 2012;  
96 Connallon and Hall 2016).

97 To test the link between different measures of sexual selection and diversification processes we use a large ( $n$   
98 = 5,812) dataset of sexual dichromatism (estimated from illustrations; Dale et al. 2015), as well as a smaller  
99 but still substantial dataset ( $n = 2,465$ ) that gives a composite measure of male-biased sexual selection,  
100 capturing variation in sexual dimorphism, social polygyny and [lack of] paternal care (Dale et al. 2015). These

101 datasets allow us to cover the majority of bird genera. Additionally, we use multiple metrics for estimating  
102 speciation and extinction rates at the tips of phylogenetic trees, including BAMM (Bayesian Analysis of  
103 Macroevolutionary Mixtures; *see*, Beaulieu and O'Meara 2015; Rabosky 2016; Moore et al. 2016; Rabosky et  
104 al. 2017), as well as older but reliable tip-rate statistics, such as diversification rate ( $\lambda_{DR}$ ) and node density  
105 ( $\lambda_{ND}$ ).

## 106 RESULTS

### 107 Variability across phylogenetic hypotheses and measures of speciation

108 Estimates of speciation rates varied across phylogenetic trees, especially in the BAMM rates ( $\lambda_{BAMM}$  and  
109  $\mu_{BAMM}$ ), where the 95 % highest posterior density (HPD) interval across 100 trees was more than 20 times  
110 larger than the 95 % confidence interval calculated for the MCC tree. This contrasts with variation across  
111 trees for the other rate estimates ( $\lambda_{DR}$  and  $\lambda_{ND}$ ), where the 95 % HPD interval across 1,000 trees was near-  
112 equivalent to the 95 % confidence interval calculated for the MCC tree ([Table S9](#)). Given the computational  
113 requirements of BAMM, the great majority of studies only derive estimates for a single consensus tree; so the  
114 high variability in BAMM estimates among trees is notable. Mean measures of speciation across 100 trees  
115 were positively correlated between measures (DR - BAMM:  $r=0.75$ , DR - ND:  $r=0.65$ , ND- BAMM:  $r=0.51$ ;  
116 [Figure S15](#)). Given that the calculation of BAMM rates can be affected by the settings of the run and the  
117 use of different priors, we compared the estimate of our MCC tree with that of previous published analyses  
118 on birds, and found a high correlation ( $r=0.81$ , [Figure S8](#)). Details of the BAMM results are presented in the  
119 supplementary materials.

### 120 Effects of sexual dichromatism/selection on speciation do not depend on en- 121 vironmental variability

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

132

133 No evidence that sexual dichromatism affects speciation

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

149 Male-biased sexual selection increases speciation

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

159 Species with smaller ranges have increased rates of speciation

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

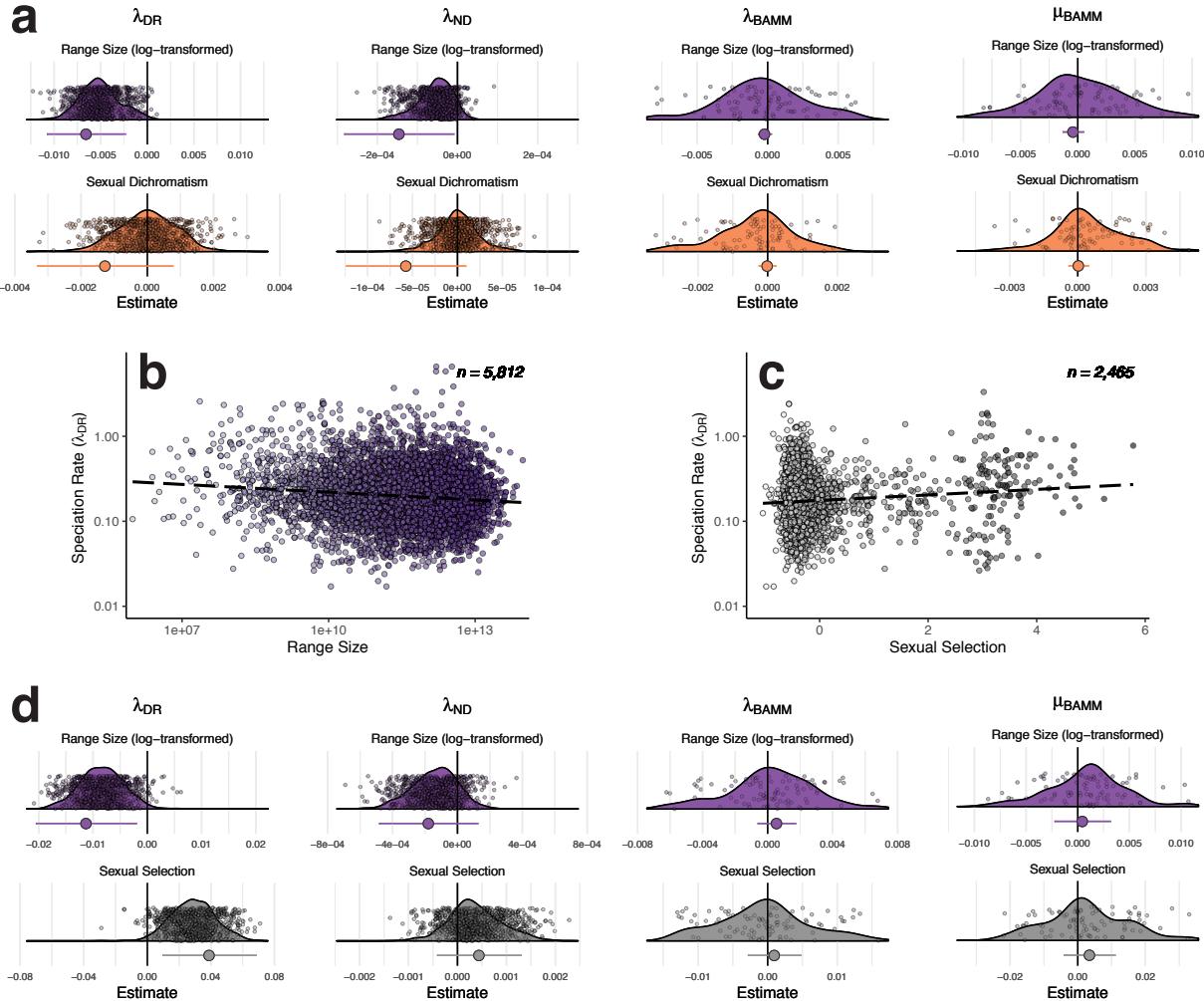
<sub>170</sub> (Figure S11, Table S11, Table S12). Because the range size dataset is the same across the three data subsets  
<sub>171</sub> we draw our conclusions from the models with the highest power using near-complete taxon sampling ( $n =$   
<sub>172</sub> 5,812).

<sub>173</sub> Phylogenetic path analysis

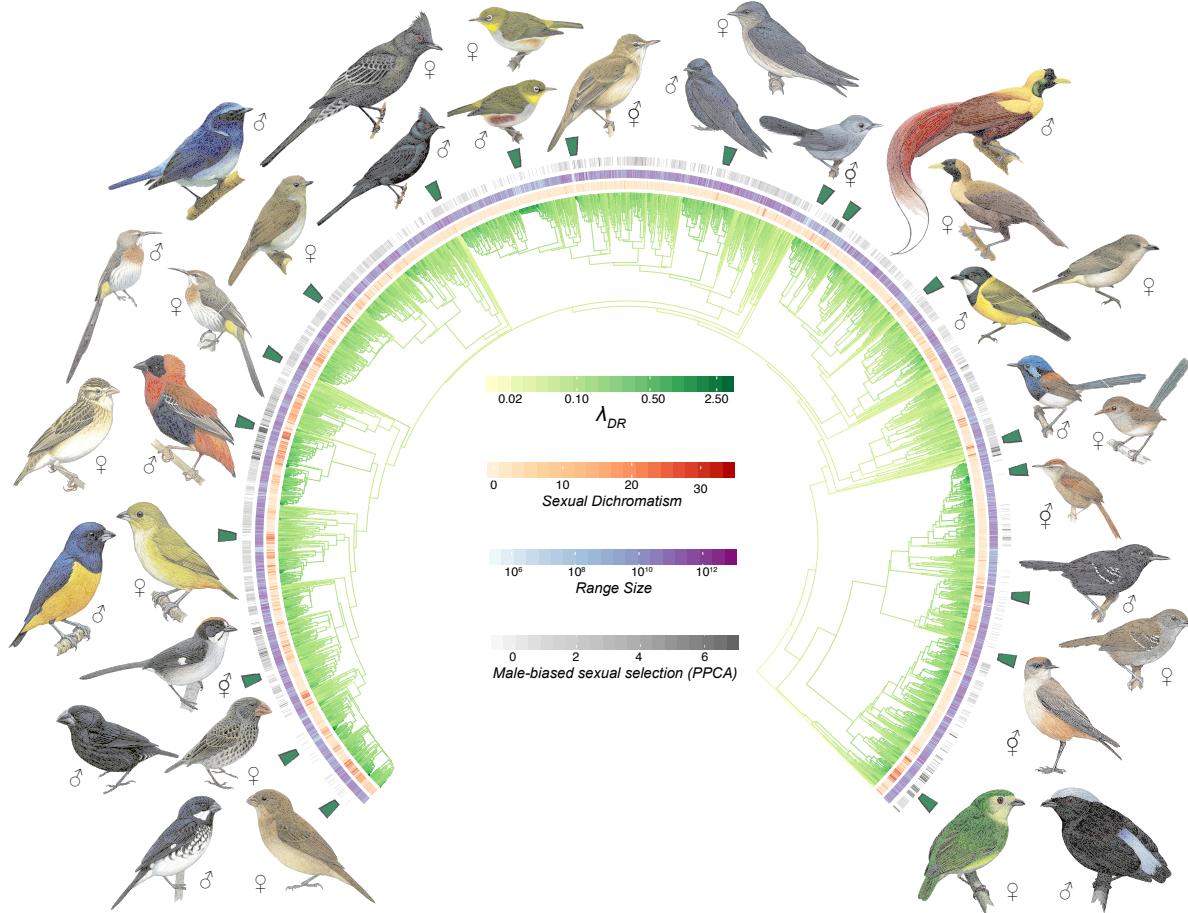
<sub>174</sub> Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS  
<sub>175</sub> (Figure 3; Figure S14). There was a modest effect of male-biased sexual selection on sexual dimorphism ( $\beta$   
<sub>176</sub> = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism ( $\beta = 0.07$ ) and strongly  
<sub>177</sub> affected range size ( $\beta = 0.52$ ). This suggests an indirect effect of temperature seasonality on  $\lambda_{DR}$  ( $\beta_{indirect} =$   
<sub>178</sub> -0.02; Figure 3), given the negative association we identified between  $\lambda_{DR}$  and range size in PGLS models.

<sub>179</sub> Extinction rate

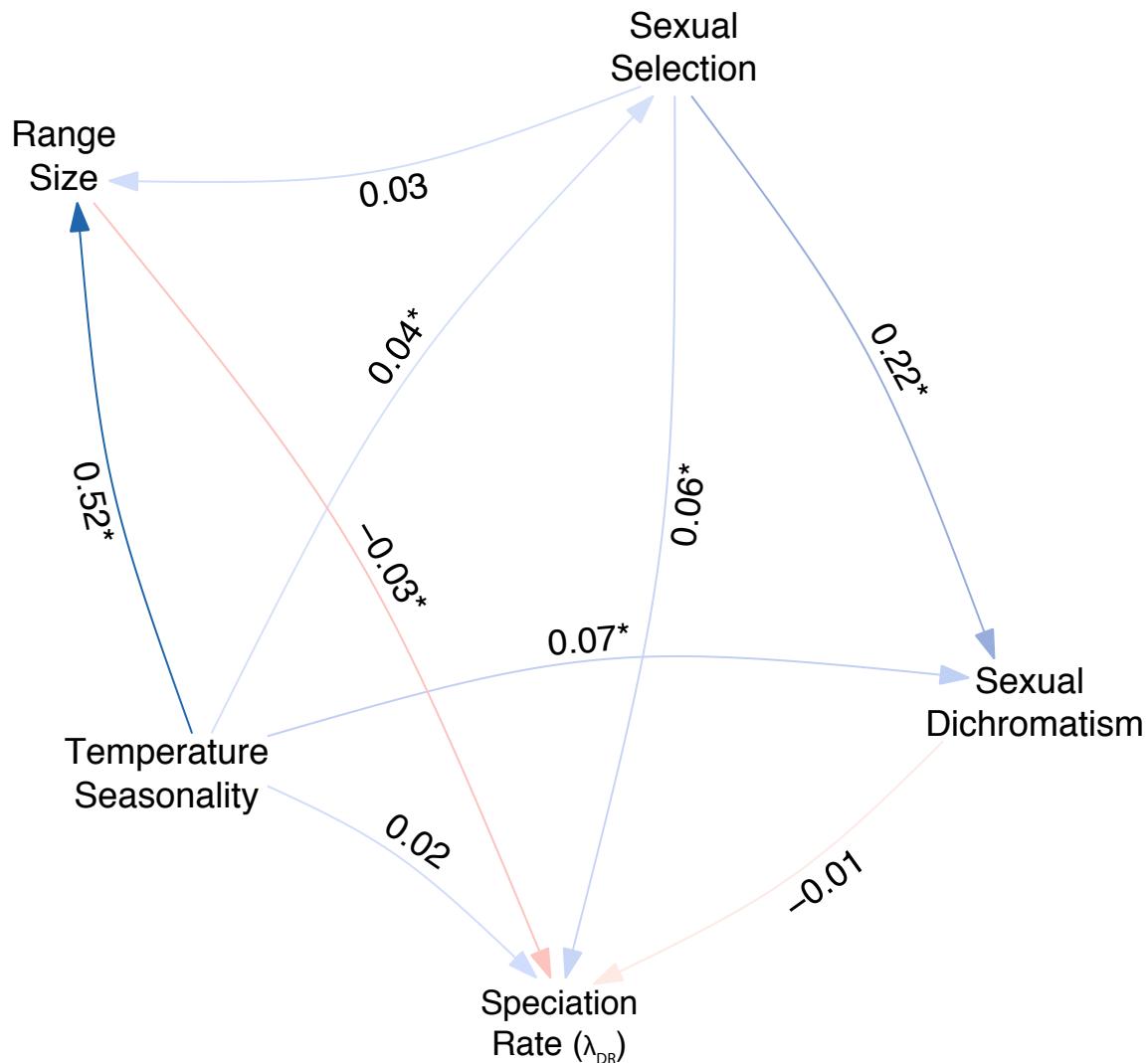
<sub>180</sub> We found no evidence that extinction ( $\mu_{BAMM}$ ) was impacted by the extent of sexual dichromatism for  
<sub>181</sub> full-taxon sampling ( $\beta = 2.385\text{e-}05$ ,  $p = 0.93$ ; Figure 1a), nor spectrophotometry-based measures of sexual  
<sub>182</sub> dichromatism (Figure S11, Table S11, Table S12) or male-biased sexual selection (Figure 1b, Table S14, Table  
<sub>183</sub> 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 ( $n = 2,465$ ).

## 184 DISCUSSION

185 We found evidence that the composite measure of male-biased sexual selection, but not the measure of sexual  
186 dichromatism, explains variation in the rate of speciation in passerine birds. The absence of a detectable  
187 correlation between sexual dichromatism and speciation rate was consistent across different measures of  
188 speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$  and  $\lambda_{BAMM}$ ) and both measures of dichromatism (spectral and RGB). These findings  
189 substantiate previous studies performed at smaller scales in birds, where sexual dichromatism measures were  
190 obtained using spectrophotometry (Huang and Rabosky 2014) and human observers (Cooney et al. 2017)  
191 and no association was found. The correlation between speciation rate and the index of male-biased sexual  
192 selection (which reflects sexual size dimorphism, social polygyny, and [lack of] paternal care) was statistically  
193 significant for  $\lambda_{DR}$ , but not for  $\lambda_{ND}$  and  $\lambda_{BAMM}$ , although the estimated direction and magnitude of  
194 the correlation was broadly similar across all speciation measures. Interestingly, we found a consistent  
195 negative relationship between range size and speciation rates, at least when this rate was quantified by  
196  $\lambda_{DR}$  and  $\lambda_{ND}$ . This suggests that species with smaller range sizes have increased speciation rates. None  
197 of the bioclimatic measures of environmental variability that we investigated (*i.e.*, temperature seasonality,  
198 long-term temperature variation, and spatial temperature variation) predicted speciation rate.

199 The association between sexual selection and sexual dichromatism in birds is a Darwinian trope (Darwin 1871)  
200 that allows it to be commonly used as a proxy for the strength of sexual selection in comparative studies (*e.g.*,  
201 Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky  
202 2014). Despite the association between sexual selection and sexual dichromatism in passerine birds (Dale et al.  
203 2015)— $r = 0.34$ —we find that sexual dichromatism does not predict any measure of speciation rate, whereas  
204 male-biased sexual selection predicts  $\lambda_{DR}$ . Given our results, we suggest that sexual dichromatism may not be  
205 a robust proxy for sexual selection at least at this broad scale, and that variation in the association between  
206 dichromatism and the strength of sexual selection may obscure any relationship with speciation rate, despite  
207 the high power of our comparative study. There are several reasons why the use of sexual dichromatism as  
208 a proxy for sexual selection is problematic. Firstly, sexual dichromatism can evolve for reasons other than  
209 sexual selection, such as when males and females occupy different ecological niches (Wallace 1889; Kottler  
210 1980; Slatkin 1984; Shine 1989) or experience different selective pressures in contexts other than competition  
211 for mates (Price and Eaton 2014). For example, in superb fairy-wrens (*Malurus cyaneus*) female colouration  
212 has probably evolved in response to spatial variation in predation pressure, increasing dichromatism (Medina  
213 et al. 2017). Ecological selection on sexual dichromatism was implicated by our path analysis, which found  
214 that sexual dichromatism is positively affected by temperature seasonality (a measure of environmental  
215 variation), albeit weakly. Secondly, colour is but one trait and sexual selection may drive the evolution of sex  
216 differences in a wide variety of traits used in mate choice or intrasexual competition (Miles and Fuxjager  
217 2018). For instance, sexual selection may promote investments in other mating signals (*e.g.* song) that  
218 trade-off against plumage colour, leading to variable investment in different sexually selected signals across  
219 species (Cooney et al. 2018). Lastly, not all plumage colouration honestly reflects mate quality. A recent  
220 meta-analysis found that converted carotenoids (but *not* carotenoids sourced from the diet) predict mate  
221 quality through improvements in parasite resistance and reproductive success (Weaver et al. 2018). Given  
222 the importance of honest signaling in sexual selection and the variability in colour production mechanisms  
223 across birds, sexual dichromatism in many species may be an unreliable measure of mate quality for female  
224 birds and sexual selection for researchers.

225 In-line with some theoretical predictions and previous studies (Kraaijeveld et al. 2011) we found that  
226 male-biased sexual selection increases speciation rate, at least for  $\lambda_{DR}$  estimates. Additionally, we found  
227 that this association appears to be independent of net primary productivity and spatiotemporal variation  
228 in the environment. The lack of an effect of these environmental variables on speciation rate (either alone  
229 or in combination with sexual selection) has several possible interpretations. Firstly, the effects of sexual  
230 selection on adaptation and thus speciation may depend on the type of environmental variability under  
231 which the species is evolving. Specifically, speciation rates may be impacted by genetic constraints on  
232 adaptation, that vary across environments. Theory suggests that sexual antagonism (often arising from  
233 increased sexual selection) may be easily purged in environments where pressures are cyclic (*e.g.* seasonality),  
234 whereas when environmental variability is directional (*e.g.* long-term climate change) sexual antagonism can  
235 indefinitely limit adaptation rates (Connallon and Hall 2016). Another possibility is that the environmental  
236 predictors used here may not account for the key ecological forces/natural selection pressures that interact  
237 with sexual selection to drive speciation. Specifically, access to dietary resources and the impacts of predation  
238 or parasitism are unaccounted for here. These are likely key processes affecting sexual selection and speciation  
239 (*reviewed in* Maan and Seehausen 2011). Finally, it is also possible that there is no effect of environmental  
240 variability on speciation rates; at least not in the species investigated here.

241 The most consistent finding uncovered in this comparative analysis is that smaller range sizes are associated  
242 with increased speciation rates. Intuitively, large range size should promote speciation by creating greater  
243 opportunities for geographic barriers to form (Rosenzweig 1995; Castiglione et al. 2017). However, the opposite  
244 pattern has also been suggested because birds with limited dispersal or more specialised niches can have more  
245 fragmented populations, which would promote vicariant divergence and higher speciation rates (Jablonski  
246 and Roy 2003; Birand et al. 2012; Claramunt et al. 2012). In amphibians (329 genera) diversification was  
247 shown to be higher in taxa with smaller range size (Greenberg and Mooers 2017). Alternatively, smaller  
248 range size may be correlated but not causally related to speciation. Under this view, high speciation rate  
249 may lead to smaller range sizes as niche filling by recently diverged species will suppress the expansion of  
250 newly speciated relatives (Rosenzweig 1995; Weir and Price 2011; Price and Eaton 2014). However, species  
251 undergoing adaptive radiation in new niches are unlikely to be limited by competition for resources from  
252 existing taxa. Across islands, we expect to see a correlation between speciation and small range size because  
253 small islands often reflect newly formed environments with empty niches. Thus, our findings could be heavily  
254 dependent on island radiations (*e.g.* “Darwin’s finches”, *Geospiza* spp.). One further explanation for the  
255 negative association between range size and sexual dichromatism/sexual selection is the potential bias of  
256 taxonomic classification, whereby over-splitting of species in clades with large ranges leads to increased recent  
257 phylogenetic branching as well as smaller ranges.

258 One outcome of our analyses was that different measures of speciation rates presented different results. This  
259 is not completely unexpected, given that each of the rates is calculated in a different way (discussed in detail  
260 in Title and Rabosky (2018)). For instance,  $\lambda_{DR}$  is weighted more towards speciation events close to the  
261 tips and allows more rate heterogeneity compared to BAMM estimates (although increasing error rate). The  
262 higher variation in  $\lambda_{DR}$  could explain why we detected a significant pattern using this metric and not the  
263 other two. We think it is unlikely that the significant correlation between  $\lambda_{DR}$  and sexual selection is spurious  
264 given the variation in  $\lambda_{DR}$  values and the consistency in the calculated estimates across the 1,000 trees.

265 In addition to speciation, sexual selection has frequently been invoked as a driver of extinction. Sexual  
266 selection may increase extinction risk as it often leads individuals (usually males) to invest in exaggerated

267 mating signals as opposed to traits — such as parental care — that elevate offspring fitness (*reviewed in*  
268 Kokko and Brooks 2003). Using the model-based approach of BAMM, we found no association between  
269 extinction rate and sexual dichromatism, male-biased sexual selection or measures of environmental variability.  
270 Extinction is notoriously difficult to estimate accurately from phylogenies, principally because many different  
271 combinations of speciation and extinction rates can give rise to similar patterns of diversity (*see* Rabosky  
272 2016). Phylogenetic methods such as BAMM allow for speciation and extinction rates to be estimated  
273 using moderately-sized phylogenies, although the ability of BAMM to model evolutionary rate shifts and  
274 extinction rates remains a subject of debate (*see*, Beaulieu and O'Meara 2015; Rabosky 2016; Moore et al.  
275 2016; Rabosky et al. 2017). Additionally, while several tip-rate estimates exist for speciation rate (*e.g.*,  $\lambda_{DR}$   
276 and  $\lambda_{ND}$ ), tip-rate estimates of extinction rate are difficult to obtain without complex Bayesian models and  
277 are fraught with issues of sampling bias (Davis et al. 2013). Although extinction rates can be estimated from  
278 alternative sources, such as the fossil record, documented recent extinctions and IUCN extinction threat  
279 status, each approach has significant limitations. Across the passerine bird phylogeny, we found that BAMM  
280 often produced homogeneous speciation and extinction rates for smaller clades showing few rate shifts, which  
281 might reduce our power to detect small differences in extinction rates among closely-related taxa (Rabosky  
282 et al. 2017; Title and Rabosky 2018). Thus, this methodological constraint likely decreases our ability to  
283 accurately measure the correlation between metrics of sexual selection and the probability of extinction.  
  
284 To summarise, we have shown that in passerines, male-biased sexual selection, but not sexual dichromatism,  
285 predicts speciation, independent of several measures of environmental variability. These findings support the  
286 idea that sexual dechromatism is not a reliable proxy for sexual selection, and that alternative measures of  
287 sexual selection are more directly related to diversification. If sexual selection promotes speciation through  
288 improvements in fitness and adaptation the implications are manifold, including for conservation (*reviewed in*,  
289 Holman and Kokko 2013) and captive breeding programs for threatened species (*reviewed in*, Charge et al.  
290 2014). Furthermore, our finding that high speciation rate is associated with smaller range size highlights the  
291 threat to the persistence of rapidly speciating lineages in a world with increased habitat loss and anthropogenic  
292 stress. This concern arises as the best predictor of extinction risk is range size (Harris and Pimm 2008) and  
293 the association found here implies that many newly-speciated clades have small range sizes and could thus be  
294 at greater risk of extinction.

## 295 MATERIALS AND METHODS

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

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

#### 302 Sexual dichromatism

303 We used a previously published measure of sexual dichromatism for 5,983 species of passerines (Dale et al.  
304 2015). Briefly, Dale et al. (2015) obtained sex-specific RGB (red, green and blue) values across six body  
305 patches (nape, crown, forehead, throat, upper breast, and lower breast) from *Handbook of the Birds of the*  
306 *World* (Del Hoyo et al. 2011). The relative contribution of male and female RGB colour values were averaged  
307 across body patches and provide ‘male-like’ and ‘female-like’ plumage scores. Here we use the absolute  
308 difference between male and female plumage scores as an estimate of sexual dichromatism. Additionally, we  
309 used another measure of dichromatism corresponding to colour distance in avian colour space derived from  
310 spectral data (Armenta et al. 2008). These measurements include variation in the ultraviolet and bird-visible  
311 range and — unlike the RGB measures — are sourced from museum samples (as opposed to colour drawings).  
312 However, this spectrophotometry data is not as extensive as the RGB measures; with only 581 passerine  
313 species available for this analysis. While there is a correlation between these two measures, there is residual  
314 variation ( $r = 0.79$ ; [Figure S10](#)).

#### 315 Male-biased sexual selection

316 Sexual dichromatism is a widely used indicator of sexual selection in birds (e.g., Barraclough et al. 1995;  
317 Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014), but only partially  
318 captures variation in the strength of sexual selection across taxa. Therefore, we also use an existing dataset  
319 (Dale et al. 2015) of male-biased sexual selection based on the first component of a phylogenetic principle  
320 component analysis (PPCA) of three characteristics positively associated with sexual selection (sexual size  
321 dimorphism, social polygyny and [lack of] paternal care). This measure of male-biased sexual selection is  
322 available for only 2,465 species and is weakly correlated with the absolute values of sexual dichromatism  
323 using RGB measures ( $r = 0.34$ ; [Figure S12](#)).

#### 324 Environmental variables

325 We obtained estimates of species range size using expert range maps (BirdLife International and Handbook  
326 of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the *Birdlife* database  
327 (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual dichromatism

dataset (Dale et al. 2015). From these distributions, we obtained estimates of climatic conditions that each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19 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 (Fick and Hijmans 2017). 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; Otto-Bliesner et al. 2006). We include estimates of climate variability during recent evolutionary history as they may be a better indicators of environmental effects on speciation than present-day environmental variability. Furthermore, 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; Zhao et al. 2005). 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).

### 343 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 (Cally et al. 2019), we used the extracted environmental variables from each species range size to develop biologically meaningful 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 (BIO 4 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. Similar 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](#).

### 363 Estimating extinction and speciation

Phylogenetic information was obtained from [www.birdtree.org](http://www.birdtree.org) (Jetz et al. 2012). We used a maximum clade credibility (MCC) tree from 2,500 samples of the posterior distribution ( $n = 5,965$ ) as the main phylogenetic

366 hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without  
 367 genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using  
 368 tip-rate measures (1000 trees) and BAMM (100 trees)(Rabosky 2014). These trees used a ‘Hackett backbone’  
 369 (Hackett et al. 2008) and were constructed using a pure birth (Yule) model. We calculated three different  
 370 tip-rate metrics of speciation and one of extinction across all trees.

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

386 Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic  
 387 trees (Rabosky 2014). This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo)  
 388 to generate probability distributions of evolutionary rate-shift configurations with variable speciation and  
 389 extinction rates. Importantly, these models provide tip-rate estimates of speciation and extinction rate. The  
 390 parameters of the 100 BAMM runs are detailed in full in the [ESM](#); briefly, we used a time-variable model with  
 391 100 expected number of shifts and prior rates set from the initial speciation and extinction values using the  
 392 **BAMMtools** R package (Rabosky et al. 2014). Each BAMM model (one MCC tree and 100 random draws of  
 393 the posterior) was run for 100 million generations, and given the computationally intensive nature of BAMM,  
 394 runs were conducted across multiple CPUs. Each run of BAMM reached convergence with effective sample  
 395 size (ESS) of MCMC (Markov Chain Monte Carlo) samples surpassing 200 (an arbitrary value, above which  
 396 posterior distributions can often be accurately inferred) for the key model parameters of log-likelihood and  
 397 number of rate shifts ([Table S3](#), [Table S4](#)). Further details of BAMM parameters and output are available in  
 398 the [ESM](#), with tip-rate means and variances provided. Additionally, given the variability in BAMM estimates,  
 399 we also provide analysis of BAMM shift configurations and tip-rate estimates from our run on the MCC  
 400 tree and within a BAMM run on the MCC tree from a genetic-only phylogeny across all birds (Harvey et al.  
 401 2017). All analyses were conducted on log-rates.

## 402 Phylogenetic comparative analysis

403 To test the association between speciation/extinction and sexual selection, environmental variability and  
 404 their interaction, we used phylogenetic least squares (PGLS) models in the **nlme** package (Pinheiro et al.  
 405 2018). Firstly we conducted model selection using  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  or  $\mu_{BAMM}$  tip-rate estimates from

the same MCC tree, which was derived from 2,500 draws of the posterior distribution (Jetz et al. 2012). For  $\lambda_{BAMM}$  and  $\mu_{BAMM}$  we were also able to use model weights sourced from the inverse of the variance of tip-rates for a given species from the posterior distribution ( $n = 1,000$ ). Model weights thus reflect the degree of precision to which each species' tip-rate is measured in BAMM. Using model selection we only compared interaction terms between a measure of sexual selection (sexual dichromatism or male-biased sexual selection) and environmental measures. That is, we fixed the individual predictors of dichromatism/male-biased sexual selection measures, log-transformed range size, seasonal temperature variation, spatial temperature variation, long-term temperature variation, and NPP while comparing 32 models with different combinations of interactions (including none). Model selection was done in MuMIn using the `dredge` function (Bartoń 2017). Using the terms from the top-ranking model (lowest AICc), we ran the equivalent model for each of the 1,000 phylogenetic trees used to derive  $\lambda_{DR}$ ,  $\lambda_{ND}$  and each of the 100 used to derive  $\lambda_{BAMM}$  and  $\mu_{BAMM}$ . In each model we used the unique response variables and phylogenetic tree correlation structure. Specifically, for models using tip-rate metrics ( $\lambda_{DR}$ ,  $\lambda_{ND}$ ) we estimated the phylogenetic signal — Pagel's  $\lambda$  (Pagel 1999) — using the `corPage1` function in the `ape` package (Paradis et al. 2004) independently for each of the 1,000 trees/models. Alternatively, for models using speciation and extinction estimates derived using BAMM ( $\lambda_{BAMM}$  and  $\mu_{BAMM}$ ) we found  $\lambda$  was consistently estimated at 1 and hence assumed Brownian motion (using the `corBrownian` function) to estimate the correlation structure. This method enabled us to present model estimates for an MCC tree alongside 1,000/100 trees from the posterior distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three datasets corresponding to each measure of sexual selection: dichromatism derived from RGB values of images ( $n = 5,812$ ); dichromatism from spectrophotometry ( $n = 581$ ) and the multivariate measure of male-biased sexual selection ( $n = 2,465$ ). Finally, using data subset for species with measurements of male-biased sexual selection, we conducted a phylogenetic path analysis using the `phylopath` R package (Bijl 2018). The phylogenetic path analysis was used to assess causal paths *between* variables not able to be modelled within the univariate response of PGLS. That is, a phylogenetic path analysis allowed us to model relationships between the predictor variables used in our PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection, and range size to have effects on each other and not just on speciation rate. To minimise path complexity we used temperature seasonality (BIO4) as the single measure for environmental variability,  $\lambda_{DR}$  as the single measure of speciation and the tip-rates from the MCC tree. Further details of the path analysis, including reasons for path directions, can be found within the [ESM](#) along with all other analyses and the relevant R code to reproduce results.

<sup>437</sup> **ACKNOWLEDGEMENTS**

<sup>438</sup> We would like to acknowledge Adnan Moussalli for his assistance in conducting BAMM runs across 100  
<sup>439</sup> phylogenetic trees. **Any others?**

## 440 REFERENCES

- 441 Agrawal, A. F. 2001. Sexual selection and the maintenance of sexual reproduction. *Nature* 411:692–695.
- 442 Armenta, J. K., P. O. Dunn, and L. A. Whittingham. 2008. Quantifying avian sexual dichromatism: A  
443 comparison of methods. *Journal of Experimental Biology* 211:2423.
- 444 Barraclough, T. G., P. H. Harvey, and S. Nee. 1995. Sexual selection and taxonomic diversity in passerine  
445 birds. *Proceedings of the Royal Society B-Biological Sciences* 259:211–215.
- 446 Bartoń, K. 2017. MuMIn: Multi-model inference.
- 447 Beaulieu, J. M., and B. C. O'Meara. 2015. Extinction can be estimated from moderately sized molecular  
448 phylogenies. *Evolution* 69:1036–1043.
- 449 Belmaker, J., and W. Jetz. 2015. Relative roles of ecological and energetic constraints, diversification rates  
450 and region history on global species richness gradients. *Ecology Letters* 18:563–571.
- 451 Berger, D., K. Grieshop, M. I. Lind, J. Goenaga, A. A. Maklakov, and G. Arnqvist. 2014. Intralocus sexual  
452 conflict and environmental stress. *Evolution* 68:2184–2196.
- 453 Bijl, W. van der. 2018. *Phylopath*: Easy phylogenetic path analysis in R. *PeerJ* 6:e4718.
- 454 Birand, A., A. Vose, and S. Gavrilets. 2012. Patterns of species ranges, speciation, and extinction. *The  
455 American Naturalist* 179:1–21.
- 456 BirdLife International and Handbook of the Birds of the World. 2017. Bird species distribution maps of the  
457 world. <http://datazone.birdlife.org/species/requestdis>.
- 458 Bonduriansky, R., and S. F. Chenoweth. 2009. Intralocus sexual conflict. *Trends in Ecology & Evolution*  
459 24:280–8.
- 460 Boughman, J. W. 2002. How sensory drive can promote speciation. *Trends in Ecology & Evolution* 17:571–577.
- 461 Cally, J. G., D. Stuart-Fox, and L. Holman. 2019. Meta-analytic evidence that sexual selection improves  
462 population fitness. *Nature communications* 10:2017. Nature Publishing Group.
- 463 Candolin, U., and J. Heuschele. 2008. Is sexual selection beneficial during adaptation to environmental  
464 change? *Trends in Ecology & Evolution* 23:446–452.
- 465 Castiglione, S., A. Mondanaro, M. Melchionna, C. Serio, M. Di Febbraro, F. Carotenuto, and P. Raia. 2017.  
466 Diversification rates and the evolution of species range size frequency distribution. *Frontiers in Ecology and  
467 Evolution* 5:147. Frontiers.
- 468 Charge, R., C. Teplitsky, G. Sorci, and M. Low. 2014. Can sexual selection theory inform genetic management  
469 of captive populations? A review. *Evolutionary Applications* 7:1120–1133.
- 470 Claramunt, S., E. P. Derryberry, J. V. Remsen, and R. T. Brumfield. 2012. High dispersal ability inhibits  
471 speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*  
472 279:1567.
- 473 Connallon, T., and M. D. Hall. 2016. Genetic correlations and sex-specific adaptation in changing environ-  
474 ments. *70:2198.*

- 475 Cooney, C. R., H. E. A. MacGregor, N. Seddon, and J. A. Tobias. 2018. Multi-modal signal evolution in  
476 birds: Re-examining a standard proxy for sexual selection. *Proceedings of the Royal Society of London B:*  
477 *Biological Sciences* 285.
- 478 Cooney, C. R., J. A. Tobias, J. T. Weir, C. A. Botero, and N. Seddon. 2017. Sexual selection, speciation and  
479 constraints on geographical range overlap in birds. *Ecology Letters* 20:863–871.
- 480 Dale, J., C. J. Dey, K. Delhey, B. Kempenaers, and M. Valcu. 2015. The effects of life history and sexual  
481 selection on male and female plumage colouration. *Nature* 527:367–370.
- 482 Darwin, C. 1871. *The descent of man and selection in relation to sex*. 1st ed. John Murray, London.
- 483 Davis, M. P., P. E. Midford, and W. Maddison. 2013. Exploring power and parameter estimation of the  
484 BiSSE method for analyzing species diversification. *BMC Evolutionary Biology* 13:38.
- 485 Del Hoyo, J., A. Elliott, and D. Christie. 2011. *Handbook of the birds of the world*. Lynx Edicions 2003-2011.
- 486 Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global  
487 land areas. *International Journal of Climatology* 37:4302–4315.
- 488 Fromhage, L., and M. D. Jennions. 2016. Coevolution of parental investment and sexually selected traits  
489 drives sex-role divergence. *Nature Communications* 7:12517.
- 490 Greenberg, D. A., and A. Ø. Mooers. 2017. Linking speciation to extinction: Diversification raises  
491 contemporary extinction risk in amphibians. *Evolution Letters* 1:40–48.
- 492 Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A.  
493 Cox, K.-L. Han, J. Harshman, C. J. Huddleston, B. D. Marks, K. J. Miglia, W. S. Moore, F. H. Sheldon,  
494 D. W. Steadman, C. C. Witt, and T. Yuri. 2008. A phylogenomic study of birds reveals their evolutionary  
495 history. *Science* 320:1763–1768.
- 496 Harris, G., and S. L. Pimm. 2008. Range size and extinction risk in forest birds. *Conservation Biology*  
497 22:163–171.
- 498 Harvey, M. G., G. F. Seeholzer, B. T. Smith, D. L. Rabosky, A. M. Cuervo, and R. T. Brumfield. 2017.  
499 Positive association between population genetic differentiation and speciation rates in new world birds.  
500 *Proceedings of the National Academy of Sciences* 114:6328–6333.
- 501 Harvey Michael, G., L. Rabosky Daniel, and N. Cooper. 2017. Continuous traits and speciation rates:  
502 Alternatives to state-dependent diversification models. *Methods in Ecology and Evolution* 9:984–993.
- 503 Holman, L., and H. Kokko. 2013. The consequences of polyandry for population viability, extinction risk and  
504 conservation. *Philosophical Transactions of the Royal Society B-Biological Sciences* 368.
- 505 Hoyo, J. del, and N. J. Collar. 2016. HBW and birdlife international illustrated checklist of the birds of the  
506 world. Lynx Edicions; BirdLife International.
- 507 Huang, H. T., and D. L. Rabosky. 2014. Sexual selection and diversification: Reexamining the correlation  
508 between dichromatism and speciation rate in birds. *The American Naturalist* 184:E101–E114.
- 509 Jablonski, D., and K. Roy. 2003. Geographical range and speciation in fossil and living molluscs. *Proceedings*  
510 *of the Royal Society of London. Series B: Biological Sciences* 270:401–406. The Royal Society.

- 511 Janicke, T., I. K. Häderer, M. J. Lajeunesse, and N. Anthes. 2016. Darwinian sex roles confirmed across the  
512 animal kingdom. *Science Advances* 2:e1500983.
- 513 Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in  
514 space and time. *Nature* 491:444–448.
- 515 Kokko, H., and R. Brooks. 2003. Sexy to die for? Sexual selection and the risk of extinction. *Annales  
516 Zoologici Fennici* 40:207–219.
- 517 Kokko, H., and M. D. Jennions. 2008. Parental investment, sexual selection and sex ratios. *Journal of  
518 Evolutionary Biology* 21:919–948.
- 519 Kottler, M. J. 1980. Darwin, Wallace, and the origin of sexual dimorphism. *Proceedings of the American  
520 Philosophical Society* 124:203–226.
- 521 Kraaijeveld, K., F. J. L. Kraaijeveld-Smit, and M. E. Maan. 2011. Sexual selection and speciation: The  
522 comparative evidence revisited. *Biological Reviews* 86:367–377.
- 523 Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National  
524 Academy of Sciences* 78:3721–3725.
- 525 Lande, R. 1982. Rapid origin of sexual isolation and character divergence in a cline. *Evolution* 36:213–223.
- 526 Long, T. A. F., A. F. Agrawal, and L. Rowe. 2012. The effect of sexual selection on offspring fitness depends  
527 on the nature of genetic variation. *Current Biology* 22:204–208.
- 528 Lorch, P. D., S. Proulx, L. Rowe, and T. Day. 2003. Condition-dependent sexual selection can accelerate  
529 adaptation. *Evolutionary Ecology Research* 5:867–881.
- 530 Maan, M. E., and O. Seehausen. 2011. Ecology, sexual selection and speciation. *Ecology Letters* 14:591–602.
- 531 Martinossi-Allibert, I., U. Savković, M. Đorđević, G. Arnqvist, B. Stojković, and D. Berger. 2017. The  
532 consequences of sexual selection in well-adapted and maladapted populations of bean beetles. *Evolution*  
533 72:518–530.
- 534 Medina, I., K. Delhey, A. Peters, K. E. Cain, M. L. Hall, R. A. Mulder, and N. E. Langmore. 2017. Habitat  
535 structure is linked to the evolution of plumage colour in female, but not male, fairy-wrens. *BMC evolutionary  
536 biology* 17:35.
- 537 Miles, M. C., and M. J. Fuxjager. 2018. Synergistic selection regimens drive the evolution of display  
538 complexity in birds of paradise. *Journal of Animal Ecology* 87:1149–1159.
- 539 Moore, B. R., S. Hohna, M. R. May, B. Rannala, and J. P. Huelsenbeck. 2016. Critically evaluating the  
540 theory and performance of bayesian analysis of macroevolutionary mixtures. *Proceedings of the National  
541 Academy of Sciences* 113:9569–9574.
- 542 Morrow, E. H., T. E. Pitcher, and G. Arnqvist. 2003. No evidence that sexual selection is an 'engine of  
543 speciation' in birds. *Ecology Letters* 6:228–234.
- 544 Otto-Bliesner, B. L., S. J. Marshall, J. T. Overpeck, G. H. Miller, A. Hu, and. 2006. Simulating arctic  
545 climate warmth and icefield retreat in the last interglaciation. *Science* 311:1751–1753.

- 546 Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: Body size, life history,  
547 sexual selection or ecology? *Proceedings of the Royal Society B-Biological Sciences* 266:933–939.
- 548 Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877.
- 549 Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of phylogenetics and evolution in R language.  
550 *Bioinformatics* 20:289–290.
- 551 Pennell, T. M., and E. H. Morrow. 2013. Two sexes, one genome: The evolutionary dynamics of intralocus  
552 sexual conflict. *Ecology and Evolution* 3:1819–1834.
- 553 Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2018. nlme: Linear and nonlinear mixed  
554 effects models.
- 555 Pischedda, A., and A. K. Chippindale. 2006. Intralocus sexual conflict diminishes the benefits of sexual  
556 selection. *PLOS Biology* 4:e356.
- 557 Price, J. J., and M. D. Eaton. 2014. Reconstructing the evolution of sexual dichromatism: Current color  
558 diversity does not reflect past rates of male and female change. *Evolution* 68:2026–2037.
- 559 Pryke, S. R., S. Andersson, and M. J. Lawes. 2001. Sexual selection of multiple handicaps in the red-collared  
560 widowbird: Female choice of tail length but not carotenoid display. *Evolution* 55:1452–1463.
- 561 Quintero, I., and W. Jetz. 2018. Global elevational diversity and diversification of birds. *Nature* 555:246.
- 562 Rabosky, D., M. Grundler, C. Anderson, P. Title, J. Shi, J. Brown, H. Huang, and J. Larson. 2014.  
563 BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in  
564 Ecology and Evolution* 5:701–707.
- 565 Rabosky, D. L. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on  
566 phylogenetic trees. *PLOS ONE* 9:e89543.
- 567 Rabosky, D. L. 2016. Challenges in the estimation of extinction from molecular phylogenies: A response to  
568 Beaulieu and O’Meara. *Evolution* 70:218–228.
- 569 Rabosky, D. L., J. Chang, P. O. Title, P. F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T. J.  
570 Near, M. Coll, and others. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*  
571 559:392.
- 572 Rabosky, D. L., J. S. Mitchell, and J. Chang. 2017. Is BAMM flawed? Theoretical and practical concerns in  
573 the analysis of multi-rate diversification models. *Systematic biology* 66:477–498.
- 574 Rankin, D. J., U. Dieckmann, and H. Kokko. 2011. Sexual conflict and the tragedy of the commons. *The  
575 American Naturalist* 177:780–791.
- 576 Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press.
- 577 Seddon, N., C. A. Botero, J. A. Tobias, P. O. Dunn, H. E. A. MacGregor, D. R. Rubenstein, J. A. C. Uy, J.  
578 T. Weir, L. A. Whittingham, and R. J. Safran. 2013. Sexual selection accelerates signal evolution during  
579 speciation in birds. *Proceedings of the Royal Society B: Biological Sciences* 280.
- 580 Seddon, N., R. M. Merrill, and J. A. Tobias. 2008. Sexually selected traits predict patterns of species richness  
581 in a diverse clade of suboscine birds. *The American Naturalist* 171:620–631.

- 582 Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *The  
583 Quarterly Review of Biology* 64:419–461.
- 584 Siller, S. 2001. Sexual selection and the maintenance of sex. *Nature* 411:689.
- 585 Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38:622–630.
- 586 Title, P. O., and D. L. Rabosky. 2018. Diversification rates and phylogenies: What are we estimating, and  
587 how good are the estimates? *bioRxiv* 369124.
- 588 Uy, J. A. C., and G. Borgia. 2000. Sexual selection drives rapid divergence in bowerbird display traits.  
589 *Evolution* 54:273–278.
- 590 Wallace, A. R. 1889. Colours and ornaments characteristic of sex. *in* Darwinism, an exponent of the theory  
591 of natural selection, with some of its applications. Macmillan; Company.
- 592 Weaver, R. J., E. S. Santos, A. M. Tucker, A. E. Wilson, and G. E. Hill. 2018. Carotenoid metabolism  
593 strengthens the link between feather coloration and individual quality. *Nature Communications* 9:73.
- 594 Weir, J. T., and T. D. Price. 2011. Limits to speciation inferred from times to secondary sympatry and ages  
595 of hybridizing species along a latitudinal gradient. *The American Naturalist* 177:462–469.
- 596 Whitlock, M. C. 2000. Fixation of new alleles and the extinction of small populations: Drift load, beneficial  
597 alleles, and sexual selection. *Evolution* 54:1855–1861.
- 598 Zhao, M., F. A. Heinsch, R. R. Nemani, and S. W. Running. 2005. Improvements of the modis terrestrial  
599 gross and net primary production global data set. *Remote Sensing of Environment* 95:164–176.