

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 rates
9 across passerine birds (up to 5,812 species, covering most genera). We tested for associations between
10 two measures of sexual selection (sexual dichromatism and a multivariate measure of male-biased sexual
11 selection), several environmental variables, and multiple measures of speciation and extinction rates. Our
12 results show that male-biased sexual selection, but not sexual dichromatism, predicts speciation rates
13 (λ_{DR}) in passerines, and found no evidence that this relationship varies with the environment. We also
14 found a strong negative relationship between range size and speciation rate. There was no correlation
15 between sexual selection and extinction rate (μ_{BAMM}). Our findings show that sexual dichromatism is
16 a poor proxy for sexual selection at least a broad-scale and support the view that sexual selection is a
17 potent evolutionary force that has 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^{1–3}. There is long-standing interest in
22 the relationship between sexual selection and the processes of speciation, extinction, and phylogenetic
23 diversification^{4–8}. Recent empirical and methodological advances, such as growing evidence that sexual
24 selection can profoundly affect many traits⁹, larger and more accurate phylogenies¹⁰, and new phylogenetic
25 methods^{11,12}, present new opportunities to test whether and how sexual selection drives diversification.

26 Several hypotheses predict a positive relationship across species between the strength of sexual selection
27 and the rate of speciation and/or extinction. For example, sexual selection is involved in reinforcement, a
28 speciation-promoting process in which members of different phylogenetic lineages evolve to avoid unproductive
29 inter-lineage mating/fertilisation¹³. Additionally, sexual selection often operates on traits that can create
30 reproductive isolation when they diverge between lineages, such as signals and preferences involved in mate
31 selection^{4,5,14}, sperm-egg interactions¹⁵, or genital morphology¹⁶. Furthermore, sexual selection has been
32 hypothesised to increase diversification by maintaining trait combinations that would be selected out under
33 pure natural selection^{17,18}, and by helping to prevent extinction by purging deleterious mutations¹⁹, fixing
34 beneficial ones²⁰, and accelerating adaptation in environments^{9,21,22}.

35 Conversely, sexual selection might hinder speciation or make extinction more likely by favouring traits that
36 improve mating success but reduce population fitness. For example, species with expensive sexual signals
37 may be less resilient to environmental change²³, and sexual selection often creates a ‘tragedy of the commons’
38 by selecting for traits that increase the reproductive success of individuals while reducing population-wide
39 productivity^{1,2,24,25}. Sexual selection might also promote extinction by causing maladaptation (‘gender load’)
40 in female traits that are genetically correlated with sexually-selected male traits^{26–30}.

41 Importantly, the relationship between sexual selection and diversification might be contingent on the
42 environment. Theoretical work predicts that sexual selection should have a more positive effect on adaptation
43 and population fitness in variable environments relative to stable ones^{31,32}, though the empirical evidence for
44 this theory is mixed and largely limited to insects⁹. The mechanism underpinning this prediction is that
45 the environment and the selective history of the population should influence the relative amounts of genetic
46 variation at sexually concordant loci (i.e. loci where the same allele is fittest for both sexes) and sexually
47 antagonistic loci (where different alleles are favoured in each sex). In stable environments, variation is thought
48 to be preferentially depleted at sexually concordant loci, leading to stronger gender load and reduced net
49 benefits of sexual selection³², and potentially to a more negative relationship between sexual selection and
50 diversification rates across species. Conversely, sexual selection might be especially important at promoting
51 local adaptation when the environment displays variability at the relevant spatial and temporal scales^{21,33–35}.

52 Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification^{7,36–39}.
53 Birds are well-suited for this purpose due to their diverse and well-characterised mating systems and
54 sexually-selected traits, and because their phylogenetic relationships are comparatively well-known. A 2011
55 meta-analysis covering 20 primary studies of birds and other taxa found a small but significant positive
56 association between sexual selection and speciation, with the average effect size in birds stronger than in
57 mammals but weaker than in insects or fish⁴⁰. However, there was large variation in effect size estimates across
58 the 20 studies, likely reflecting differences in methodology, such as metrics used to characterise speciation and

59 sexual selection, in addition to true biological differences. More recently, 39 found no association between
60 sexual dichromatism and speciation ($n = 918$ species) in a study using spectrophotometric measurements of
61 museum specimens⁴¹ and tip-rate estimates from a molecular-only phylogeny¹⁰. Similarly, 42 found no effect
62 of sexual dichromatism on diversification across 1,306 pairs of species, using dichromatism scores provided by
63 human observers.

64 Here, we investigate the association between sexual selection and diversification in birds while building upon
65 previous approaches in multiple ways. We use two measures of the strength of sexual selection: sexual
66 dichromatism⁴³, as well as an index of male-biased sexual selection⁴³, which captures (co)variation in sexual
67 size dimorphism, social polygyny and paternal care. These two measures are used because sexual dichromatism
68 does not always signal the presence of strong sexual selection and *vice versa*⁴³. For example, male and
69 female dunnocks (*Prunella modularis*) are similarly coloured yet sexual selection appears to be strong⁴⁴.
70 Furthermore, a recent comparative study found a negative relationship between dichromatism and another
71 sexually-selected trait (song) across species, suggesting that a multi-trait focus would improve estimates of
72 sexual selection intensity⁸. Additionally, our analysis includes multiple ecological and environmental variables
73 on diversification, allowing us to adjust for potential confounds, to identify environmental factors driving
74 diversification, and to test whether environmental factors interact with sexual selection as theory predicts³².
75 We use multiple approaches for quantifying speciation and extinction rates at the tips of phylogenetic trees,
76 including BAMM^{45–48}, as well as older but reliable tip-rate statistics, such as diversification rate (λ_{DR}) and
77 node density (λ_{ND}).

78 RESULTS

79 Variability across phylogenetic trees and speciation rate measures

80 [Is it possible to move this later in the Results? It's possibly not ideal to start by highlighting
81 the dependence of our conclusions on the methods we choose, and not mentioning our main
82 non-null finding regarding the SS index. Having said that I can see a case for leaving it here
83 too. - Luke] [We initially had this at the end but moved it up to the start. What do you think
84 Devi? - Justin]

85 Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially in
86 the BAMM rates (λ_{BAMM} and μ_{BAMM}), where the 95 % highest posterior density (HPD) interval across
87 phylogenetic least squares (PGLS) model estimates from 100 trees was often > 20 times larger than the 95
88 % confidence interval for estimates from a single PGLS model using the MCC (maximum clade credibility)
89 tree. This contrasts with variation across trees for the other rate estimates (λ_{DR} and λ_{ND}), where the
90 95 % HPD interval of model estimates for pgls models using 1,000 trees was near-equivelant to the 95 %
91 confidence interval calculated for pgls model estimates of the MCC tree (Table S9). Given the computational
92 requirements of BAMM, the great majority of earlier studies have based their estimates on a single consensus
93 tree, and so the inconsistency of the BAMM estimates between different phylogenies with similar statistical
94 support is notable. Mean measures of speciation rate across 100 trees were positively correlated between
95 measures (DR - BAMM: $r=0.75$, DR - ND: $r=0.65$, ND- BAMM: $r=0.51$; Figure S15). Given that the
96 calculation of BAMM rates can be affected by the settings of the run and the use of different priors, we

97 compared the estimate of our MCC tree with that of previous published analyses on birds, and found a high
98 correlation ($r=0.81$, [Figure S8](#)). Full details of the BAMM results are presented as supplementary materials.

99 No evidence that the relationship between sexual selection and speciation
100 depends on environmental variability

101 [I think this part should go after the next 2 sections, as it's a more confusing being about
102 interactions, and we should preserve the order of ideas from the Abstract and Intro. - Luke]
103 [Statistically, I think it is best to rule out the interactions first but Yes I see your point -
104 Justin]

105 We next fit PGLS models with 2-way interaction terms between each measure of sexual dichromatism/selection
106 and the five measures of environmental variability (seasonal temperature variation, log-range size, long-term
107 temperature variation, spatial temperature variation, and NPP) were included in the full model for posterior
108 model selection. However, no interaction terms were present in the top models ($\Delta \text{AICc} > 4$) for any measure
109 of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) or sexual selection (RGB values, spectrophotometry and male-biased
110 sexual selection; $\Delta \text{AICc} > 4$; [Table S5](#), [Table S6](#), [Table S10](#), [Table S13](#)). Thus we found no evidence
111 that the effect of sexual selection on speciation is dependent on our measures of environmental variation.
112 Furthermore, we found no evidence that these environmental factors (seasonal temperature variation, long-
113 term temperature variation, spatial temperature variation, and NPP) predict speciation independently from
114 sexual dichromatism/selection ([Figure 1](#), [Figure S11](#)).

115

116 No evidence that sexual dichromatism affects speciation

117 We found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation.
118 Using three different measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) as the response variable, the effect of sexual
119 dichromatism was not significant in any PGLS model based on tip-rate estimates and correlation structures
120 from the MCC tree. Specifically, sexual dichromatism showed no association with λ_{DR} ($\beta = -1.279e-03$, $p =$
121 0.147; [Figure 1a](#), [Figure 2a](#)) or λ_{ND} ($\beta = -5.745e-05$, $p = 0.078$; [Figure 1a](#)). Furthermore, speciation rates
122 from BAMM (λ_{BAMM}) were also unaffected by sexual dichromatism ($\beta = -1.429e-05$, $p = 0.872$; [Figure 1a](#)).
123 PGLS analyses using sexual dichromatism ($n = 581$) measured by spectrophotometry⁴¹ yielded results
124 concordant with the full dataset; i.e. no association between sexual dichromatism and speciation ([Figure S11](#)).
125 Our results from models based on the MCC tree are largely corroborated by model estimates from PGLS
126 analyses of the rates and correlation structures from 1,000 trees (for λ_{DR} , λ_{ND}) and 100 trees for λ_{BAMM} .
127 The HPD intervals show model estimates are distributed around zero when using complete taxon sampling
128 models and RGB measures of sexual dichromatism (λ_{DR} : HPD Interval = $-1.635e-03$, $1.658e-03$, λ_{ND} : HPD
129 Interval = $-4.256e-05$, $5.499e-05$, [Figure 1a](#), [Table S8](#)). For PGLS models using spectrophotometry-based
130 measures of sexual dichromatism, the estimates from the 100 trees in the λ_{DR} models are positively skewed
131 (HPD Interval = $-1.780e-02$, $3.489e-02$) but normally distributed around zero for λ_{ND} and λ_{BAMM} ([Table](#)
132 [S12](#)).

¹³³ Male-biased sexual selection increases speciation rate

¹³⁴ We found a significant positive association between male-biased sexual selection ($n = 2,465$) and λ_{DR} for
¹³⁵ the MCC tree ($\beta = 3.887\text{e-}02$, $p = 0.012$; [Figure 1b](#)). However, this association was not significant for the
¹³⁶ other two measures of speciation rate (λ_{ND} : $\beta = 4.383\text{e-}04$, $p = 0.351$; λ_{BAMM} : $\beta = 9.423\text{e-}04$, $p = 0.764$;
¹³⁷ [Figure 1b](#)). The distribution of estimates from PGLS models on 1,000 trees was similar to the estimate from
¹³⁸ the MCC tree: among the 1,000 trees there was a positive association between sexual selection and λ_{DR}
¹³⁹ (HPD Interval = $4.513\text{e-}03$, $5.718\text{e-}02$), and the distribution skewed towards a positive association between
¹⁴⁰ sexual selection and λ_{ND} (HPD Interval = $-5.044\text{e-}04$, $1.585\text{e-}03$;) as well as the 100 models using λ_{BAMM}
¹⁴¹ (HPD Interval = $-1.295\text{e-}02$, $3.088\text{e-}02$). Complete HPD intervals for models using male-bias sexual selection
¹⁴² PPCA as a predictor can be found within [Table S15](#).

¹⁴³ Species with smaller ranges have increased rates of speciation

¹⁴⁴ Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation, we found a negative association between range size and
¹⁴⁵ speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This negative
¹⁴⁶ association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.579\text{e-}03$, $p = 0.001$; λ_{ND} :
¹⁴⁷ $\beta = -1.462\text{e-}04$, $p = 0.034$; [Figure 1a](#), [Figure 2](#)). This association was also evident across the estimates from
¹⁴⁸ models using the 1,000 trees (λ_{DR} : HPD Interval = $-8.871\text{e-}03$, $-6.610\text{e-}04$; λ_{ND} : HPD Interval = $-1.514\text{e-}04$,
¹⁴⁹ $1.724\text{e-}05$; [Figure 1a](#)). Subset models with reduced sample size and different measures of sexual selection —
¹⁵⁰ but the same measure of range size — showed equivocal evidence that range size is negatively associated
¹⁵¹ with speciation. Range size significantly predicted λ_{DR} ([Figure 1b](#)) using data subset for male-biased sexual
¹⁵² selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} . Models using data subset for spectrophotometry-based
¹⁵³ dichromatism ($n = 581$) gave non-significant estimates for the effect of range size on all measures of speciation
¹⁵⁴ ([Figure S11](#), [Table S11](#), [Table S12](#)). Because the range size dataset is the same across the three data subsets
¹⁵⁵ we draw our conclusions from the models with the highest power using near-complete taxon sampling ($n =$
¹⁵⁶ 5,812).

¹⁵⁷ Phylogenetic path analysis

¹⁵⁸ Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
¹⁵⁹ ([Figure 3](#); [Figure S14](#)). There was a modest effect of male-biased sexual selection on sexual dimorphism (β
¹⁶⁰ = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism ($\beta = 0.07$) and strongly
¹⁶¹ affected range size ($\beta = 0.52$). This suggests an indirect effect of temperature seasonality on λ_{DR} ($\beta_{indirect} =$
¹⁶² -0.02; [Figure 3](#)), given the negative association we identified between λ_{DR} and range size in PGLS models.

¹⁶³ Extinction rate

¹⁶⁴ We found no evidence that extinction (μ_{BAMM}) was impacted by the extent of sexual dichromatism for
¹⁶⁵ full-taxon sampling ($\beta = 2.385\text{e-}05$, $p = 0.93$; [Figure 1a](#)), nor spectrophotometry-based measures of sexual

¹⁶⁶ dichromatism (Figure S11, Table S11, Table S12) or male-biased sexual selection (Figure 1b, Table S14, Table
¹⁶⁷ S15).

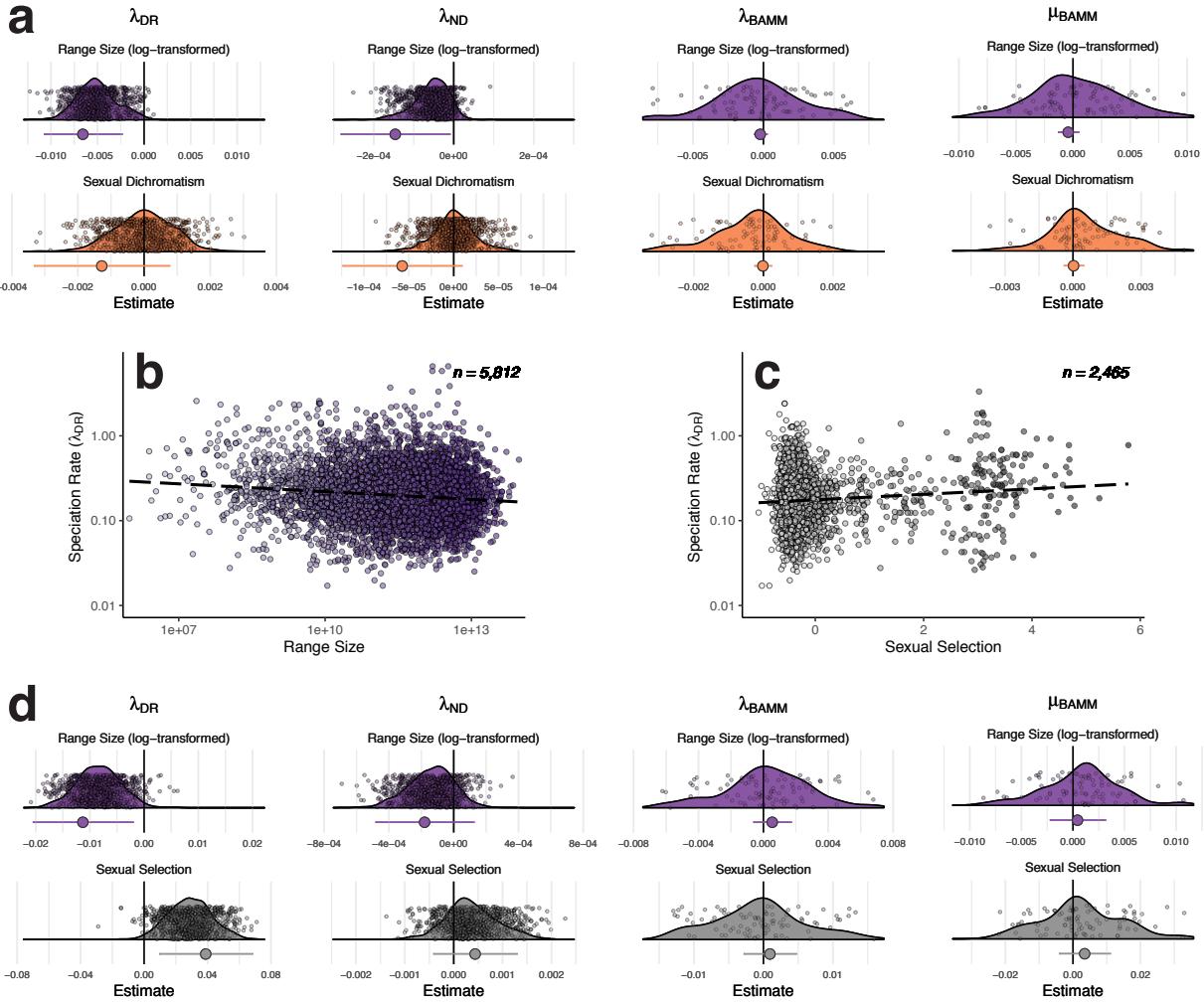


Figure 1: Model estimates (a) for the effect of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset (RGB values, $n = 5,812$). (b) depicts the scatter plot of speciation rate (λ_{DR}) and log-range size with the model estimate presented as a dashed line. (c) shows the scatter plot of speciation rate (λ_{DR}) and male-biased sexual selection ($n = 2,465$). Similar to (a), (d) presents model estimates for PGLS analyses using a restricted dataset with measures of male-biased sexual selection ($n = 2,465$) and shows the effect of log-range size and male-biased sexual selection on speciation and extinction rates. Both datasets were used for analyses with three measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one measure of extinction (μ_{BAMM}) as response variables. The numerical values for the model estimates using the MCC tree and HPD intervals of estimates from 1,000 randomly sampled trees (for λ_{DR} and λ_{ND}) or 100 randomly sampled trees for λ_{BAMM} and μ_{BAMM} can be found in the ESM. Density curves are based on model estimates from 1,000/100 trees and the circle below with error bars is the estimate and 95% CIs from the MCC tree. For this figure we removed outliers from estimates coming from the 100 randomly sampled trees for BAMM models in order to be able to visualise the MCC 95% CIs.

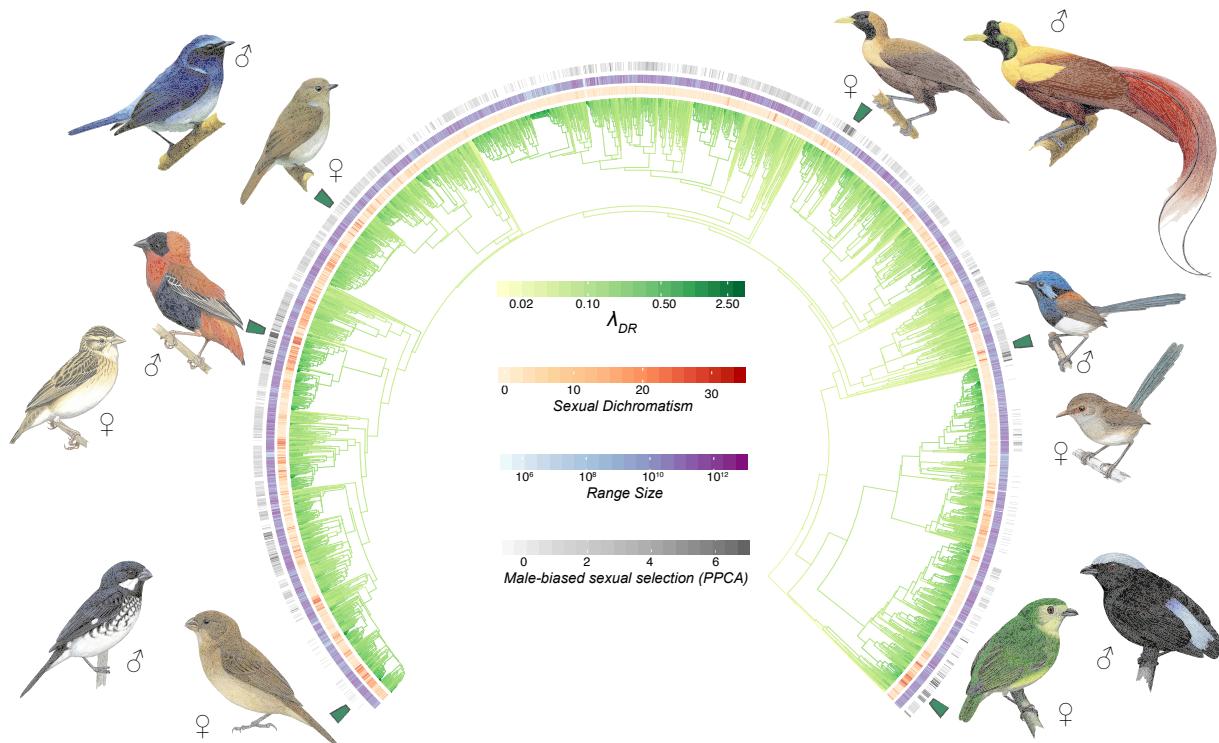


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism, range size available for 5,812 species and male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative association between λ_{DR} and log-range size as well as a significant positive association between λ_{DR} and male-biased sexual selection but no significant association between λ_{DR} and sexual dichromatism based on RGB measures. λ_{DR} are those from the MCC tree and images of birds are from the *Handbook of the Birds of the World*. Clockwise the six species are: *Sporophila bouvronides*, *Euplectes franciscanus*, *Phainopepla nitens*, *Paradisaea rubra*, *Malurus pulcherrimus*, *Lepidothrix coeruleocapilla*. Edge colours for the terminal branch correspond to λ_{DR} but all precluding branches have been generated for graphical purposes using ancestral character state estimation and should not be interpreted.

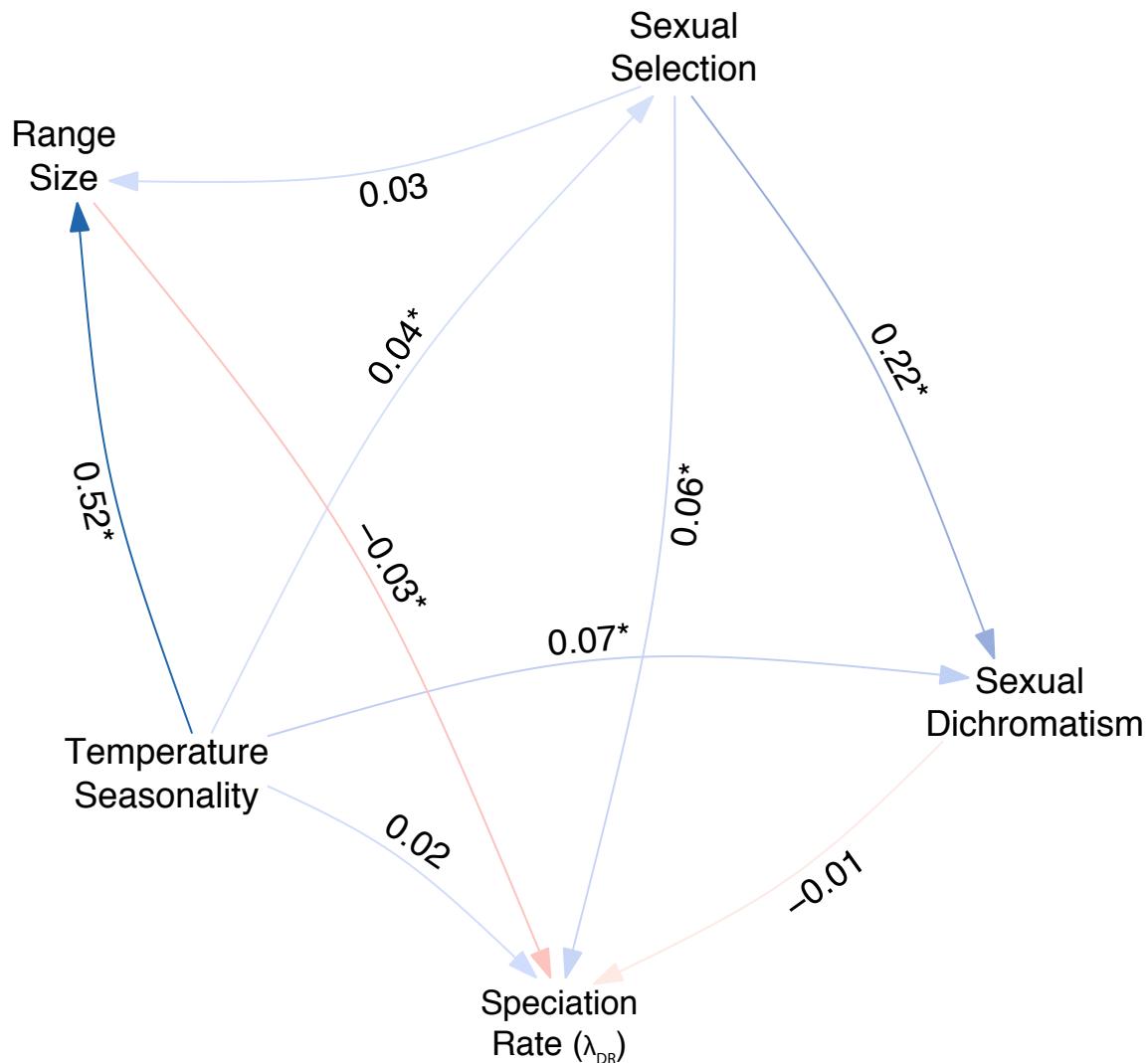


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with the direction of effect corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95% confidence intervals 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 ($n = 2,465$).

168 DISCUSSION

169 We found evidence that the composite index of male-biased sexual selection, but not measures of sexual
170 dichromatism, is correlated with the rate of speciation in passerine birds. The absence of a detectable
171 correlation between sexual dichromatism and speciation rate was consistent across different measures of
172 speciation (λ_{DR} , λ_{ND} and λ_{BAMM}) and both measures of dichromatism (spectral and RGB), and it cannot
173 be explained by a difference in statistical power since the sample size for the dichromatism analyses was much
174 larger. These findings reaffirm the conclusions of previous, smaller studies in which sexual dichromatism was
175 measured using spectrophotometry³⁹ or human observers⁴². The correlation between speciation rate and the
176 index of male-biased sexual selection (which encapsulates variation in sexual size dimorphism, social polygyny,
177 and paternal care) was statistically significant for λ_{DR} , but not for λ_{ND} and λ_{BAMM} , although the estimated
178 direction and magnitude of the correlation was broadly similar across all three measures. Interestingly, we
179 also found a consistent negative relationship between range size and speciation rate, at least when this rate
180 was quantified using λ_{DR} and λ_{ND} . None of the bioclimatic measures of environmental variability that
181 we investigated (i.e., temperature seasonality, long-term temperature variation, and spatial temperature
182 variation) significantly predicted speciation rate.

183 The difference in findings between the analyses of sexual dichromatism *versus* the index of sexual selection
184 is noteworthy, because the majority of earlier studies used dichromatism alone as their proxy for sexual
185 selection^{36–39,49}. Given our findings, and the modest correlation between dichromatism and the sexual
186 selection index⁴³, we hypothesise that sexual dichromatism may not be a robust proxy for sexual selection.
187 Although dichromatism clearly reflects sexual selection to some extent, it is possibly that it is too indirect
188 a measure to detect any association with speciation rate, even with a high sample size. There are several
189 reasons why the use of sexual dichromatism as a proxy for sexual selection is problematic. Firstly, sexual
190 dichromatism can evolve for reasons other than sexual selection, such as when males and females occupy
191 different ecological niches^{50–53} or experience different selective pressures in contexts other than competition
192 for mates⁵⁴. For example, in superb fairy-wrens (*Malurus cyaneus*) female colouration has probably evolved
193 in response to spatial variation in predation pressure, increasing dichromatism⁵⁵. Ecological selection on
194 sexual dichromatism was implicated by our path analysis, which found that sexual dichromatism is positively
195 affected by temperature seasonality (a measure of environmental variation), albeit weakly. Secondly, colour is
196 only one of the traits subject to sexual selection^{9,56}. For instance, sexual selection may promote investments
197 in other mating signals (e.g. song) that trade-off against plumage colour, leading to variable investment in
198 different sexually selected signals across species⁸. Lastly, not all plumage colouration honestly reflects mate
199 quality. A recent meta-analysis found that converted carotenoids (but not carotenoids sourced from the diet)
200 predict mate quality through improvements in parasite resistance and reproductive success⁵⁷. Given the
201 importance of honest signaling in sexual selection and the variability in colour production mechanisms across
202 birds, sexual dichromatism in many species may be an unreliable measure of mate quality for female birds
203 and sexual selection for researchers.

204 In-line with some theoretical predictions and previous studies⁴⁰ we found that male-biased sexual selection
205 increases speciation rate, at least when speciation is measured by λ_{DR} . Additionally, we found that this
206 association appears to be independent of net primary productivity and spatiotemporal variation in the
207 environment. The lack of an effect of these environmental variables on speciation rate has several possible
208 interpretations. Firstly, the effects of sexual selection on adaptation and speciation may depend on the type of

209 environmental variability under which the species is evolving. Specifically, speciation rates might be impacted
210 by genetic constraints on adaptation, that vary across environments. Theory suggests that sexual antagonism
211 (which is often exacerbated in species with strong sexual selection) may be lower in habitats experiencing
212 cyclical environmental variation (e.g. seasonality), relative to those experiencing directional change in the
213 environment³². Another possibility is that the environmental predictors we chose may not account for the
214 key ecological sources of selection that interact with sexual selection to drive speciation. For example, our
215 study does not include direct measure of food availability or the severity of predation and parasitism, which
216 are both hypothesised to affect sexual selection and speciation³⁴. Finally, it is possible that environmental
217 variability genuinely has little effect on speciation rates, at least in the taxa investigated here.

218 The most robust finding in our study is the finding that species with smaller ranges have elevated speciation
219 rates. This result is similar to a study of 329 amphibian genera, which found higher diversification rates
220 in taxa with smaller range size⁵⁸. Intuitively, large range size should promote speciation by creating more
221 opportunities for geographic barriers to form^{59,60}. However, the opposite pattern is also plausible because
222 birds with limited dispersal or more specialised niches can have more fragmented populations, which would
223 promote vicariant divergence and higher speciation rates^{61–63}. It is also possible that high speciation rates
224 cause smaller range sizes, rather than the other way around, for example because repeatedly-speciating
225 lineages tend to fill niches in ways that hinder the geographical expansion of new species^{54,59,64}. However,
226 species undergoing adaptive radiation in new habitats are unlikely to be limited by competition for resources
227 from existing taxa. One further explanation for the negative association between range size and sexual
228 dichromatism/sexual selection is the potential bias of taxonomic classification, whereby over-splitting of
229 species in clades with large ranges leads to increased recent phylogenetic branching as well as smaller ranges.

230 In addition to speciation, sexual selection is hypothesised to affect extinction. Using the model-based
231 approach of BAMM, we found no association between the estimated extinction rate and sexual dichromatism,
232 male-biased sexual selection, or our measures of environmental variability. However, these extinction results
233 should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from
234 phylogenies, principally because different combinations of speciation and extinction rates can give rise to
235 similar patterns of diversity⁴⁶. Phylogenetic methods such as BAMM allow for speciation and extinction rates
236 to be estimated using moderately-sized phylogenies, although the ability of BAMM to model evolutionary rate
237 shifts and extinction rates is debated^{45–48}. Additionally, while several tip-rate estimates exist for speciation
238 rate (e.g., λ_{DR} and λ_{ND}), tip-rate estimates of extinction rate are difficult to obtain without complex Bayesian
239 models which are sensitive to sampling bias⁶⁵. Although extinction rates can be inferred from alternative
240 sources, such as the fossil record⁶⁶, direct observation extinction, or IUCN red list status⁵⁸, each approach
241 has its limitations. Across the passerine bird phylogeny, we found that BAMM often produced homogeneous
242 speciation and extinction rates for smaller clades showing few rate shifts, which might reduce our power
243 to detect small differences in extinction rates among closely-related taxa^{48,67}. Thus, this methodological
244 constraint likely decreases our ability to accurately measure the correlation between metrics of sexual selection
245 and the probability of extinction.

246 One outcome of our analyses was that different measures of speciation rates presented different results. This
247 is not completely surprising, because each of the rates is calculated differently (see 67). For instance, λ_{DR}
248 is weighted more towards speciation events close to the tips and allows more rate heterogeneity compared
249 to BAMM estimates. This leads to greater variation in λ_{DR} relative to the BAMM estimates, potentially
250 explaining the difference in results. The BAMM estimates were also more sensitive to phylogenetic uncertainty.

251 To summarise, we have shown that male-biased sexual selection, but not sexual dichromatism, predicts
252 speciation in passerines, and that this relationship is not markedly affected by environmental variability.
253 These findings imply that sexual dechromatism is not a reliable proxy for sexual selection, and that alternative
254 measures of sexual selection are more directly related to diversification. Our results also add indirect support
255 to the hypothesis that sexual selection promotes adaptation, which has implications for conservation²⁵ and
256 captive breeding programs for threatened species⁶⁸. Furthermore, our finding that high speciation rate is
257 associated with smaller range size highlights the threat to the persistence of rapidly-speciating lineages in
258 a world with increased habitat loss and anthropogenic stress. This concern arises as the best predictor of
259 extinction risk is range size⁶⁹ and the association found here implies that many newly-speciated clades have
260 small range sizes and could thus be at greater risk of extinction.

261 MATERIALS AND METHODS

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

267 Compiling data for sexual selection and environmental stress

268 Sexual dichromatism

269 We used a previously-published measure of sexual dichromatism for 5,983 species of passerines⁴³. Briefly, 43
270 obtained sex-specific RGB (red-green-blue) values across six body patches (nape, crown, forehead, throat,
271 upper breast, and lower breast) from *Handbook of the Birds of the World*⁷⁰. The relative contribution of male
272 and female RGB colour values were averaged across body patches and provide ‘male-like’ and ‘female-like’
273 plumage scores. Here we use the absolute difference between male and female plumage scores as an estimate
274 of sexual dichromatism. Additionally, we used another measure of dichromatism corresponding to colour
275 distance in avian colour space derived from spectral data⁴¹. These measurements include variation in the
276 ultraviolet and bird-visible range and — unlike the RGB measures — are sourced from museum specimens
277 as opposed to illustrations. The spectrophotometry data covers only 581 passerine species (10-fold fewer
278 than the RGB data), although there was a substantial correlation between the two dichromatism measures
279 ($r = 0.79$; [Figure S10](#)).

280 Male-biased sexual selection

281 Because sexual dichromatism is presumably imperfectly correlated with variation in the strength of sexual
282 selection across taxa, we sourced an additional measure of sexual selection, also from 43, referred to here as
283 the ‘index of male-biased sexual selection’. This index is the first principal component from a phylogenetic
284 principal component analysis (PPCA) of three characteristics positively associated with sexual selection
285 (sexual size dimorphism, social polygyny and [lack of] paternal care). This measure of male-biased sexual
286 selection is available for only 2,465 species, and shows a moderate correlation with the RGB measure of
287 sexual dichromatism ($r = 0.34$; [Figure S12](#)).

288 Environmental variables

289 We obtained estimates of species range size using expert range maps⁷¹. Because of taxonomic changes
290 to 1,230 species in the Birdlife database⁷² we manually matched these taxa with the names used in the
291 sexual dichromatism dataset⁴³. From these distributions, we obtained estimates of climatic conditions that
292 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19
293 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 resolution⁷³. 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 interglacial⁷⁴. 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 3⁷⁵. 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).

305 Generating biologically relevant predictors for environmental stress

Given that stressful environments are expected to interact with sexual selection and have a positive effect on adaptation⁹, we used the extracted environmental variables from each species range size to create predictors of environmental variation/stress. Firstly we used (i) the average NPP in each species' range and (v) the log-transformed range size as potentially informative predictors of speciation rates. We also used three environmental predictors derived from bioclimatic data. These predictors relate to seasonal climate variation, spatial climate variation and long-term climate variation. To obtain seasonal climate variation we used (iii) mean values of temperature seasonality (BIO4) for each range. (iv) To estimate levels of spatial environmental variation a species may endure we used the first principle component (PC1) from a PCA on standard deviations from all bioclimatic variables, excluding temperature and precipitation seasonality (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. Similarly to spatial variation, the long-term climate variation is primarily loaded to temperature differences between the LIG and current climates (Table S2, Figure S2). The five predictors of environmental variability are not strongly correlated (Figure S3). Details and R code to generate these predictors can be found within the ESM.

325 Estimating extinction and speciation

Phylogenetic information was obtained from www.birdtree.org¹⁰. We used a maximum clade credibility (MCC) tree from 2,500 samples of the posterior distribution ($n = 5,965$) as the main phylogenetic hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using tip-rate measures (1000 trees) and BAMM (100 trees)¹¹. These trees used a 'Hackett backbone'⁷⁶ and were constructed using a pure birth (Yule) model. We calculated three different tip-rate metrics of speciation and one of extinction

332 across all trees.

333 Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes
 334 and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating the
 335 density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES), also
 336 known as diversification rate (DR)^{10,77,78}, is derived from the sum of edge lengths branching from a node,
 337 with each edge towards the root having the length down-weighted. Studies have suggested that DR and ND
 338 (henceforth referred to as λ_{DR} and λ_{ND}) are more reflective estimates of speciation than diversification; this
 339 is because λ_{DR} and λ_{ND} cannot account for whole-clade extinctions and thus under-estimate extinction rate,
 340 which makes the composite measure of diversification more dependent on speciation^{67,79}. Therefore, λ_{DR} is a
 341 measure of speciation rate more heavily weighted to recent speciation events while λ_{ND} measures speciation
 342 across the root-to-tip path. These tip-rate measures are alternatives to state-dependent diversification models
 343 such as Quantitative State Speciation-Extinction (QuaSSE); but, based on previous simulation studies, λ_{DR}
 344 and λ_{ND} are robust and intuitive measures that provide high power and low false discovery rate with large
 345 phylogenies when incorporated into Phylogenetic Generalized Least Squares (PGLS) models¹².

346 Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic
 347 trees¹¹. This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo) to generate
 348 probability distributions of evolutionary rate-shift configurations with variable speciation and extinction rates.
 349 Importantly, these models provide tip-rate estimates of speciation and extinction rate. The parameters of the
 350 100 BAMM runs are detailed in full in the [ESM](#); briefly, we used a time-variable model with 100 expected
 351 number of shifts and prior rates set from the initial speciation and extinction values using the **BAMMtools**
 352 R package⁸⁰. Each BAMM model (one MCC tree and 100 random draws of the posterior) was run for 100
 353 million generations, and given the computationally intensive nature of BAMM, runs were conducted across
 354 multiple CPUs. Each run of BAMM reached convergence with effective sample size (ESS) of MCMC (Markov
 355 Chain Monte Carlo) samples surpassing 200 (an arbitrary value, above which posterior distributions can often
 356 be accurately inferred) for the key model parameters of log-likelihood and number of rate shifts ([Table S3](#),
 357 [Table S4](#)). Further details of BAMM parameters and output are available in the [ESM](#), with tip-rate means
 358 and variances provided. Additionally, given the variability in BAMM estimates, we also provide analysis of
 359 BAMM shift configurations and tip-rate estimates from our run on the MCC tree and within a BAMM run
 360 on the MCC tree from a genetic-only phylogeny across all birds⁸¹. All analyses were conducted on log-rates.

361 Phylogenetic comparative analysis

362 To test the association between speciation/extinction and sexual selection, environmental variability and
 363 their interaction, we used phylogenetic least squares (PGLS) models in the **n1me** package⁸². Firstly, we
 364 conducted model selection to compare models in which λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} were the response
 365 variable: these tip-rate estimates all came from the same MCC tree (derived from 2,500 draws of the posterior
 366 distribution in 10). For models of λ_{BAMM} and μ_{BAMM} we used the inverse of the variance associated
 367 with each tip rate estimate as weights, to account for the variable precision of the estimates provided by
 368 BAMM. The most complicated model in each set under comparison contained one of the measures of sexual
 369 selection (sexual dichromatism or the index of male-biased sexual selection), all of the environmental measures
 370 (i.e. log-transformed range size, seasonal temperature variation, spatial temperature variation, long-term
 371 temperature variation, and NPP), and all of the 2-way interactions between sexual selection and each of the

environmental measures. The simpler models contained all of the same main effects, but had fewer 2-way interaction terms (potentially none). Model selection was done in MuMIn using the `dredge` function⁸³. Using the terms from the top-ranked model (ranked by AICc), we ran the equivalent model for each of the 1,000 phylogenetic trees used to derive λ_{DR} , λ_{ND} and each of the 100 trees used to derive λ_{BAMM} and μ_{BAMM} . In each model we used the unique response variables and phylogenetic tree correlation structure. Specifically, for models using tip-rate metrics (λ_{DR} , λ_{ND}) we estimated the phylogenetic signal — Pagel's λ ⁸⁴ — using the `corPage1` function in the `ape` package⁸⁵ independently for each of the 1,000 trees/models. Alternatively, for models using speciation and extinction estimates derived using BAMM (λ_{BAMM} and μ_{BAMM}) we found λ 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 the subset of species with measurements of male-biased sexual selection, we conducted a phylogenetic path analysis using the `phylopath` R package⁸⁶. 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, λ_{DR} as the single measure of speciation and the tip-rates from the MCC tree. Further details of the path analysis, including our rationale for each path's directions, can be found within the [ESM](#) along with all other analyses and the relevant R code to reproduce results.

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