

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

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

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

4 **Abstract**

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

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

17 INTRODUCTION

18 Sexual selection is a fundamental evolutionary process; yet there is long-standing debate about how it shapes
19 patterns of species diversity^{1–5}. Sexual selection can promote speciation because it operates on traits that
20 can create reproductive isolation when they diverge between lineages, such as signals and preferences involved
21 in mate selection^{1,2,6}, sperm-egg interactions⁷, or genital morphology⁸. Sexual selection could also promote
22 speciation or prevent extinction by purging deleterious mutations⁹, fixing beneficial ones¹⁰, and accelerating
23 adaptation in different environments^{11–13}. Conversely, sexual selection might hinder speciation or make
24 extinction more likely by favouring traits that improve mating success but reduce population fitness^{14–17}.
25 For example, species with costly sexual signals may be less resilient to environmental change¹⁸. Sexual
26 selection might also promote extinction by causing maladaptation ('gender load') in female traits that are
27 genetically correlated with sexually-selected male traits^{19–23}. Although numerous studies have examined
28 the relationship between sexual selection and speciation or extinction rates^{4,24–28}, the availability of more
29 complete phenotypic, ecological and phylogenetic data²⁹, together with significant advances in phylogenetic
30 methods^{30,31}, present new opportunities to test whether and how sexual selection drives diversification.

31 The relationship between sexual selection and diversification may depend on the environment. Theoretical
32 work predicts that sexual selection should have a more positive effect on adaptation and population fitness
33 in variable environments relative to stable ones^{32,33}. In stable environments, consistent selection depletes
34 genetic variation at sexually concordant loci (i.e. loci where the same allele is fittest for both sexes). In these
35 environments, genetic variation remains disproportionately at sexually antagonistic loci, leading to stronger
36 gender load and reduced net benefits of sexual selection³³. By contrast, in spatially or temporally variable
37 environments, sexual selection can enhance local adaptation. For example, in Darwin's finches (*Geospiza*
38 *fortis*) divergent beak morphology is an adaptation to local food availability that has been maintained through
39 assortative mating³⁴. Despite the potential interaction between sexual selection and environmental variability
40 in diversification, comparative tests are currently lacking.

41 Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification^{4,24,25,27,28}
42 because their biology and phylogenetic relationships are comparatively well-known. A 2011 meta-analysis
43 covering 20 primary studies of birds and other taxa found a small but significant positive association between
44 sexual selection and speciation, with the average effect size in birds stronger than in mammals but weaker
45 than in insects or fish²⁶. However, there was large variation in effect size estimates across the 20 studies, likely
46 reflecting differences in methodology, such as metrics used to characterise speciation and sexual selection,
47 in addition to true biological differences. More recently, Huang & Rabosky²⁸ found no association between
48 sexual dichromatism and speciation ($n = 918$ species) in a study using spectrophotometric measurements of
49 museum specimens³⁵ and tip-rate estimates from a molecular-only phylogeny²⁹. Similarly, Cooney et al.³⁶
50 found no effect of sexual dichromatism on diversification across 1,306 pairs of species, using dichromatism
51 scores provided by human observers.

52 Here, we investigate the association between sexual selection and diversification in birds while building upon
53 previous approaches in multiple ways. We use two measures of the strength of sexual selection: sexual
54 dichromatism³⁷, as well as an index of male-biased sexual selection³⁷, which captures (co)variation in sexual
55 size dimorphism, social polygyny and paternal care. We use these two measures because sexual dichromatism
56 does not always signal the presence of strong sexual selection and *vice versa*³⁷. For example, male and

57 female dunnocks (*Prunella modularis*) are similarly coloured yet sexual selection appears to be strong³⁸.
58 Furthermore, a recent comparative study found a negative relationship between dichromatism and another
59 sexually-selected trait (song) across species, suggesting that a multi-trait focus would improve estimates of
60 sexual selection intensity⁵. Additionally, our analysis includes multiple ecological and environmental variables,
61 allowing us to adjust for potential confounds, to identify environmental factors driving diversification, and
62 to test whether environmental factors interact with sexual selection as theory predicts³³. We use multiple
63 approaches for quantifying speciation and extinction rates at the tips of phylogenetic trees, including BAMM
64 (Bayesian Analysis of Macroevolutionary Mixtures)^{39–42}, as well as older but reliable tip-rate statistics, namely
65 diversification rate (λ_{DR}) and node density (λ_{ND})²⁹.

66 RESULTS

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

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

80 The two measures of sexual dichromatism were from previously published data, one based on RGB (red-
81 green-blue) values from images in *Handbook of the Birds of the World*⁴³ ($n = 5,983$), and the other based
82 on spectrophotometry and avian colour space ($n = 581$)³⁵. The index of male-biased sexual selection is
83 associated with greater sexual size dimorphism, social polygyny and lack of paternal care ($n = 2,465$).

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

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

91 We found a significant positive association between the index of male-biased sexual selection ($n = 2,465$) and
92 λ_{DR} for the MCC tree ($\beta = 3.887\text{e-}02$, $p = 0.012$; Figure 1b). However, this association was not significant

93 for the other two measures of speciation rate (λ_{ND} : $\beta = 4.383\text{e-}04$, $p = 0.351$; λ_{BAMM} : $\beta = 9.423\text{e-}04$, $p =$
 94 0.764; [Figure 1b](#)). The distribution of estimates from PGLS models on 1,000 trees was similar to the estimate
 95 from the MCC tree: among the 1,000 trees there was a positive association between sexual selection and λ_{DR}
 96 (highest posterior density (HPD) Interval = $4.513\text{e-}03$, $5.718\text{e-}02$), and the distribution skewed towards a
 97 positive association between sexual selection and λ_{ND} (HPD Interval = $-5.044\text{e-}04$, $1.585\text{e-}03$;) as well as the
 98 100 models using λ_{BAMM} (HPD Interval = $-1.295\text{e-}02$, $3.088\text{e-}02$; [Table S15](#)).

99 In contrast to male-biased sexual selection, we found no evidence that species with increased sexual dichro-
 100 matism have higher or lower rates of speciation. Sexual dichromatism showed no association with λ_{DR} (β
 101 = $-1.279\text{e-}03$, $p = 0.147$; [Figure 1a](#), [Figure 2](#)), λ_{ND} ($\beta = -5.745\text{e-}05$, $p = 0.078$; [Figure 1a](#)) or λ_{BAMM} (β
 102 = $-1.429\text{e-}05$, $p = 0.872$; [Figure 1a](#)). PGLS analyses using sexual dichromatism ($n = 581$) measured by
 103 spectrophotometry³⁵ yielded results concordant with the full dataset; i.e. no association between sexual
 104 dichromatism and speciation ([Figure S11](#)). Our results from models based on the MCC tree are largely
 105 corroborated by model estimates from PGLS analyses of the rates and correlation structures from 1,000 trees
 106 (for λ_{DR} , λ_{ND}) and 100 trees for λ_{BAMM} . The HPD intervals show model estimates are distributed around
 107 zero when using complete taxon sampling models and RGB measures of sexual dichromatism (λ_{DR} : HPD
 108 Interval = $-1.635\text{e-}03$, $1.658\text{e-}03$, λ_{ND} : HPD Interval = $-4.256\text{e-}05$, $5.499\text{e-}05$, [Figure 1a](#), [Table S8](#)). For PGLS
 109 models using spectrophotometry-based measures of sexual dichromatism, the estimates from the 100 trees
 110 in the λ_{DR} models are positively skewed (HPD Interval = $-1.780\text{e-}02$, $3.489\text{e-}02$) but normally distributed
 111 around zero for λ_{ND} and λ_{BAMM} ([Table S12](#)).

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

119 Species with smaller ranges have increased rates of speciation

120 Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation, we found a negative association between range size
 121 and speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This
 122 negative association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.579\text{e-}03$, $p =$
 123 0.001; λ_{ND} : $\beta = -1.462\text{e-}04$, $p = 0.034$; [Figure 1a](#), [Figure 2](#)). This association was also evident across the
 124 estimates from models using the 1,000 trees (λ_{DR} : HPD Interval = $-8.871\text{e-}03$, $-6.610\text{e-}04$; λ_{ND} : HPD Interval
 125 = $-1.514\text{e-}04$, $1.724\text{e-}05$; [Figure 1a](#)). Subset models with reduced sample size and different measures of sexual
 126 selection — but the same measure of range size — showed equivocal evidence that range size is negatively
 127 associated with speciation. Range size significantly predicted λ_{DR} ([Figure 1b](#)) using data subset for species
 128 with an index of male-biased sexual selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} . Models using data subset
 129 for spectrophotometry-based dichromatism ($n = 581$) gave non-significant estimates for the effect of range
 130 size on all measures of speciation ([Figure S11](#), [Table S11](#), [Table S12](#)). Because the range size dataset is the
 131 same across the three data subsets we draw our conclusions from the models with the highest power using
 132 near-complete taxon sampling ($n = 5,812$).

133 Phylogenetic path analysis

134 Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
135 ([Figure 3](#); [Figure S14](#)). There was a modest effect of male-biased sexual selection on sexual dimorphism (β
136 = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism (β = 0.07) and strongly
137 affected range size (β = 0.52). This suggests an indirect effect of temperature seasonality on λ_{DR} ($\beta_{indirect}$ =
138 -0.02; [Figure 3](#)), given the negative association we identified between λ_{DR} and range size in PGLS models.

139 Extinction rate

140 We found no evidence that extinction (μ_{BAMM}) was impacted by the extent of sexual dichromatism for
141 full-taxon sampling (β = 2.385e-05, p = 0.93; [Figure 1a](#)), nor spectrophotometry-based measures of sexual
142 dichromatism ([Figure S11](#), [Table S11](#), [Table S12](#)) or male-biased sexual selection ([Figure 1b](#), [Table S14](#), [Table](#)
143 [S15](#)).

144 Variability across phylogenetic trees and speciation rate measures

145 Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially
146 in the BAMM rates (λ_{BAMM} and μ_{BAMM}), where the 95 % HPD interval across PGLS model estimates
147 from 100 trees was often > 20 times larger than the 95 % confidence interval for estimates from a single
148 PGLS model using the MCC tree. This contrasts with variation across trees for the other rate estimates
149 (λ_{DR} and λ_{ND}), where the 95 % HPD interval of model estimates for pgls models using 1,000 trees was
150 near-equivalent to the 95 % confidence interval calculated for pgls model estimates of the MCC tree ([Table](#)
151 [S9](#)). Given the computational requirements of BAMM, the great majority of earlier studies have based their
152 estimates on a single consensus tree, and so the inconsistency of the BAMM estimates between different
153 phylogenies with similar statistical support is notable. Mean measures of speciation rate across 100 trees
154 were positively correlated between measures (λ_{DR} - λ_{BAMM} : $r=0.75$, λ_{DR} - λ_{ND} : $r=0.65$, λ_{ND} - λ_{BAMM} :
155 $r=0.51$; [Figure S15](#)). Given that the calculation of BAMM rates can be affected by the settings of the run
156 and the use of different priors, we compared the estimate of our MCC tree with that of previous published
157 analyses on birds, and found a high correlation ($r=0.81$, [Figure S8](#)). Full details of the BAMM results are
158 presented as supplementary materials.

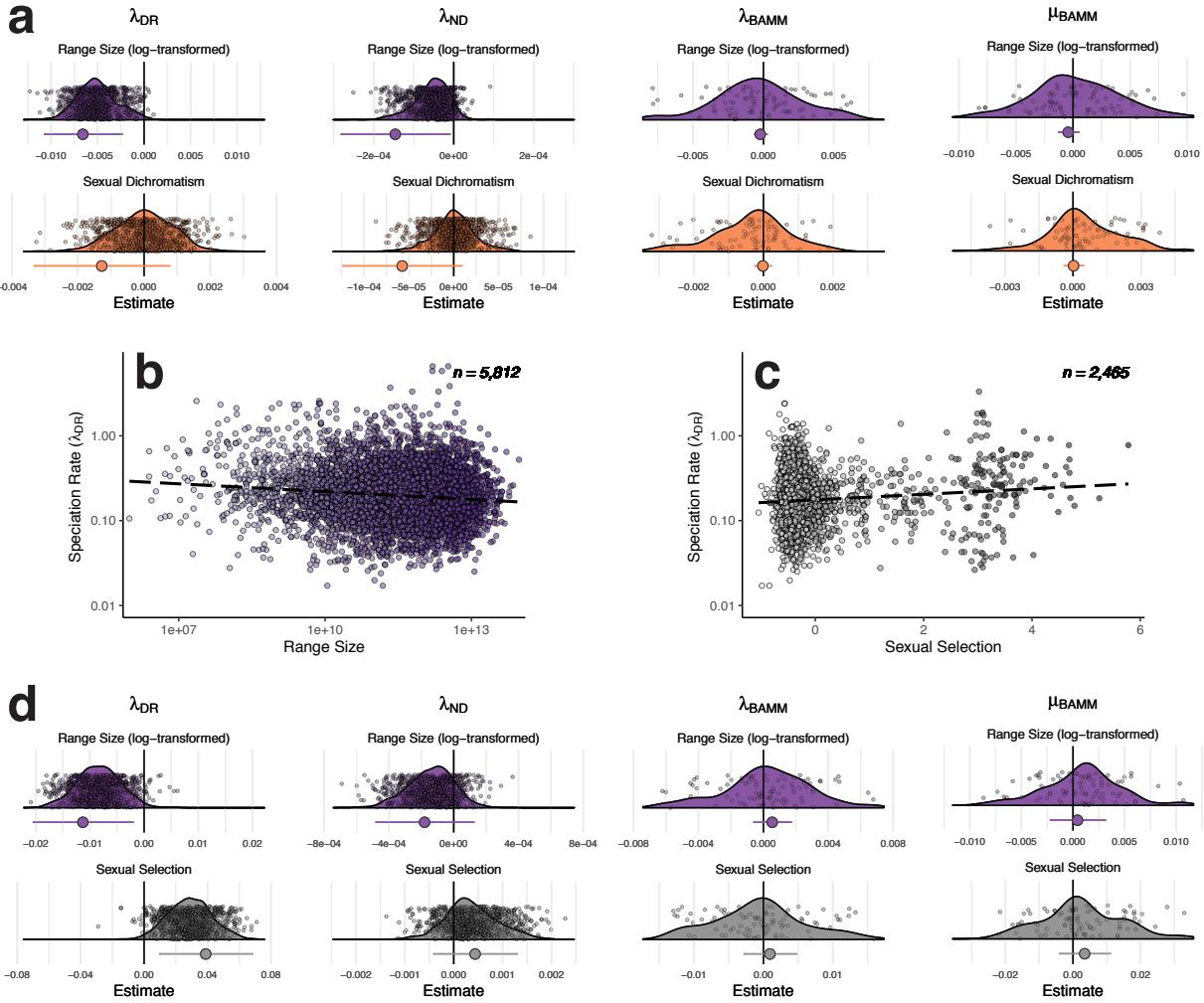


Figure 1: Model estimates (a) for the effect of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset (RGB values, $n = 5,812$). (b) depicts the scatter plot of speciation rate (λ_{DR}) and log-range size with the model estimate 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 an index of male-biased sexual selection ($n = 2,465$) and shows the effect of log-range size and male-biased sexual selection on speciation and extinction rates. Both datasets were used for analyses with three measures of speciation (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.

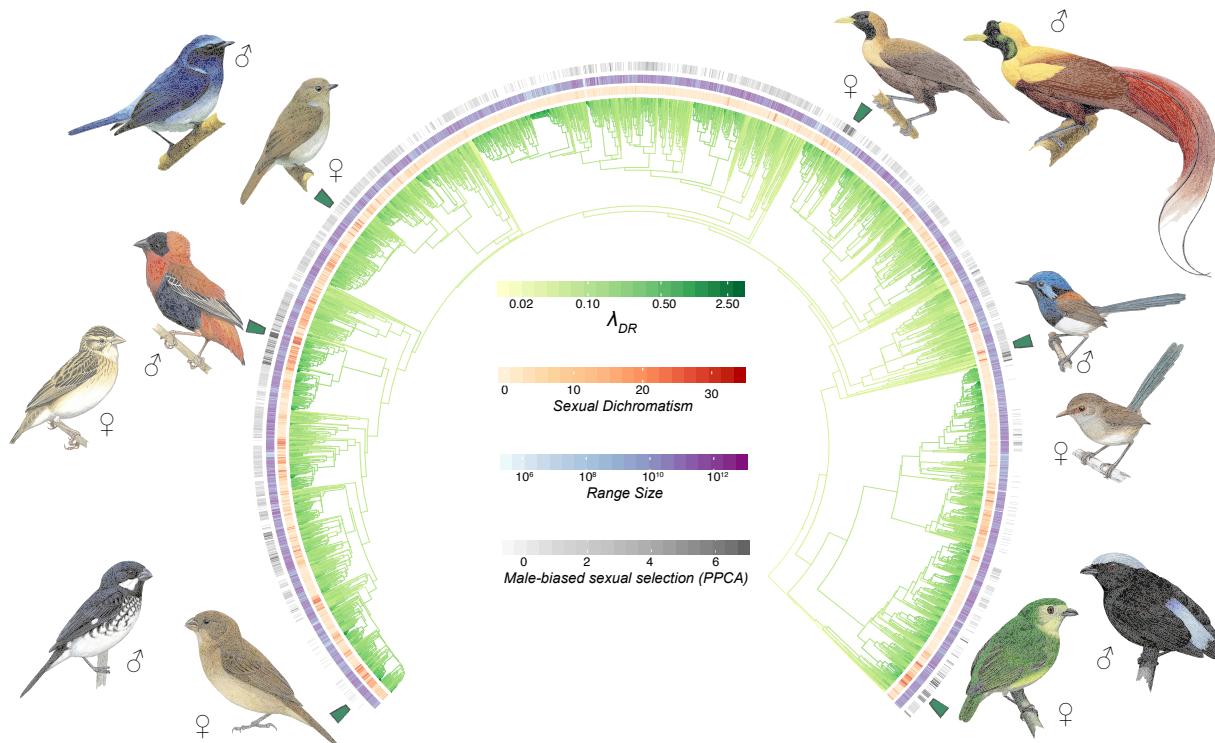


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism, range size available for 5,812 species and an index of male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative association 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.

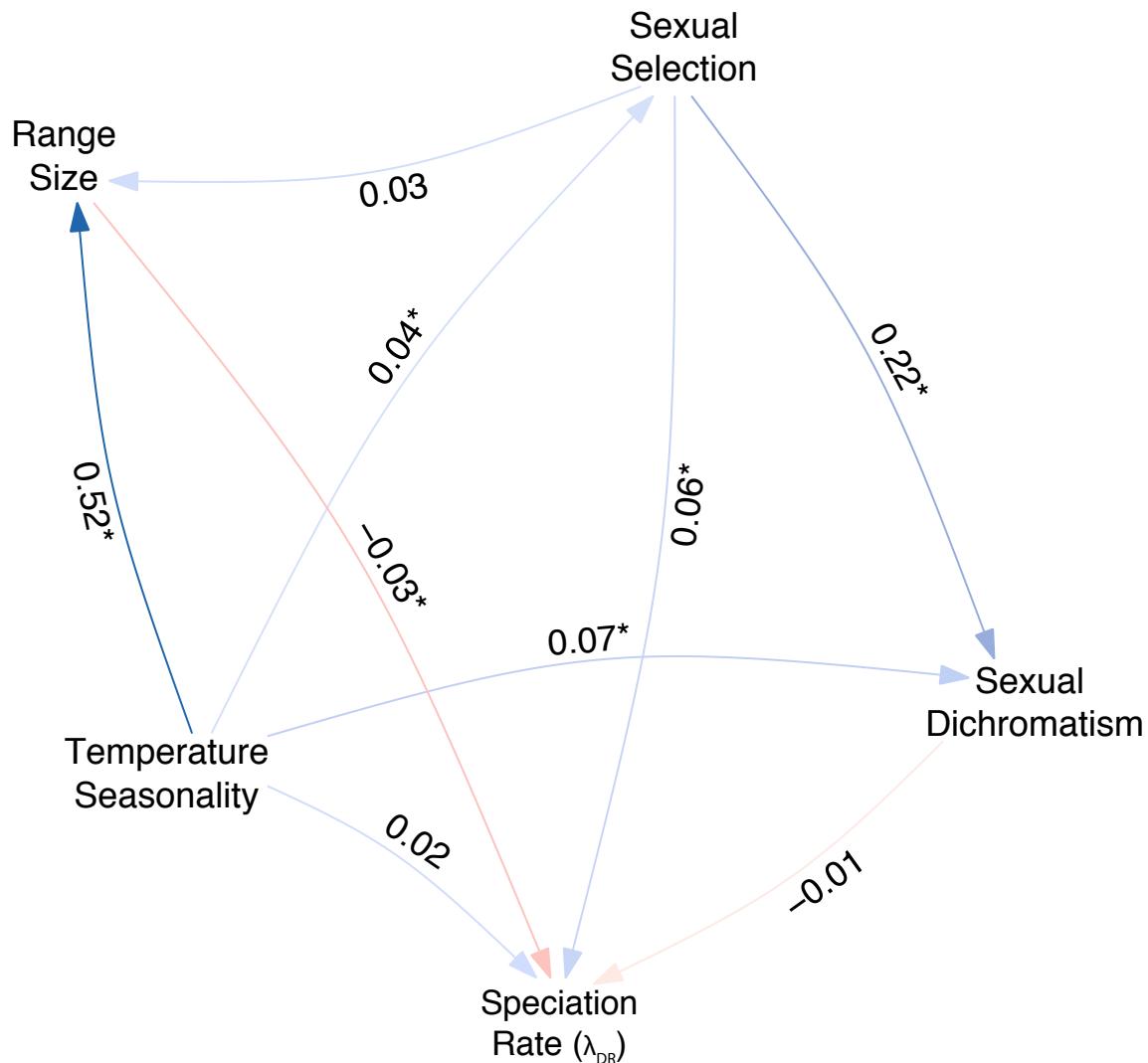


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with the direction of effect corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95% confidence intervals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

159 DISCUSSION

160 We found evidence that the composite index of male-biased sexual selection, but not measures of sexual
161 dichromatism, is correlated with the rate of speciation in passerine birds. The absence of a detectable
162 correlation between sexual dichromatism and speciation rate was consistent across different measures of
163 speciation (λ_{DR} , λ_{ND} and λ_{BAMM}) and both measures of dichromatism (spectral and RGB), and it cannot
164 be explained by a difference in statistical power since the sample size for the dichromatism analyses was much
165 larger. These findings reaffirm the conclusions of previous, smaller studies in which sexual dichromatism
166 was measured using spectrophotometry²⁸ or human observers³⁶. The correlation between speciation rate
167 and the index of male-biased sexual selection (which encapsulates variation in sexual size dimorphism, social
168 polygyny, and paternal care) was statistically significant for λ_{DR} , but not for λ_{ND} and λ_{BAMM} . Interestingly,
169 we also found a consistent negative relationship between range size and speciation rate, at least when this
170 rate was quantified using λ_{DR} and λ_{ND} . None of the bioclimatic measures of environmental variability that
171 we investigated (i.e., temperature seasonality, long-term temperature variation, and spatial temperature
172 variation) significantly predicted speciation rate.

173 The difference in findings between the analyses of sexual dichromatism *versus* the index of sexual selection
174 is noteworthy, because the majority of earlier studies used dichromatism alone as their proxy for sexual
175 selection^{24,25,27,28,44}. Given our findings, and the modest correlation between dichromatism and the sexual
176 selection index³⁷, we suggest that sexual dichromatism may not be a robust proxy for sexual selection.
177 Although dichromatism clearly reflects sexual selection to some extent, it may be too indirect a measure to
178 detect any association with speciation rate, even with large sample size. There are several reasons why the use
179 of sexual dichromatism as a proxy for sexual selection is problematic. Firstly, sexual dichromatism can evolve
180 for reasons other than sexual selection, such as when males and females occupy different ecological niches^{45–48}
181 or experience different selective pressures in contexts other than competition for mates⁴⁹. For example,
182 in superb fairy-wrens (*Malurus cyaneus*) female colouration has probably evolved in response to spatial
183 variation in predation pressure, increasing dichromatism⁵⁰. Ecological selection on sexual dichromatism was
184 implicated by our path analysis, which found that sexual dichromatism is positively affected by temperature
185 seasonality (a measure of environmental variation), albeit weakly. Secondly, colour is only one of the traits
186 subject to sexual selection^{13,51}. For instance, sexual selection may promote investments in other mating
187 signals (e.g. song) that trade-off against plumage colour, leading to variable investment in different sexually
188 selected signals across species⁵. Lastly, not all plumage colouration honestly reflects mate quality. A recent
189 meta-analysis found that converted carotenoids (but not carotenoids sourced from the diet) predict mate
190 quality through improvements in parasite resistance and reproductive success⁵². Given the importance of
191 honest signaling in sexual selection and the variability in colour production mechanisms across birds, sexual
192 dichromatism in many species may be an unreliable measure of mate quality for female birds and sexual
193 selection for researchers.

194 In-line with some theoretical predictions and previous studies²⁶ we found that male-biased sexual selection
195 increases speciation rate, at least when speciation is measured by λ_{DR} . Additionally, we found that this
196 association appears to be independent of net primary productivity and spatiotemporal variation in the
197 environment. The lack of an effect of these environmental variables on speciation rate has several possible
198 interpretations. Firstly, the effects of sexual selection on adaptation and speciation may depend on the type of
199 environmental variability under which the species is evolving. Specifically, speciation rates might be impacted

200 by genetic constraints on adaptation, that vary across environments. Theory suggests that sexual antagonism
201 (which is often exacerbated in species with strong sexual selection) may be lower in habitats experiencing
202 cyclical environmental variation (e.g. seasonality), relative to those experiencing directional change in the
203 environment³³. Another possibility is that the environmental predictors we chose may not account for the
204 key ecological sources of selection that interact with sexual selection to drive speciation. For example, our
205 study does not include direct measure of food availability or the severity of predation and parasitism, which
206 are both hypothesised to affect sexual selection and speciation⁵³. Finally, it is possible that environmental
207 variability genuinely has little effect on speciation rates, at least in the taxa investigated here.

208 The most robust finding in our study is the finding that species with smaller ranges have elevated speciation
209 rates. This result is similar to a study of 329 amphibian genera, which found higher diversification rates
210 in taxa with smaller range size⁵⁴. Intuitively, large range size should promote speciation by creating more
211 opportunities for geographic barriers to form^{55,56}. However, the opposite pattern is also plausible because
212 birds with limited dispersal or more specialised niches can have more fragmented populations, which would
213 promote vicariant divergence and higher speciation rates^{57–59}. It is also possible that high speciation rates
214 cause smaller range sizes, rather than the other way around, for example because repeatedly-speciating
215 lineages tend to fill niches in ways that hinder the geographical expansion of new species^{49,55,60}. However,
216 species undergoing adaptive radiation in new habitats are unlikely to be limited by competition for resources
217 from existing taxa. One further explanation for the negative association between range size and sexual
218 dichromatism/sexual selection is the potential bias of taxonomic classification, whereby over-splitting of
219 species in clades with large ranges leads to increased recent phylogenetic branching as well as smaller ranges.

220 In addition to speciation, sexual selection is hypothesised to affect extinction. Using the model-based
221 approach of BAMM, we found no association between the estimated extinction rate and sexual dichromatism,
222 male-biased sexual selection, or our measures of environmental variability. However, these extinction results
223 should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from
224 phylogenies, principally because different combinations of speciation and extinction rates can give rise to
225 similar patterns of diversity⁴⁰. Phylogenetic methods such as BAMM allow for speciation and extinction rates
226 to be estimated using moderately-sized phylogenies, although the ability of BAMM to model evolutionary rate
227 shifts and extinction rates is debated^{39–42}. Additionally, while several tip-rate estimates exist for speciation
228 rate (e.g., λ_{DR} and λ_{ND}), tip-rate estimates of extinction rate are difficult to obtain without complex Bayesian
229 models which are sensitive to sampling bias⁶¹. Although extinction rates can be inferred from alternative
230 sources, such as the fossil record⁶², direct observation extinction, or IUCN red list status⁵⁴, each approach
231 has its limitations. Across the passerine bird phylogeny, we found that BAMM often produced homogeneous
232 speciation and extinction rates for smaller clades showing few rate shifts, which might reduce our power
233 to detect small differences in extinction rates among closely-related taxa^{42,63}. Thus, this methodological
234 constraint likely decreases our ability to accurately measure the correlation between metrics of sexual selection
235 and the probability of extinction.

236 One outcome of our analyses was that different measures of speciation rates presented different results. This is
237 not completely surprising, because each of the rates is calculated differently⁶³. For instance, λ_{DR} is weighted
238 more towards speciation events close to the tips and allows more rate heterogeneity compared to BAMM
239 estimates. This leads to greater variation in λ_{DR} relative to the BAMM estimates, potentially explaining the
240 difference in results. The BAMM estimates were also more sensitive to phylogenetic uncertainty.

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

²⁴² speciation in passerines, that the magnitude of this effect is modest, and that this relationship is not markedly
²⁴³ affected by environmental variability. These findings imply that sexual dechromatism is not a reliable proxy for
²⁴⁴ sexual selection, and that alternative measures of sexual selection are more directly related to diversification.
²⁴⁵ Our results also add indirect support to the hypothesis that sexual selection promotes adaptation, which
²⁴⁶ has implications for conservation¹⁶ and captive breeding programs for threatened species⁶⁴. Furthermore, our
²⁴⁷ finding that high speciation rate is associated with smaller range size highlights the threat to the persistence
²⁴⁸ of rapidly-speciating lineages in a world with increased habitat loss and anthropogenic stress. This concern
²⁴⁹ arises as the best predictor of extinction risk is range size⁶⁵ and the association found here implies that many
²⁵⁰ newly-speciated clades have small range sizes and could thus be at greater risk of extinction.

251 MATERIALS AND METHODS

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

257 Compiling data for sexual selection and environmental stress

258 Sexual dichromatism

259 We used a previously-published measure of sexual dichromatism for 5,983 species of passerines³⁷. Briefly, Dale
260 et al.³⁷ obtained sex-specific RGB (red-green-blue) values across six body patches (nape, crown, forehead,
261 throat, upper breast, and lower breast) from *Handbook of the Birds of the World*⁴³. The relative contribution
262 of male and female RGB colour values were averaged across body patches and provide ‘male-like’ and
263 ‘female-like’ plumage scores. Here we use the absolute difference between male and female plumage scores as
264 an estimate of sexual dichromatism. Additionally, we used another measure of dichromatism corresponding to
265 colour distance in avian colour space derived from spectral data³⁵. These measurements include variation in
266 the ultraviolet and bird-visible range and — unlike the RGB measures — are sourced from museum specimens
267 as opposed to illustrations. The spectrophotometry data covers only 581 passerine species (10-fold fewer
268 than the RGB data), although there was a substantial correlation between the two dichromatism measures
269 ($r = 0.79$; [Figure S10](#)).

270 Male-biased sexual selection

271 Because sexual dichromatism is presumably imperfectly correlated with variation in the strength of sexual
272 selection across taxa, we sourced an additional measure of sexual selection³⁷, referred to here as the ‘index
273 of male-biased sexual selection’. This index is the first principal component from a phylogenetic principal
274 component analysis (PPCA) of three characteristics positively associated with sexual selection (sexual size
275 dimorphism, social polygyny and [lack of] paternal care). This measure of male-biased sexual selection
276 is available for only 2,465 species, and shows a moderate correlation with the RGB measure of sexual
277 dichromatism ($r = 0.34$; [Figure S12](#)).

278 Environmental variables

279 We obtained estimates of species range size using expert range maps⁶⁶. Because of taxonomic changes
280 to 1,230 species in the Birdlife database⁶⁷ we manually matched these taxa with the names used in the
281 sexual dichromatism dataset³⁷. From these distributions, we obtained estimates of climatic conditions that
282 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19
283 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 resolution⁶⁸. 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)⁶⁹. 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)⁷⁰. Using these data, which we provide as a potentially useful data resource (see [ESM](#)), we generated five predictors of speciation associated with different patterns in environmental variability (see below).

Generating biologically relevant predictors for environmental stress

Given that stressful environments are expected to interact with sexual selection and have a positive effect on adaptation¹³, we used the extracted environmental variables from each species range size to create predictors of environmental variation/stress. Firstly we used (i) the average NPP in each species' range and (v) the log-transformed range size as potentially informative predictors of speciation rates. We also used three environmental predictors derived from bioclimatic data. These predictors relate to seasonal climate variation, spatial climate variation and long-term climate variation. To obtain seasonal climate variation we used (iii) mean values of temperature seasonality (BIO4) for each range. (iv) To estimate levels of spatial environmental variation a species may endure we used the first principle component (PC1) from a PCA on standard deviations from all bioclimatic variables, excluding temperature and precipitation seasonality (BIO4 and BIO15). PC1 was heavily loaded towards bioclimatic variables relating to temperature, thus PC1 reflects the variation in temperature across a species' range ([Table S1](#)). Species range is a potentially informative predictor of speciation and extinction, so we controlled for the correlation between environmental spatial variation and range size — where larger ranges have larger variation in PC1 — by using the residuals of a fitted general additive model (GAM; [Figure S1](#)) as a predictor. To obtain long-term variation in climates for each species range we take (v) the first principal component of the absolute difference in the bioclimatic variables between the LIG and current values. Similarly to spatial variation, the long-term climate variation is primarily loaded to temperature differences between the LIG and current climates ([Table S2](#), [Figure S2](#)). The five predictors of environmental variability are not strongly correlated ([Figure S3](#)). Details and R code to generate these predictors can be found within the [ESM](#).

Estimating extinction and speciation

Phylogenetic information was obtained from www.birdtree.org²⁹. We used a maximum clade credibility (MCC) tree from 2,500 samples of the posterior distribution ($n = 5,965$) as the main phylogenetic hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using tip-rate measures (1,000 trees) and BAMM (100 trees)³⁰. These trees used a 'Hackett backbone'⁷¹ and were constructed using a pure birth (Yule) model. We calculated three different tip-rate metrics of speciation and one of extinction across all trees.

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

and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES), also known as diversification rate (DR)^{29,72,73}, is derived from the sum of edge lengths branching from a node, with each edge towards the root having the length down-weighted. Studies have suggested that DR and ND (henceforth referred to as λ_{DR} and λ_{ND}) are more reflective estimates of speciation than diversification; this is because λ_{DR} and λ_{ND} cannot account for whole-clade extinctions and thus under-estimate extinction rate, which makes the composite measure of diversification more dependent on speciation^{63,74}. Therefore, λ_{DR} is a measure of speciation rate more heavily weighted to recent speciation events while λ_{ND} measures speciation across the root-to-tip path. These tip-rate measures are alternatives to state-dependent diversification models such as Quantitative State Speciation-Extinction (QuaSSE); but, based on previous simulation studies, λ_{DR} and λ_{ND} are robust and intuitive measures that provide high power and low false discovery rate with large phylogenies when incorporated into Phylogenetic Generalized Least Squares (PGLS) models³¹.

Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic trees³⁰. This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo) to generate probability distributions of evolutionary rate-shift configurations with variable speciation and extinction rates. Importantly, these models provide tip-rate estimates of speciation and extinction rate. The parameters of the 100 BAMM runs are detailed in full in the [ESM](#); briefly, we used a time-variable model with 100 expected number of shifts and prior rates set from the initial speciation and extinction values using the **BAMMtools** R package⁷⁵. Each BAMM model (one MCC tree and 100 random draws of the posterior) was run for 100 million generations, and given the computationally intensive nature of BAMM, runs were conducted across multiple CPUs. Each run of BAMM reached convergence with effective sample size (ESS) of MCMC (Markov Chain Monte Carlo) samples surpassing 200 (an arbitrary value, above which posterior distributions can often be accurately inferred) for the key model parameters of log-likelihood and number of rate shifts ([Table S3](#), [Table S4](#)). Further details of BAMM parameters and output are available in the [ESM](#), with tip-rate means and variances provided. Additionally, given the variability in BAMM estimates, we also provide analysis of BAMM shift configurations and tip-rate estimates from our run on the MCC tree and within a BAMM run on the MCC tree from a genetic-only phylogeny across all birds⁷⁶. All analyses were conducted on log-rates.

349 Phylogenetic comparative analysis

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we used phylogenetic least squares (PGLS) models in the **nlme** package⁷⁷. Firstly, we conducted model selection to compare models in which λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} were the response variable: these tip-rate estimates all came from the same MCC tree (derived from 2,500 draws of the posterior distribution²⁹). For models of λ_{BAMM} and μ_{BAMM} we used the inverse of the variance associated with each tip rate estimate as weights, to account for the variable precision of the estimates provided by BAMM. The most complicated model in each set under comparison contained one of the measures of sexual selection (sexual dichromatism or the index of male-biased sexual selection), all of the environmental measures (i.e. log-transformed range size, seasonal temperature variation, spatial temperature variation, long-term temperature variation, and NPP), and all of the 2-way interactions between sexual selection and each of the environmental measures. The simpler models contained all of the same main effects, but had fewer 2-way interaction terms (potentially none). Model selection was done in **MuMIn** using the **dredge** function⁷⁸. Using the terms from the top-ranked

362 model (ranked by AICc), we ran the equivalent model for each of the 1,000 phylogenetic trees used to derive
363 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
364 response variables and phylogenetic tree correlation structure. Specifically, for models using tip-rate metrics
365 (λ_{DR} , λ_{ND}) we estimated the phylogenetic signal — Pagel's λ^{79} — using the `corPagel` function in the `ape`
366 package⁸⁰ independently for each of the 1,000 trees/models. Alternatively, for models using speciation and
367 extinction estimates derived using BAMM (λ_{BAMM} and μ_{BAMM}) we found λ was consistently estimated at 1
368 and hence assumed Brownian motion (using the `corBrownian` function) to estimate the correlation structure.
369 This method enabled us to present model estimates for an MCC tree alongside 1,000/100 trees from the
370 posterior distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three
371 datasets corresponding to each measure of sexual selection: dichromatism derived from RGB values of images
372 ($n = 5,812$); dichromatism from spectrophotometry ($n = 581$) and the index of male-biased sexual selection
373 ($n = 2,465$).

374 Finally, using the subset of species with an index of male-biased sexual selection, we conducted a phylogenetic
375 path analysis using the `phylopath` R package⁸¹. The phylogenetic path analysis was used to assess causal paths
376 between variables not able to be modelled within the univariate response of PGLS. That is, a phylogenetic
377 path analysis allowed us to model relationships between the predictor variables used in our PGLS analysis as
378 we anticipate environmental variability, sexual dichromatism/selection, and range size to have effects on each
379 other and not just on speciation rate. To minimise path complexity we used temperature seasonality (BIO4)
380 as the single measure for environmental variability, λ_{DR} as the single measure of speciation and the tip-rates
381 from the MCC tree. Further details of the path analysis, including our rationale for each path's directions,
382 can be found within the [ESM](#) along with all other analyses and the relevant R code to reproduce results.

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