

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

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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 (λ_{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.

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19 INTRODUCTION

20 Sexual selection results from competition for matings, fertilisations, or associated resources, and is typically
21 stronger in males than females (Kokko and Jennions 2008; Fromhage and Jennions 2016; Janicke et al. 2016).

22 This evolutionary force has been proposed to facilitate speciation through the evolution of divergent signals
23 associated with improved mating success (Lande 1981, 1982). Experiments suggest that sexual selection
24 can influence the evolution of a surprisingly diverse set of traits (Cally et al. 2019), and may therefore
25 strongly influence extant patterns of species diversity. For instance, in antbirds (Thamnophilidae), genera
26 with complex songs and striking dichromatism are more species-rich (Seddon et al. 2008). Divergent mating
27 signals in one sex (usually males) co-evolves with divergent preferences for those signals in the opposite sex,
28 leading to behavioural reproductive isolation (Safran et al. 2013).

29 Alongside facilitating the evolution of divergent mating signals, sexual selection can increase the extent
30 populations diverge by enlarging the available phenotypic space for mating signals. These predictions emerge
31 as sexual selection may increase genetic diversity as a result of trade-offs between naturally- and sexually-
32 selected traits or trade-offs under *intra-locus* sexual conflict between male and female trait expressions
33 (Lorch et al. 2003; Bonduriansky 2011; Radwan et al. 2016). Additionally, sexual selection can have both
34 positive and negative consequences for adaptation (*e.g.*, Kokko and Brooks 2003; Whitlock and Agrawal
35 2009; Holman and Kokko 2013). For example, sexual selection can elevate average fitness by helping to
36 purge deleterious mutations (Agrawal 2001; Siller 2001) and fix beneficial ones (Whitlock 2000), which should
37 mitigate extinction risk and facilitate adaptation to environmental change. However, sexual selection might
38 also promote extinction by selecting for male traits that have detrimental pleiotropic effects on female traits
39 (Pischedda and Chippindale 2006; Bonduriansky and Chenoweth 2009; Pennell and Morrow 2013; Berger
40 et al. 2014), or selecting for male phenotypes with improved mating success but which harm population
41 productivity, such as under-investing in parental care (Kokko and Rankin 2006).

42 Importantly, the effects of sexual selection on adaptation and speciation may depend on environmental
43 conditions. Both theoretical and empirical studies suggest that under stressful/changing environments, sexual
44 selection may have greater fitness benefits than under benign environments. Stressful environments strengthen
45 the positive correlation between male mating success and female fitness, reducing the burden of negative
46 pleiotropic effects (Long et al. 2012; Berger et al. 2014; Connallon and Hall 2016; Martinossi-Allibert et
47 al. 2017). Conversely, benign or stable environments ensure consistent selection, preferentially eroding
48 genetic variation at sexually concordant loci (*i.e.* loci where the optimum genotype is equivalent for both
49 sexes). In these stable environments, genetic variation remains disproportionately at sexually antagonistic
50 loci; causing displacement of male and female traits from their optimum. It follows from these predictions
51 that populations with stronger sexual selection would have fitness benefits, allowing them to adapt to novel
52 environments (*reviewed in* Candolin and Heuschele 2008). Additionally, sexual selection can reinforce local
53 adaptations through mate choice on phenotypes that effectively advertise quality in a specific ecological
54 context (Boughman 2002; Maan and Seehausen 2011). For instance, beak morphology is a trait that arose
55 under natural selection in several taxa and is now a trait under sexual selection (a.k.a. *magic traits*; Servedio
56 et al. 2011). In Darwin's finches (*Geospiza fortis*) divergent beak morphology is an adaptation to local
57 food availability that has been maintained through assortative mating (Huber et al. 2007). Through these
58 synergetic effects sexual selection and natural selection (*e.g.* environmental variation over space and time)
59 may lead to increased speciation rates.

60 Birds are a speciose and well-characterised group of organisms with remarkable and variable sexually-selected
61 traits such as song and colourful plumage, thus are a popular focus for macroevolutionary studies of sexual
62 selection and diversification (e.g., Barraclough et al. 1995; Morrow et al. 2003; Seddon et al. 2008, 2013;
63 Huang and Rabosky 2014). A 2011 meta-analysis, covering 20 studies of birds and other taxa, found a small
64 but significant positive association between sexual selection and speciation, with the average effect size in
65 birds stronger than in mammals but weaker than in insects and fish (Kraaijeveld et al. 2011). However,
66 Kraaijeveld et al. (2011) found large variation in effect sizes between studies, likely because of differences in
67 the metrics used as estimates of speciation and the strength of sexual selection. More recently, Huang and
68 Rabosky (2014) found no association between sexual dichromatism and speciation ($n = 918$ species) when
69 using spectrophotometry measures on taxonomic specimens (Armenta et al. 2008) and tip-rate estimates
70 from a molecular-only phylogeny (Jetz et al. 2012). Similarly, Cooney et al. (2017) found no effect of sexual
71 dichromatism on diversification across 1,306 pairs of species, using dichromatism scores from human observers.
72 Here, we investigate the association between sexual selection and diversification in birds while extending
73 previous work in multiple ways. Firstly, multiple macroevolutionary studies estimate the strength of sexual
74 selection using proxies such as sexual dimorphism or dichromatism, but sexual selection in birds can involve
75 many other traits, such as song, or the use of ornaments like long tail feathers, bows, crests and displays
76 (e.g., Uy and Borgia 2000; Pryke et al. 2001). In fact, it was recently highlighted that song divergence is
77 inversely correlated to sexual dichromatism in passerines, suggesting that there is a trade-off between signalling
78 modalities (Cooney et al. 2018). Our study compares the role of sexual dichromatism and other sexual
79 selection proxies in the generation of species. Additionally, we test the relative contribution of environmental
80 variables to the generation of diversity, and how environment and sexual selection could interact to drive
81 speciation processes (Long et al. 2012; Connallon and Hall 2016).
82 To test the link between different measures of sexual selection and diversification processes we use a large (n
83 = 5,812) dataset of sexual dichromatism (estimated from illustrated drawings; Dale et al. 2015), as well as
84 a reduced but still substantial dataset ($n = 2,465$) that gives a composite measure of male-biased sexual
85 selection, capturing variation in sexual dimorphism, social polygyny and [lack of] paternal care (Dale et al.
86 2015). These datasets allow us to cover the majority of bird genera. Additionally, we use multiple metrics
87 for estimating speciation and extinction rates at the tips of phylogenetic trees, including BAMM (Bayesian
88 Analysis of Macroevolutionary Mixtures; see, Beaulieu and O'Meara 2015; Rabosky 2016; Moore et al. 2016;
89 Rabosky et al. 2017), as well as older but reliable tip-rate statistics, such as diversification rate (λ_{DR}) and
90 node density (λ_{ND}).

91 MATERIALS AND METHODS

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

97 Compiling data for sexual selection and environmental stress

98 Sexual dichromatism

99 We used a previously published measure of sexual dichromatism for 5,983 species of passerines (Dale et al.
100 2015). Briefly, Dale et al. (2015) obtained sex-specific RGB (red, green and blue) values across six body
101 patches (nape, crown, forehead, throat, upper breast, and lower breast) from *Handbook of the Birds of the*
102 *World* (Del Hoyo et al. 2011). The relative contribution of male and female RGB colour values were averaged
103 across body patches and provide ‘male-like’ and ‘female-like’ plumage scores. Here we use the absolute
104 difference between male and female plumage scores as an estimate of sexual dichromatism. Additionally, we
105 used another measure of dichromatism corresponding to colour distance in avian colour space derived from
106 spectral data (Armenta et al. 2008). These measurements include variation in the ultraviolet and bird-visible
107 range and — unlike the RGB measures — are sourced from museum samples (as opposed to colour drawings).
108 However, this spectrophotometry data is not as extensive as the RGB measures; with only 581 passerine
109 species available for this analysis. While there is a correlation between these two measures, there is residual
110 variation ($r = 0.79$; [Figure S10](#)).

111 Male-biased sexual selection

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

120 Environmental variables

121 We obtained estimates of species range size using expert range maps (BirdLife International and Handbook
122 of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the *Birdlife* database
123 (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual dichromatism
124 dataset (Dale et al. 2015). From these distributions, we obtained estimates of climatic conditions that
125 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19
126 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature
127 and precipitation) with 30-second ($\sim 1 \text{ km}^2$) spatial resolution (Fick and Hijmans 2017). From these values,
128 we obtained means and standard deviations for each species. Using the same spatial sampling, we extracted
129 means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial
130 (LIG; 120,000 - 140,000 years ago; Otto-Bliesner et al. 2006). We include estimates of climate variability
131 during recent evolutionary history as they may be a better indicators of environmental effects on speciation
132 than present-day environmental variability. Furthermore, to estimate variability in the energy available to

133 species, we obtained the mean and standard deviation of net primary productivity (NPP) values between
134 2000 - 2015 across each species distribution. Estimates of NPP had 30-second resolution and were obtained
135 through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production products stage 3
136 (MOD17A3; Zhao et al. 2005). Using these data, which we provide as a potentially useful data resource
137 (see [ESM](#)), we generated five predictors of speciation associated with different patterns in environmental
138 variability (see below).

139 Generating biologically relevant predictors for environmental stress

140 Given that stressful environments are expected to interact with sexual selection and have a positive effect
141 on adaptation (Cally et al. 2019), we used the extracted environmental variables from each species range
142 size to develop biologically meaningful predictors of environmental variation/stress. Firstly we used (*i*)
143 the average NPP in each species' range and (*v*) the log-transformed range size as potentially informative
144 predictors of speciation rates. We also used three environmental predictors derived from bioclimatic data.
145 These predictors relate to seasonal climate variation, spatial climate variation and long-term climate variation.
146 To obtain seasonal climate variation we used (*iii*) mean values of temperature seasonality (BIO4) for each
147 range. (*iV*) To estimate levels of spatial environmental variation a species may endure we used the first
148 principle component (PC1) from a PCA on standard deviations from all bioclimatic variables, excluding
149 temperature and precipitation seasonality (BIO 4 and BIO15). PC1 was heavily loaded towards bioclimatic
150 variables relating to temperature, thus PC1 reflects the variation in temperature across a species' range
151 ([Table S1](#)). Species range is a potentially informative predictor of speciation and extinction, so we controlled
152 for the correlation between environmental spatial variation and range size — where larger ranges have larger
153 variation in PC1 — by using the residuals of a fitted general additive model (GAM; [Figure S1](#)) as a predictor.
154 To obtain long-term variation in climates for each species range we take (*v*) the first principal component of
155 the absolute difference in the bioclimatic variables between the LIG and current values. Similar to spatial
156 variation, the long-term climate variation is primarily loaded to temperature differences between the LIG
157 and current climates ([Table S2](#), [Figure S2](#)). The five predictors of environmental variability are not strongly
158 correlated ([Figure S3](#)). Details and R code to generate these predictors can be found within the [ESM](#).

159 Estimating extinction and speciation

160 Phylogenetic information was obtained from www.birdtree.org (Jetz et al. 2012). We used a maximum clade
161 credibility (MCC) tree from 2,500 samples of the posterior distribution ($n = 5,965$) as the main phylogenetic
162 hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without
163 genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using
164 tip-rate measures (1000 trees) and BAMM (100 trees)(Rabosky 2014). These trees used a 'Hackett backbone'
165 (Hackett et al. 2008) and were constructed using a pure birth (Yule) model. We calculated three different
166 tip-rate metrics of speciation and one of extinction across all trees.

167 Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes
168 and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating
169 the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES),
170 also known as diversification rate (DR) (e.g., Jetz et al. 2012; Quintero and Jetz 2018; Rabosky et al. 2018),

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 (Belmaker and Jetz 2015; Title and Rabosky 2018). Therefore, λ_{DR} is a measure of speciation rate more heavily weighted to recent speciation events and λ_{ND} is a measure of 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) models (Harvey Michael et al. 2017).

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

Phylogenetic comparative analysis

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we used phylogenetic least squares (PGLS) models in the [nlme](#) package (Pinheiro et al. 2018). Firstly we conducted model selection using λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{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 λ_{BAMM} and μ_{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

211 2017). Using the terms from the top-ranking model (lowest AICc), we ran the equivalent model for each
212 of the 1,000 phylogenetic trees used to derive λ_{DR} , λ_{ND} and each of the 100 used to derive λ_{BAMM} and
213 μ_{BAMM} . In each model we used the unique response variables and phylogenetic tree correlation structure.
214 Specifically, for models using tip-rate metrics (λ_{DR} , λ_{ND}) we estimated the phylogenetic signal — Pagel's λ
215 (Pagel 1999) — using the `corPage1` function in the `ape` package (Paradis et al. 2004) independently for each
216 of the 1,000 trees/models. Alternatively, for models using speciation and extinction estimates derived using
217 BAMM (λ_{BAMM} and μ_{BAMM}) we found λ was consistently estimated at 1 and hence assumed Brownian
218 motion (using the `corBrownian` function) to estimate the correlation structure. This method enabled us to
219 present model estimates for an MCC tree alongside 1,000/100 trees from the posterior distribution of trees to
220 account for phylogenetic uncertainty. This approach was repeated on three datasets corresponding to each
221 measure of sexual selection: dichromatism derived from RGB values of images ($n = 5,812$); dichromatism
222 from spectrophotometry ($n = 581$) and the multivariate measure of male-biased sexual selection ($n = 2,465$).
223 Finally, using data subset for species with measurements of male-biased sexual selection, we conducted a
224 phylogenetic path analysis using the `phylopath` R package (Bijl 2018). The phylogenetic path analysis was
225 used to assess causal paths *between* variables not able to be modelled within the univariate response of PGLS.
226 That is, a phylogenetic path analysis allowed us to model relationships between the predictor variables used
227 in our PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection, and range
228 size to have effects on each other and not just on speciation rate. To minimise path complexity we used
229 temperature seasonality (BIO4) as the single measure for environmental variability, λ_{DR} as the single measure
230 of speciation and the tip-rates from the MCC tree. Further details of the path analysis, including reasons
231 for path directions, can be found within the [ESM](#) along with all other analyses and the relevant R code to
232 reproduce results.

233 RESULTS

234 Variability across phylogenetic hypotheses and measures of speciation

235 Estimates of speciation rates varied across phylogenetic trees, especially in the BAMM rates (λ_{BAMM} and
236 μ_{BAMM}), where the 95 % highest posterior density (HPD) interval across 100 trees was more than 20 times
237 larger than the 95 % confidence interval calculated for the MCC tree. This contrasts with variation across
238 trees for the other rate estimates (λ_{DR} and λ_{ND}), where the 95 % HPD interval across 1,000 trees was near-
239 equivaleant to the 95 % confidence interval calculated for the MCC tree ([Table S9](#)). Given the computational
240 requirements of BAMM, the great majority of studies only derive estimates for a single consensus tree; so the
241 high variability in BAMM estimates among trees is notable. Mean measures of speciation across 100 trees
242 were positively correlated between measures (DR - BAMM: $r=0.75$, DR - ND: $r=0.65$, ND- BAMM: $r=0.51$;
243 [Figure S15](#)). Given that the calculation of BAMM rates can be affected by the settings of the run and the
244 use of different priors, we compared the estimate of our MCC tree with that of previous published analyses
245 on birds, and found a high correlation ($r=0.81$, [Figure S8](#)). Details of the BAMM results are presented in the
246 supplementary materials.

²⁴⁷ Effects of sexual dichromatism/selection on speciation do not depend on environmental variability
²⁴⁸

²⁴⁹ PGLS models with interaction terms between each measure of sexual dichromatism/selection and the five
²⁵⁰ measures of environmental variability (seasonal temperature variation, log-range size, long-term temperature
²⁵¹ variation, spatial temperature variation, and NPP) were included in model selection. However, no interaction
²⁵² terms were significant or present in the top models ($\delta \text{ AICc} > 4$) for any measure of speciation (λ_{DR} , λ_{ND} ,
²⁵³ λ_{BAMM}) or sexual selection (RGB values, spectrophotometry and male-biased sexual selection; $\delta \text{ AICc}$
²⁵⁴ > 4 ; [Table S5](#), [Table S6](#), [Table S10](#), [Table S13](#)). Thus we found no evidence that the effect of sexual
²⁵⁵ selection on speciation is dependent on our measures of environmental variation. Furthermore, we found no
²⁵⁶ evidence that these environmental factors (seasonal temperature variation, long-term temperature variation,
²⁵⁷ spatial temperature variation, and NPP) predict speciation independently from sexual dichromatism/selection
²⁵⁸ ([Figure 1](#), [Figure S11](#)).

²⁵⁹

²⁶⁰ No evidence that sexual dichromatism affects speciation

²⁶¹ We found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation.
²⁶² Using three response measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}), the effect of sexual dichromatism was not
²⁶³ significant in any PGLS model based on tip-rate estimates and correlation structures from the MCC tree.
²⁶⁴ Specifically, sexual dichromatism showed no association with λ_{DR} ($\beta = -1.279\text{e-}03$, $p = 0.147$; [Figure 1a](#),
²⁶⁵ [Figure 2a](#)) or λ_{ND} ($\beta = -5.745\text{e-}05$, $p = 0.078$; [Figure 1a](#)). Furthermore, speciation rates from BAMM
²⁶⁶ (λ_{BAMM}) were also unaffected by sexual dichromatism ($\beta = -1.429\text{e-}05$, $p = 0.872$; [Figure 1a](#)). PGLS analyses
²⁶⁷ using sexual dichromatism ($n = 581$) measured by spectrophotometry (Armenta et al. 2008) yielded results
²⁶⁸ concordant with the full dataset; *i.e.* no association between sexual dichromatism and speciation ([Figure S11](#)).
²⁶⁹ Our results from models based on the MCC tree are largely corroborated by model estimates from PGLS
²⁷⁰ analyses of the rates and correlation structures from 1,000 random trees (for λ_{DR} , λ_{ND}) and 100 random
²⁷¹ trees for λ_{BAMM} . The HPD (highest posterior density) intervals show model estimates are distributed around
²⁷² zero when using complete taxon sampling models and RGB measures of sexual dichromatism ([Figure 1a](#),
²⁷³ [Table S8](#)). For PGLS models using spectrophotometry-based measures of sexual dichromatism, the estimates
²⁷⁴ from the 100 trees in the λ_{DR} models are positively skewed (HPD Interval = $-1.780\text{e-}02$, $3.489\text{e-}02$) but
²⁷⁵ normally distributed around zero for λ_{ND} and λ_{BAMM} ([Table S12](#)).

²⁷⁶ Male-biased sexual selection increases speciation

²⁷⁷ We found a significant positive association between male-biased sexual selection ($n = 2,465$) and λ_{DR} for
²⁷⁸ the MCC tree ($\beta = 3.887\text{e-}02$, $p = 0.012$; [Figure 1b](#)). However, this association was not significant for the
²⁷⁹ other two measures of speciation rate (λ_{ND} : $\beta = 4.383\text{e-}04$, $p = 0.351$; λ_{BAMM} : $\beta = 9.423\text{e-}04$, $p = 0.764$;
²⁸⁰ [Figure 1b](#)). The distribution of estimates from PGLS models on 1,000 random trees was similar to the
²⁸¹ estimate from the MCC tree: among the 1,000 trees there was a positive association between sexual selection
²⁸² and λ_{DR} (HPD Interval = $4.513\text{e-}03$, $5.718\text{e-}02$), and a smaller positive association between sexual selection

283 and λ_{ND} (HPD Interval = -5.044e-04, 1.585e-03;) as well as the 100 models using λ_{BAMM} (HPD Interval
284 = -1.295e-02, 3.088e-02). Complete HPD intervals for models using male-bias sexual selection PPCA as a
285 predictor can be found within [Table S15](#).

286 Species with smaller ranges have increased rates of speciation

287 Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation, we found a negative association between range size and
288 speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This negative
289 association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.579e-03$, $p = 0.001$; λ_{ND} :
290 $\beta = -1.462e-04$, $p = 0.034$; [Figure 1a](#), [Figure 2](#)). This association was also evident across the estimates from
291 models using the 1,000 trees (λ_{DR} : HPD Interval = -8.871e-03, -6.610e-04; λ_{ND} : HPD Interval = -1.514e-04,
292 1.724e-05; [Figure 1a](#)). Subset models with reduced sample size and different measures of sexual selection
293 — but the same measure of range size — showed variable evidence that range size is negatively associated
294 with speciation. Range size significantly predicted λ_{DR} ([Figure 1b](#)) using data subset for male-biased sexual
295 selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} . Models using data subset for spectrophotometry-based
296 dichromatism ($n = 581$) gave non-significant estimates for the effect of range size on all measures of speciation
297 ([Figure S11](#), [Table S11](#), [Table S12](#)). Because the range size dataset is the same across the three data subsets
298 we draw our conclusions from the models with the highest power using near-complete taxon sampling ($n =$
299 5,812).

300 Phylogenetic path analysis

301 Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
302 ([Figure 3](#); [Figure S14](#)). There was a modest effect of male-biased sexual selection on sexual dimorphism (β
303 = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism ($\beta = 0.07$) and strongly
304 affected range size ($\beta = 0.52$). This suggests an indirect effect of temperature seasonality on λ_{DR} ($\beta_{indirect} =$
305 -0.02; [Figure 3](#)), given the negative association we identified between λ_{DR} and range size in PGLS models.

306 Extinction rate

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

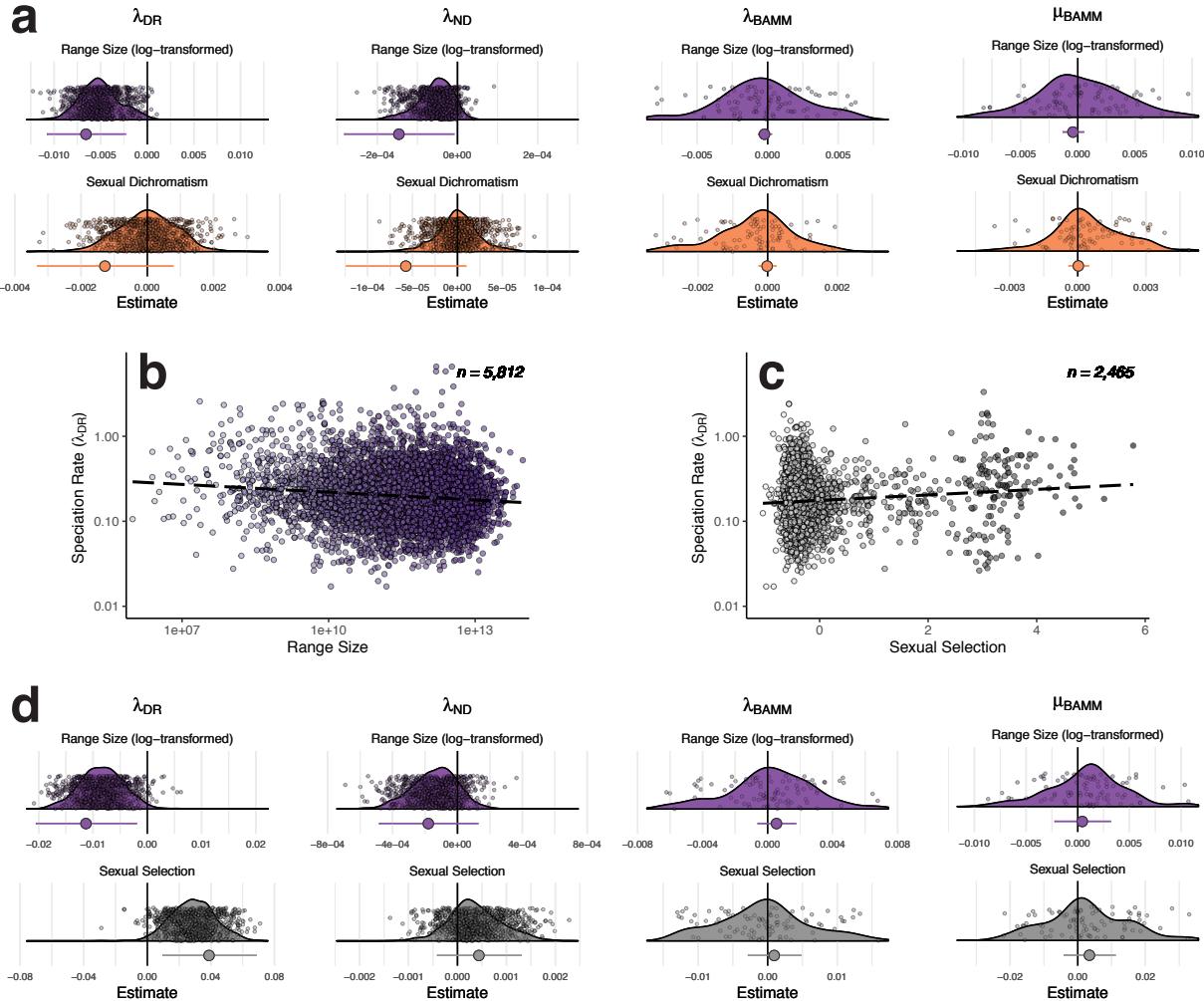


Figure 1: Model estimates (a) for the effect of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset (RGB values, $n = 5,812$). (b) depicts the scatter plot of speciation rate (λ_{DR}) and log-range size with the model estimate 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 random trees (for λ_{DR} and λ_{ND}) or 100 random 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 random trees for BAMM models in order to be able to visualise the MCC 95 % CIs.

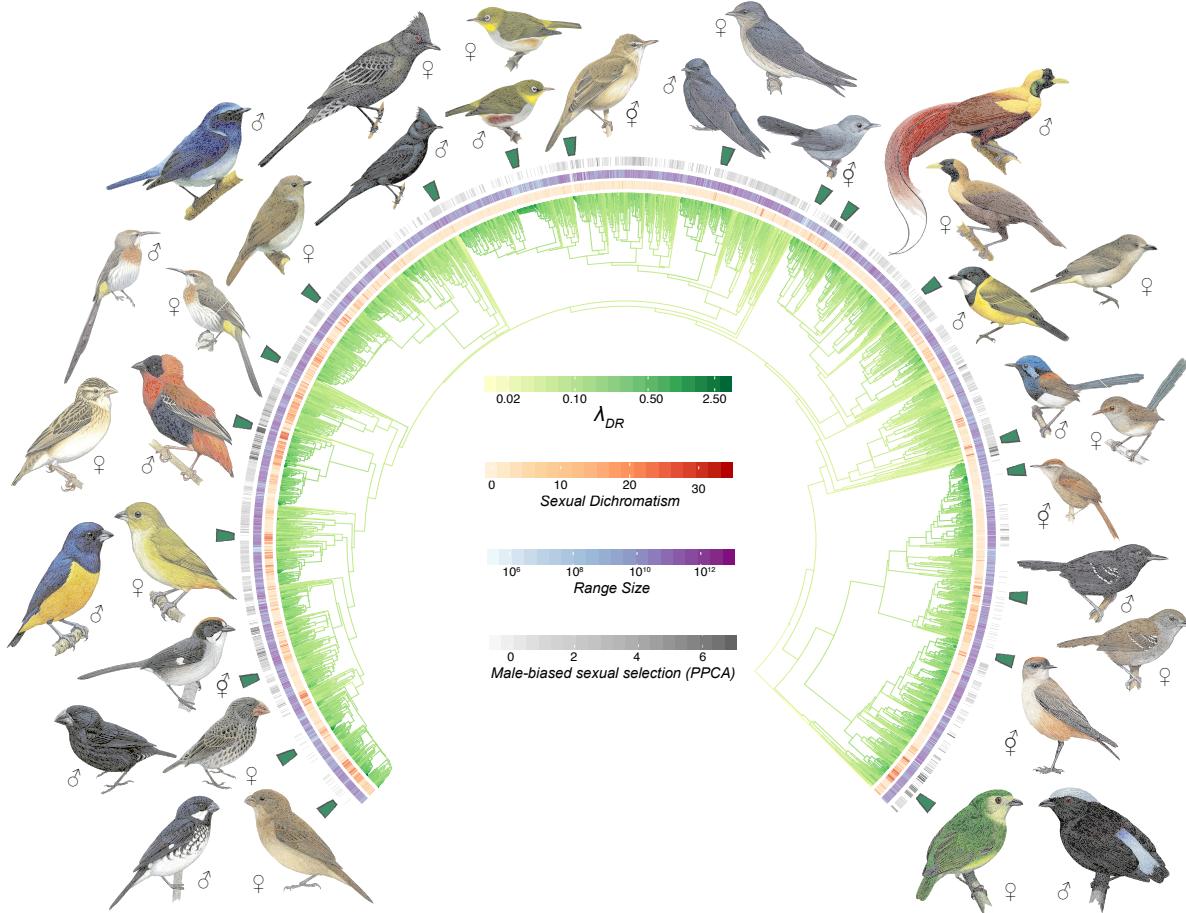


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism, range size available for 5,812 species and male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative association between λ_{DR} 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 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 λ_{DR} but all precluding branches have been generated for graphical purposes using ancestral character state estimation and should not be interpreted.

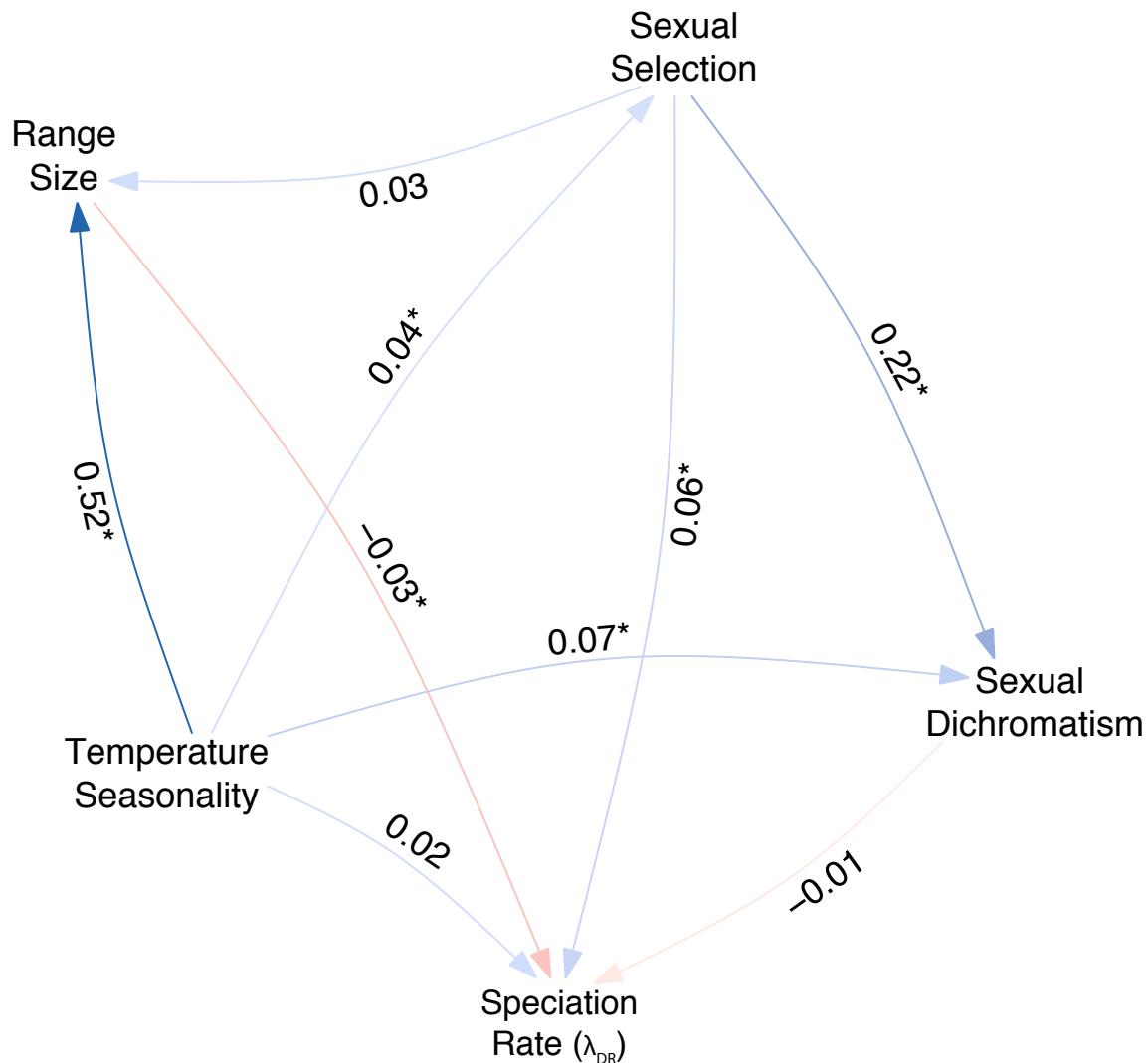


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with the direction of effect corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95 % confidence intervals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

311 DISCUSSION

312 We found evidence that the composite measure of male-biased sexual selection, but not the measure of sexual
313 dichromatism, explains variation in the rate of speciation in passerine birds. The absence of a detectable
314 correlation between sexual dichromatism and speciation rate was consistent across different measures of
315 speciation (λ_{DR} , λ_{ND} and λ_{BAMM}) and both measures of dichromatism (spectral and RGB). These findings
316 substantiate previous studies performed at smaller scales in birds, where sexual dichromatism measures were
317 obtained using spectrophotometry (Huang and Rabosky 2014) and human observers (Cooney et al. 2017)
318 and no association was found. The correlation between speciation rate and the index of male-biased sexual
319 selection (which reflects sexual size dimorphism, social polygyny, and [lack of] paternal care) was statistically
320 significant for λ_{DR} , but not for λ_{ND} and λ_{BAMM} , although the estimated direction and magnitude of
321 the correlation was broadly similar across all speciation measures. Interestingly, we found a consistent
322 negative relationship between range size and speciation rates, at least when this rate was quantified by
323 λ_{DR} and λ_{ND} . This suggests that species with smaller range sizes have increased speciation rates. None
324 of the bioclimatic measures of environmental variability that we investigated (*i.e.*, temperature seasonality,
325 long-term temperature variation, and spatial temperature variation) predicted speciation rate.

326 The association between sexual selection and sexual dichromatism in birds is a Darwinian trope (Darwin 1871)
327 that allows it to be commonly used as a proxy for the strength of sexual selection in comparative studies (*e.g.*,
328 Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky
329 2014). Despite the association between sexual selection and sexual dichromatism in passerine birds (Dale et al.
330 2015)— $r = 0.34$ —we find that sexual dichromatism does not predict any measure of speciation rate, whereas
331 male-biased sexual selection predicts λ_{DR} . Given our results, we suggest that sexual dichromatism may not be
332 a robust proxy for sexual selection at least at this broad scale, and that variation in the association between
333 dichromatism and the strength of sexual selection may obscure any relationship with speciation rate, despite
334 the high power of our comparative study. There are several reasons why the use of sexual dichromatism as
335 a proxy for sexual selection is problematic. Firstly, sexual dichromatism can evolve for reasons other than
336 sexual selection, such as when males and females occupy different ecological niches (Wallace 1889; Kottler
337 1980; Slatkin 1984; Shine 1989) or experience different selective pressures in contexts other than competition
338 for mates (Price and Eaton 2014). For example, in superb fairy-wrens (*Malurus cyaneus*) female colouration
339 has probably evolved in response to spatial variation in predation pressure, increasing dichromatism (Medina
340 et al. 2017). Ecological selection on sexual dichromatism was implicated by our path analysis, which found
341 that sexual dichromatism is positively affected by temperature seasonality (a measure of environmental
342 variation), albeit weakly. Secondly, colour is but one trait and sexual selection may drive the evolution of sex
343 differences in a wide variety of traits used in mate choice or intrasexual competition (Miles and Fuxjager
344 2018). For instance, sexual selection may promote investments in other mating signals (*e.g.* song) that
345 trade-off against plumage colour, leading to variable investment in different sexually selected signals across
346 species (Cooney et al. 2018). Lastly, not all plumage colouration honestly reflects mate quality. A recent
347 meta-analysis found that converted carotenoids (but *not* carotenoids sourced from the diet) predict mate
348 quality through improvements in parasite resistance and reproductive success (Weaver et al. 2018). Given
349 the importance of honest signaling in sexual selection and the variability in colour production mechanisms
350 across birds, sexual dichromatism in many species may be an unreliable measure of mate quality for female
351 birds and sexual selection for researchers.

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

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

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

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

394 mating signals as opposed to traits — such as parental care — that elevate offspring fitness (*reviewed in*
395 Kokko and Brooks 2003). Using the model-based approach of BAMM, we found no association between
396 extinction rate and sexual dichromatism, male-biased sexual selection or measures of environmental variability.
397 Extinction is notoriously difficult to estimate accurately from phylogenies, principally because many different
398 combinations of speciation and extinction rates can give rise to similar patterns of diversity (*see* Rabosky
399 2016). Phylogenetic methods such as BAMM allow for speciation and extinction rates to be estimated
400 using moderately-sized phylogenies, although the ability of BAMM to model evolutionary rate shifts and
401 extinction rates remains a subject of debate (*see*, Beaulieu and O'Meara 2015; Rabosky 2016; Moore et al.
402 2016; Rabosky et al. 2017). Additionally, while several tip-rate estimates exist for speciation rate (*e.g.*, λ_{DR}
403 and λ_{ND}), tip-rate estimates of extinction rate are difficult to obtain without complex Bayesian models and
404 are fraught with issues of sampling bias (Davis et al. 2013). Although extinction rates can be estimated from
405 alternative sources, such as the fossil record, documented recent extinctions and IUCN extinction threat
406 status, each approach has significant limitations. Across the passerine bird phylogeny, we found that BAMM
407 often produced homogeneous speciation and extinction rates for smaller clades showing few rate shifts, which
408 might reduce our power to detect small differences in extinction rates among closely-related taxa (Rabosky
409 et al. 2017; Title and Rabosky 2018). Thus, this methodological constraint likely decreases our ability to
410 accurately measure the correlation between metrics of sexual selection and the probability of extinction.

411 To summarise, we have shown that in passerines, male-biased sexual selection, but not sexual dichromatism,
412 predicts speciation, independent of several measures of environmental variability. These findings support the
413 idea that sexual dechromatism is not a reliable proxy for sexual selection, and that alternative measures of
414 sexual selection are more directly related to diversification. If sexual selection promotes speciation through
415 improvements in fitness and adaptation the implications are manifold, including for conservation (*reviewed in*,
416 Holman and Kokko 2013) and captive breeding programs for threatened species (*reviewed in*, Charge et al.
417 2014). Furthermore, our finding that high speciation rate is associated with smaller range size highlights the
418 threat to the persistence of rapidly speciating lineages in a world with increased habitat loss and anthropogenic
419 stress. This concern arises as the best predictor of extinction risk is range size (Harris and Pimm 2008) and
420 the association found here implies that many newly-speciated clades have small range sizes and could thus be
421 at greater risk of extinction.

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