

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

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⁴ **Abstract**

⁵ Many theories related to sexual selection predict that it shapes phylogenetic diversity by altering
⁶ speciation or extinction rates. The predicted effects on diversity are often contradictory; for example,
⁷ sexual selection might promote speciation by creating reproductive isolation, or hinder it by selecting
⁸ for traits that facilitate gene flow. Similarly, sexual selection might precipitate extinction by favouring
⁹ competitive phenotypes with poor survival, or stave it off by helping populations shed deleterious mutations.
¹⁰ Here, we investigate the relationship between sexual selection and rates of speciation and extinction in
¹¹ passerine birds. We use two measures of sexual selection – sexual dichromatism ($n = 5,812$ species) and a
¹² multivariate measure of male-biased sexual selection (sexual dimorphism, polygyny and paternal care; n
¹³ = 2,465) – as well as three distinct measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}), and one measure of
¹⁴ extinction (μ_{BAMM}). We also tested whether the effects of sexual selection is contingent on ecological
¹⁵ variables such as spatiotemporal temperature variation, primary productivity, and range size. We find
¹⁶ that male-biased sexual selection but not sexual dichromatism predicts speciation. Additionally, we find
¹⁷ that birds with smaller ranges have higher speciation rates; although the direction of causality is unclear.

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

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19 Introduction

20 Selection pressures are the main engine of speciation. As populations diverge they accumulate genetic and
21 phenotypic changes that ultimately erect barriers against gene flow (Presgraves 2010; *but see* Shaw and Mullen
22 2011). In this view, populations will speciate and adapt more readily to new and different environments if
23 selection is strong and/or persistant. Hence, the rate at which speciation occurs is likely dependent on both
24 the population's response to selection (adaptation) and the potential for divergent phenotypic traits to evolve
25 (*e.g.*, morphology or colour Hugall and Stuart-Fox 2012; Rabosky et al. 2013). Experiments suggest that
26 sexual selection can influence the evolution of a surprisingly diverse set of traits (Cally et al. 2018 *in review*),
27 and may therefore strongly influence extant patterns of phylogenetic diversity.

28 Sexual selection results from competition for matings, fertilisations, or associated resources, and is typically
29 stronger in males than females (Kokko and Jennions 2008; Fromhage and Jennions 2016; Janicke et al. 2016).
30 This evolutionary force has been proposed to facilitate speciation through the evolution of divergent signals
31 associated with improved mating success (Lande 1981, 1982). For instance, in antbirds (Thamnophilidae),
32 genera with complex songs and striking dichromatism, are more species rich (Seddon et al. 2008). Under this
33 model of speciation, divergent mating signals in one sex (usually males) co-evolve with divergent preferences for
34 those signals in the opposite sex, leading to behavioural reproductive isolation (Safran et al. 2013). Alongside
35 facilitating the evolution of divergent mating signals, sexual selection can increase the extent populations
36 diverge by enlarging the available phenotypic space for mating signals. These predictions emerge as sexual
37 selection may increase genetic diversity as a result of trade-offs between naturally- and sexually-selected traits
38 or trade-offs under *intra-locus* sexual conflict between male and female trait expressions (Lorch et al. 2003;
39 Bonduriansky 2011; Radwan et al. 2016). Additionally, sexual selection can have both positive and negative
40 consequences for adaptation (*e.g.*, Kokko and Brooks 2003; Whitlock and Agrawal 2009; Holman and Kokko
41 2013). For example, sexual selection can elevate average fitness by helping to purge deleterious mutations
42 (Agrawal 2001; Siller 2001) and fix beneficial ones (Whitlock 2000), which should mitigate extinction risk and
43 facilitate adaptation to environmental change. However, sexual selection might also promote extinction, by
44 selecting for male traits that have detrimental pleiotropic effects on female traits (Pischedda and Chippindale
45 2006; Bonduriansky and Chenoweth 2009; Pennell and Morrow 2013; Berger et al. 2014), or selecting for male
46 phenotypes with improved mating success but which harm population productivity, such as under-investing
47 in parental care (Kokko and Rankin 2006).

48 Importantly, the effects of sexual selection on adaptation and speciation may depend on environmental
49 conditions. Both theoretical and empirical studies suggest that under stressful/changing environments, sexual
50 selection may have greater fitness benefits than under benign environments. Stressful environments strengthen
51 the positive correlation between male mating success and female fitness, reducing the burden of negative
52 pleiotropic effects (Long et al. 2012; Berger et al. 2014; Connallon and Hall 2016; Martinossi-Allibert et al.
53 2017). Conversely, benign or stable environments ensure consistent selection, preferentially eroding genetic
54 variation at sexually concordant loci (*i.e.* loci where the optimum genotype is equivalent for both sexes). In
55 these stable environments, genetic variation remains disproportionately at sexually antagonistic loci; causing
56 displacement of male and female traits from their optimum. It follows from these predictions that populations
57 with stronger sexual selection would have fitness benefits, allowing them to adapt to novel environments
58 (*reviewed in* Candolin and Heuschele 2008). Additionally, sexual selection can reinforce locally adapted
59 phenotypes through mate choice on phenotypes that effectively advertise quality in a specific ecological

60 context (Boughman 2002; Maan and Seehausen 2011). For instance, beak morphology is a trait that arose
61 under natural selection in several taxa and is now a trait under sexual selection (a.k.a. *magic traits*; Servedio
62 et al. 2011). In Darwin's finches (*Geospiza fortis*) divergent beak morphology is an adaptation to local
63 food availability that has been maintained through assortative mating (Huber et al. 2007). Through these
64 synergetic effects sexual selection and natural selection — such as environmental change over space and
65 time — may lead to increased adaptation and speciation rates.

66 As a speciose and well-characterised group of organisms with remarkable and variable sexually-selected traits
67 such as song and colourful plumage, birds are a popular focus for macroevolutionary studies of sexual selection
68 and diversification (Barraclough et al. 1995; Morrow et al. 2003; e.g. Seddon et al. 2008, 2013; Huang
69 and Rabosky 2014). A 2011 meta-analysis, covering 20 studies of birds and other taxa, found a small but
70 significant positive association between sexual selection and speciation, though the average effect size was
71 weaker in birds than in insects and fish but stronger than in mammals (Kraaijeveld et al. 2011). Birds
72 are often thought to be more conducive in benefiting from sexual selection due to their sex determination
73 system. In male homogametic species (ZZ/ZW) — such as birds — males are predicted to have increased
74 heritability of male-specific genotypes on the Z chromosome associated with mating success: such as elaborate
75 ornamentation or plumage colouration (Hastings 1994; Reeve and Pfennig 2003). As such, we might expect
76 bird populations experiencing stronger sexual selection to have increased adaptation and speciation rates
77 compared to male heterogametic taxa. However, Kraaijeveld et al. (2011) found large variation in effect sizes
78 between studies, likely because of differences in the metrics used as estimates of speciation and the strength of
79 sexual selection. More recently, Huang and Rabosky (2014) found no association between sexual dichromatism
80 and speciation ($n = 918$ species) when using spectrophotometry measures on taxonomic specimens (Armenta
81 et al. 2008) and tip-rate estimates from a molecular-only phylogeny (Jetz et al. 2012). Similarly, Cooney
82 et al. (2017) found no effect of sexual dichromatism on diversification across 1,306 pairs of species, using
83 dichromatism scores from human observers.

84 Here, we investigate the association between sexual selection and diversification in birds while extending
85 previous work in multiple ways. Firstly, many macroevolutionary studies estimate the strength of sexual
86 selection using proxies such as sexual dimorphism or dichromatism, but these are imperfect correlates. We
87 used a very large ($n = 5,812$) dataset of sexual dichromatism measures (sourced from illustrated drawings;
88 Dale et al. 2015), as well as a smaller but still substantial dataset ($n = 2,465$) that gives a composite measure
89 of male-biased sexual selection, capturing variation in sexual dimorphism, social polygyny and [lack of]
90 paternal care. These datasets allow us to cover the great majority of bird genera, in contrast to previous
91 work that has often focused on particular clades (e.g. Seddon et al. 2008). Secondly, we use the latest
92 methods for estimating speciation and extinction rates at the tips of phylogenetic trees, including BAMM
93 (Bayesian Analysis of Macroevolutionary Mixtures) (see, Beaulieu and O'Meara 2015; Rabosky 2016; Moore
94 et al. 2016; Rabosky et al. 2017), as well as older but less controversial tip-rate statistics, commonly referred
95 to as diversification rate (λ_{DR}) and node density (λ_{ND}). We also conduct analyses that allow phylogenetic
96 uncertainty in the avian tree (Jetz et al. 2012; but see Rubolini et al. 2015) to affect the precision of
97 our estimates, rather than implicitly assuming that the single best-supported phylogenetic tree is correct.
98 Thirdly, our analysis includes several potentially important environmental variables as predictors: range size,
99 seasonal variation in temperature, spatial temperature variation (across a species' range), long-term variation
100 in temperature between now and the last inter-glacial (LIG) as well net primary productivity (NPP). By
101 including these environmental variables in our models, we statistically account for their effects on variation in

102 diversification rates and thereby improve our estimates of the effects of sexual selection. We also test whether
103 the effects of sexual selection are contingent on the environment, as predicted by some theories (*e.g.* the
104 theory that sexual selection is more likely to elevate adaptation in changeable relative to static environments;
105 Long et al. 2012; Connallon and Hall 2016).

106 Materials and methods

107 We examined the effect of sexual selection on speciation and extinction rate in 97 % of passerines ($n = 5,812$
108 species; 58 % of all birds). Specifically, we (*i*) compiled datasets for sexual dichromatism/selection strength
109 and environmental variability, (*ii*) obtained estimates of speciation and extinction rates across passerines,
110 and (*iii*) conducted phylogenetic generalized least-squares (PGLS) regressions. Analyses are documented
111 with reproducible code in the [electronic supplementary material \(ESM\)](#).

112 Compiling data for sexual selection and environmental stress

113 Sexual dichromatism

114 We used a previously published measure of sexual selection for 5,983 species of passerines (Dale et al. 2015).
115 Briefly, Dale et al. (2015) obtained sex-specific RGB (red, green and blue) values across six body patches
116 (nape, crown, forehead, throat, upper breast and lower breast) from *Handbook of the Birds of the World*
117 (volumes 8–16) (Del Hoyo et al. 2011). The relative contribution of male and female RGB colour values
118 were averaged across body patches and provide ‘male-like’ and ‘female-like’ plumage scores. Here we use
119 the absolute difference between male and female plumage scores as an estimate of sexual dichromatism.
120 Additionally, we used a measure of dichromatism from spectral data, used to estimate colour distance in
121 avian colour space (Armenta et al. 2008). These measurements include variation in the ultraviolet and
122 bird-visible range and — unlike the RGB measures — are sourced from taxonomic samples (as opposed to
123 colour drawings). However, this spectrophotometry data is not as extensive as the RGB measures; with only
124 581 passerine species available for this analysis. While there is a correlation between these two measures,
125 there is residual variation ($r = 0.79$; [Figure S9](#)).

126 Male-biased sexual selection

127 Sexual dichromatism is a widely used indicator of sexual selection in birds (*e.g.*, Barraclough et al. 1995;
128 Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014), but only partially
129 captures variation in the strength of sexual selection across taxa. Therefore, we also use an existing dataset
130 (Dale et al. 2015) of male-biased sexual selection based on the first component of a phylogenetic principle
131 component analysis (PPCA) of three characteristics associated with sexual selection (sexual size dimorphism,
132 social polygyny and [lack of] paternal care). This measure of male-biased sexual selection is available for only
133 2,465 species and is weakly correlated with the absolute values of sexual dichromatism using RGB measures
134 ($r = 0.34$; [Figure S11](#)).

135 Environmental variables

136 We obtained estimates of species range size using expert range maps (BirdLife International and Handbook
137 of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the *Birdlife* database
138 (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual dichromatism
139 dataset (Dale et al. 2015). From these distributions we obtained estimates of climatic conditions that
140 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19
141 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature
142 and precipitation) with 30 seconds (~1 km²) spatial resolution (Fick and Hijmans 2017). From these values
143 we obtained means and standard deviations for each species. Using the same spatial sampling we extracted
144 means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial
145 (LIG; 120,000 - 140,000 years ago) (Otto-Bliesner et al. 2006). Furthermore, to estimate variability in the
146 energy available to species we obtained the mean and standard deviation of net primary productivity (NPP)
147 values between 2000 - 2015 across each species distribution. Estimates of NPP had 30 second resolution
148 and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production
149 products stage 3 (MOD17A3) (Zhao et al. 2005). Using this data, which we provide as a potentially useful
150 data resource (see ESM), we generated five predictors of speciation associated with different patterns in
151 environmental variability (see below).

152 Generating biologically relevant predictors for environmental variation

153 Using the extracted environmental variables from each species range size we developed biologically meaningful
154 predictors of environmental variation/stress relating to (*i*) seasonal climate variation, (*ii*) spatial climate
155 variation and (*iii*) long-term climate variation. To obtain seasonal climate variation we used mean values
156 of temperature seasonality (BIO4) for each range. To estimate levels of spatial environmental variation a
157 species may endure we used the first principle component (PC1) from a PCA on standard deviations from all
158 bioclimatic variables, excluding temperature (BIO4) and precipitation seasonality (BIO15). PC1 was heavily
159 loaded towards bioclimatic variables relating to temperature, thus PC1 reflects the variation in temperature
160 across a species' range (Table S1). Given that species range is a potentially informative predictor of speciation
161 and extinction we controlled for the correlation between spatial variation and range size — where larger
162 ranges have larger variation in PC1 — by taking the residuals of a fitted general additive model (GAM; Figure
163 S1). To obtain long-term variation in climates for each species range we take the first principal component of
164 the absolute difference in the bioclimatic variables between the LIG and current values. Similarly to spatial
165 variation, the long-term climate variation is primarily loaded to temperature differences between the LIG
166 and current climates (Table S2, Figure S2). The five predictors of environmental variability are not strongly
167 correlated (Figure S3). Details and code to generate these predictors can be found within the ESM.

168 Estimating extinction and speciation.

169 Phylogenetic information was obtained from www.birdtree.org (Jetz et al. 2012). We used a maximum clade
170 credibility (MCC) tree from 2,500 samples of the posterior distribution that were subset to the passerine bird
171 order ($n = 5,965$) as the main phylogenetic tree in our comparative analysis. Additionally, a random draw of
172 100 full trees (including species without genetic data) from the posterior distribution of phylogenetic trees

173 was used for diversification analyses using tip-rate measures and BAMM (Rabosky 2014). These trees used
174 a ‘Hackett backbone’ (Hackett et al. 2008) and were constructed using the a pure birth (Yule) model. We
175 calculated three different tip-rate metrics of speciation and one of extinction across all trees.

176 Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes
177 and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating
178 the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES),
179 also known as diversification rate (DR) (*e.g.*, Jetz et al. 2012; Quintero and Jetz 2018; Rabosky et al. 2018),
180 is derived from the sum of edge lengths branching from a node, with each more basal node having the sum of
181 lengths down-weighted. Studies have suggested that DR and ND (henceforth referred to as λ_{DR} and λ_{ND})
182 are more reflective estimates of speciation than diversification (Belmaker and Jetz 2015; Rabosky and others
183 2018). Therefore, λ_{DR} is a measure of speciation rate more heavily weighted to recent speciation events
184 and λ_{ND} is a measure of speciation across the root-to-tip path. These tip-rate measures are alternatives
185 to state-dependent diversification models such as Quantitative State Speciation-Extinction (QuaSSE). But,
186 based on previous simulation studies λ_{DR} and λ_{ND} are robust and intuitive measures that provide high
187 power and low false discovery rate with large phylogenies when incorporated into Phylogenetic Generalized
188 Least Squares (PGLS) models (Harvey Michael et al. 2017).

189 Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic
190 trees (Rabosky 2014). This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo)
191 to generate probability distributions of evolutionary rate-shift configurations with variable speciation and
192 extinction rates. Importantly, these models provide tip-rate estimates of speciation and extinction rate. The
193 parameters of the 100 BAMM runs are detailed in full in the [ESM](#); briefly we used a time-variable model
194 with 100 expected number of shifts and prior rates set from the initial speciation and extinction values using
195 the **BAMMtools** R package (Rabosky et al. 2014). Each BAMM model (one MCC and 100 random draws of
196 the posterior) was run for 100 million generations, and given the computationally intensive nature of BAMM,
197 runs were conducted across multiple CPU’s. Each run of BAMM reached convergence with effective sample
198 size (ESS) of MCMC (Markov Chain Monte Carlo) samples surpassing 200 (an arbitrary value, above which
199 posterior distributions can often be accurately inferred) for the key model parameters of log-likelihood and
200 number of rate shifts ([Table S3](#), [Table S4](#)). Further details of BAMM parameters and output are available in
201 the [ESM](#), with tip-rate means and variances provided. Additionally, given the variability in BAMM estimates,
202 we also provide some analysis of BAMM shift configurations and tip-rate estimates from our run on the MCC
203 tree and within a BAMM run on the MCC tree from a genetic-only phylogeny across all birds (Harvey et al.
204 2017). All analyses were conducted on log-rates.

205 Statistical analysis

206 Phylogenetic comparative analysis

207 To test the association between speciation/extinction and sexual selection, environmental variability and
208 their interaction, we used phylogenetic least squares (PGLS) models in the **n1m** package (Pinheiro et al.
209 2018). We began by estimating the phylogenetic signal — Pagel’s λ (Pagel 1999) — using the **corPagel**
210 function in the **ape** package (Paradis et al. 2004) on the MCC tree. The estimate of λ was then fixed for
211 model selection, which was conducted on the same MCC tree derived from 2,500 draws of the posterior

212 distribution (Jetz et al. 2012). Model selection used either λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} tip-rate estimates
213 from the MCC tree as the response variable. For λ_{BAMM} and μ_{BAMM} we were also able to use model weights
214 sourced from the inverse of the variance of tip-rates for a given species from the posterior distribution (n
215 = 1,000). Model weights thus reflect the degree of precision to which each species tip-rate is measured in
216 BAMM. Using model selection we only compared interaction terms between a measure of sexual selection
217 (sexual dichromatism or male-biased sexual selection) and environmental measures. That is, we fixed the
218 individual predictors of: dichromatism/male-biased sexual selection measures, log-transformed range size,
219 seasonal temperature variation, spatial temperature variation, long-term temperature variation and NPP
220 while comparing 32 models with different combinations of interactions (including none). Model selection was
221 done in MuMIn using the `dredge` function (Bartoń 2017). Using the terms from the top-ranking model (lowest
222 AICc), we ran the equivalent model for each of the 100 phylogenetic trees used to derive λ_{DR} , λ_{ND} , λ_{BAMM}
223 and μ_{BAMM} , using the unique response variables and phylogenetic tree correlation structure in each model.
224 This method enabled us to present model estimates for an MCC tree alongside 100 trees from the posterior
225 distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three datasets
226 corresponding to each measure of sexual selection: dichromatism derived from RGB values of images (n =
227 5,812); dichromatism from spectrophotometry (n = 581) and the multivariate measure of male-biased sexual
228 selection (n = 2,465).

229 Finally, using data subsetted for species with measurements of male-biased sexual selection, we conducted
230 a phylogenetic path analysis using the phylopath R package (Bijl 2018). The phylogenetic path analysis
231 was used to assess causal paths *between* variables not able to be modelled within the univariate response of
232 PGLS. That is, a phylogenetic path analysis allowed us to model relationships between the predictor variables
233 used in our PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection and
234 range size to have effects on each other and not just on speciation rate. To minimise path complexity we use
235 temperature seasonality (BIO4) as the single measure for environmental variability and use λ_{DR} as the single
236 measure of speciation. The phylogenetic path analysis used tip-rates and correlation structure from the MCC
237 tree. Further details of the path analysis including reasons for path directions can be found within the ESM
238 along with all other analyses and the relevant R code to reproduce results.

239 Results

240 Effects of sexual dichromatism/selection on speciation are not dependent on 241 environmental variability

242 PGLS models with interaction terms between each measure of sexual dichromatism/selection and the five
243 measures of environmental variability (seasonal temperature variation, log-range size, long-term temperature
244 variation, spatial temperature variation and NPP) were included in model selection. However, no interaction
245 terms were significant or present in the top models (δ AICc > 4) for any measure of speciation (λ_{DR} , λ_{ND} ,
246 λ_{BAMM}) or sexual selection (RGB values, spectrophotometry and male-biased sexual selection; δ AICc
247 > 4; [Table S5](#), [Table S6](#), [Table S10](#), [Table S13](#)). Thus we found no evidence that the effect of sexual
248 selection on speciation is dependent on our measures of environmental variation. Furthermore, we found no
249 evidence that these environmental factors (seasonal temperature variation, long-term temperature variation,
250 spatial temperature variation and NPP) predict speciation independently from sexual dichromatism/selection

251 (Figure 1, Figure S10).

252 No evidence that sexual dichromatism affects speciation

253 We found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation.
 254 Using three response measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}), the effect of sexual dichromatism was not
 255 significant in any PGLS model based on tip-rate estimates and correlation structures from the MCC tree.
 256 Specifically, sexual dichromatism showed no association with λ_{DR} ($\beta = -1.279e-03$, $p = 0.147$; Figure 1a,
 257 Figure 2a) or λ_{ND} ($\beta = -5.745e-05$, $p = 0.078$; Figure 1a). Furthermore, speciation rates from BAMM
 258 (λ_{BAMM}) were also unaffected by sexual dichromatism ($\beta = -1.430e-05$, $p = 0.872$; Figure 1a). PGLS analyses
 259 using subsetted data ($n = 581$), where sexual dichromatism was measured using spectrophotometry (Armenta
 260 et al. 2008) yielded results concordant to the full data set; *i.e.* no association between sexual dichromatism
 261 and speciation or extinction (Figure S10). Our results from MCC models are largely corroborated by model
 262 estimates from PGLS analyses of the rates and correlation structures from 100 random trees. The HPD
 263 (highest posterior density) intervals show model estimates are distributed around zero when using complete
 264 taxon sampling models and RGB measures of sexual dichromatism (Figure 1a, Table S8). For PGLS models
 265 using spectrophotometry-based measures of sexual dichromatism, the estimates from the 100 trees in the
 266 λ_{DR} models are positively skewed (-1.781e-02, 3.488e-02) but normally distributed around zero for λ_{ND} and
 267 λ_{BAMM} (Table S12).

268 Male-biased sexual selection increases speciation

269 We found a significant positive association between male-biased sexual selection ($n = 2,465$) and λ_{DR} (β
 270 = 3.887e-02, $p = 0.012$; Figure 1b). However, this associate was not significant for the other two measures
 271 of speciation rate (λ_{ND} : $\beta = 4.381e-04$, $p = 0.351$; λ_{BAMM} : $\beta = 9.422e-04$, $p = 0.764$; Figure 1b). The
 272 distribution of estimates from PGLS models on 100 random trees was similar to the estimate from an MCC
 273 tree: among the 100 trees there was a positive association between sexual selection and λ_{DR} (HPD Interval =
 274 9.115e-03, 6.085e-02), and a smaller positive association between sexual selection and λ_{ND} (HPD Interval =
 275 -3.104e-04, 1.536e-03;) as well as λ_{BAMM} (HPD Interval = -1.297e-02, 3.089e-02). Complete HPD intervals
 276 for models using male-bias sexual selection PPCA as a predictor can be found within Table S15.

277 Species with smaller ranges have increased rates of speciation

278 Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation we found a negative association between range size and
 279 speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This negative
 280 association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.578e-03$, $p = 0.001$; λ_{ND} :
 281 $\beta = -1.462e-04$, $p = 0.034$; Figure 1a, Figure 2). This association was also evident across the estimates from
 282 models using the 100 trees (λ_{DR} : HPD Interval = -8.438e-03, -1.823e-03; λ_{ND} : HPD Interval = -1.899e-04,
 283 9.112e-06; Figure 1a). Subsetted models with reduced sample size and different measures of sexual selection —
 284 but the same measure of range size — showed variable evidence that range size is negatively associated with
 285 speciation. Range size significantly predicted λ_{DR} (Figure 1b) using data subsetted for male-biased sexual
 286 selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} . Models using data subsetted for spectrophotometry-based

287 dichromatism ($n = 581$) gave non-significant estimates for the effect of range size on all measures of speciation
288 (Figure S10, Table S11, Table S12). Because the range size dataset is the same across the three data subsets
289 we draw our conclusions from the models with highest power using near-complete taxon sampling ($n = 5,812$).

290 Phylogenetic path analysis

291 Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
292 (Figure 3; Figure S13). Notably, environmental variability (temperature seasonality) directly affected sexual
293 dichromatism ($\beta = 0.07$) and the path from male-biased sexual selection to sexual dichromatism was relatively
294 weak, ($\beta = 0.22$). Additionally, the large direct effect of temperature seasonality on range size ($\beta = 0.52$)
295 suggests an indirect effect of temperature seasonality on λ_{DR} ($\beta = -0.02$; Figure 3), given the negative we
296 identified between λ_{DR} and range size in PGLS models.

297 Extinction rate

298 We found no evidence that extinction (μ_{BAMM}) was impacted by the extent of sexual dichromatism for
299 full-taxon sampling ($\beta = 2.390\text{e-}05$, $p = 0.93$; Figure 1a), nor spectrophotometry-based measures of sexual
300 dichromatism (Figure S10, Table S11, Table S12) or male-biased sexual selection (Figure 1b, Table S14, Table
301 S15).

302 Variability across trees and methods

303 We tested our hypothesis that sexual selection is associated with speciation using several methods and across
304 100 trees drawn from the post burn-in posterior (Jetz et al. 2012). We used a range of methods to overcome
305 uncertainty in the power and precision of various tip-rate estimates as well as the variation between trees.
306 We found that the tip-rate estimates across the 100 trees were quite variable for both λ_{DR} and λ_{BAMM}
307 (Figure S14). Despite this, tip-rate estimates of speciation from the two methods were moderately correlated
308 across the 100 trees ($r = 0.75$) and for the MCC tree ($r = 0.68$; Figure S15). However, in comparison to λ_{DR} ,
309 the value of λ_{BAMM} was the *mean* drawn from a posterior distribution ($n = 1,000$) of BAMM generations,
310 thus estimates of λ_{BAMM} (and μ_{BAMM}) have an added level of variation. To account for this variation,
311 weights (using the inverse of the variance) were used for the PGLS models. From 1,000 posterior samples
312 of the MCC BAMM run the coefficient of variation (CV) for all log-rates of λ_{BAMM} was relatively low
313 (*mean CV* = 21.49, *median CV* = 15.76 ; see Figures S5 and Figure S7). Despite the convergence of the
314 BAMM model in all runs — where effective sample sizes of the number of shifts and log-likelihood were all
315 greater than 200 (Table S3, Table S4) — we found that the unique combinations of rate shifts across the
316 large phylogenetic tree ($n = 5,966$ species) was high. This means that although the number of rate shifts
317 reached convergence (*median* = 59; Figure S6), the locations of the rate shifts (*i.e.* the credible shift set)
318 across the tree are highly heterogeneous. The variability in the locations for the shift configurations is a
319 likely source of uncertainty in downstream tip-rates used as the response variable in PGLS models. Notably,
320 the 95 % HPD interval for model estimates using BAMM rates from 100 trees was about 20-fold the 95 %
321 confidence intervals of the estimate from the MCC tree; whereas for λ_{DR} and λ_{ND} the HPD 95 % interval
322 width was equal to or less than the MCC 95 % CI (Figure 1, Table S9).

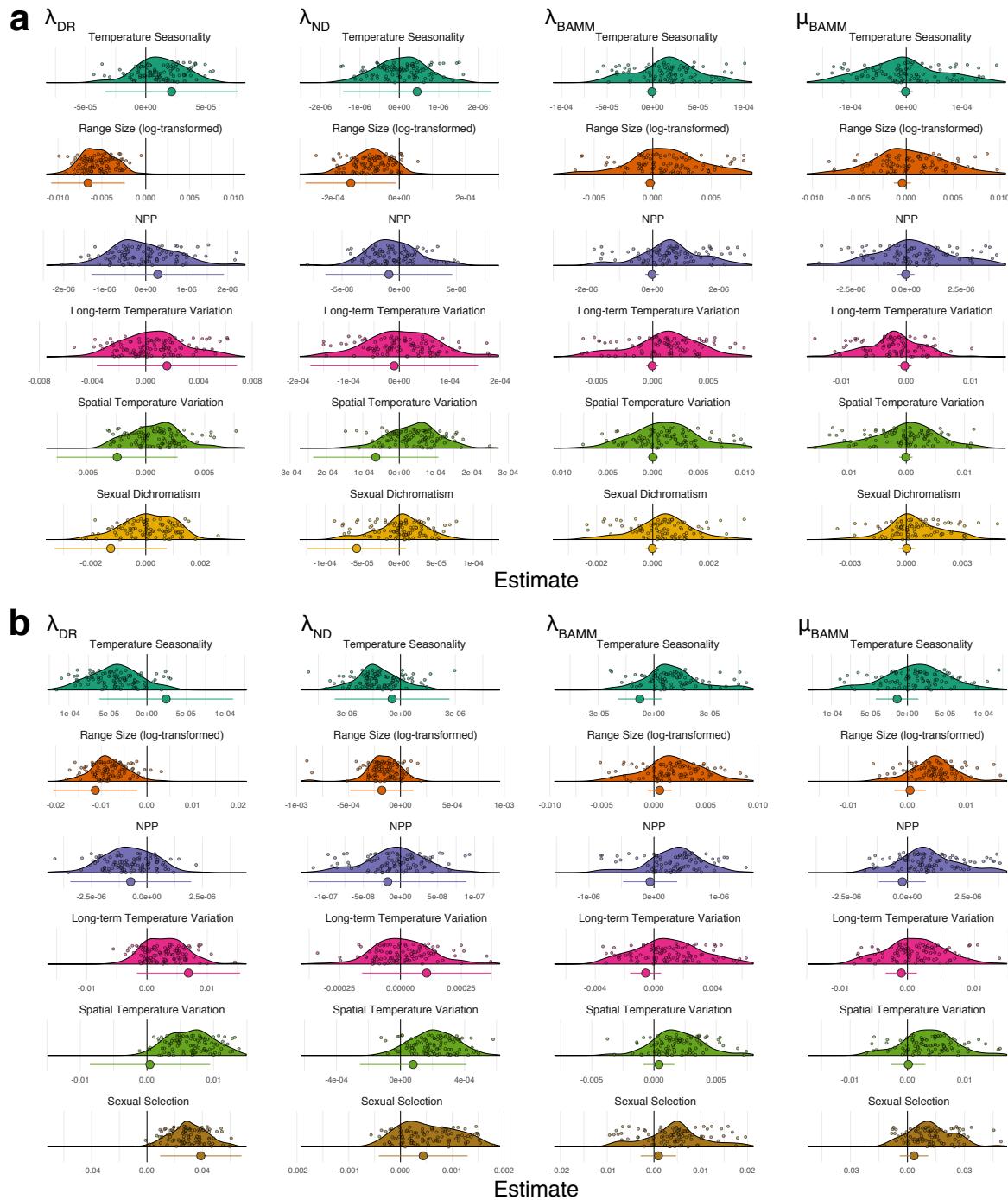


Figure 1: Model estimates for (a) PGLS analyses using sexual dichromatism ($n = 5,812$) and (b) PGLS analyses using measures of male-biased sexual selection ($n = 2,465$). Both datasets were used for analyses with three measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one measure of extinction (μ_{BAMM}) as response variables. The numerical values for the model estimates using the MCC tree and HPD intervals of estimates from 100 random trees can be found in the ESM. Density curves are based on estimates from 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 interpret the MCC 95 % CIs.

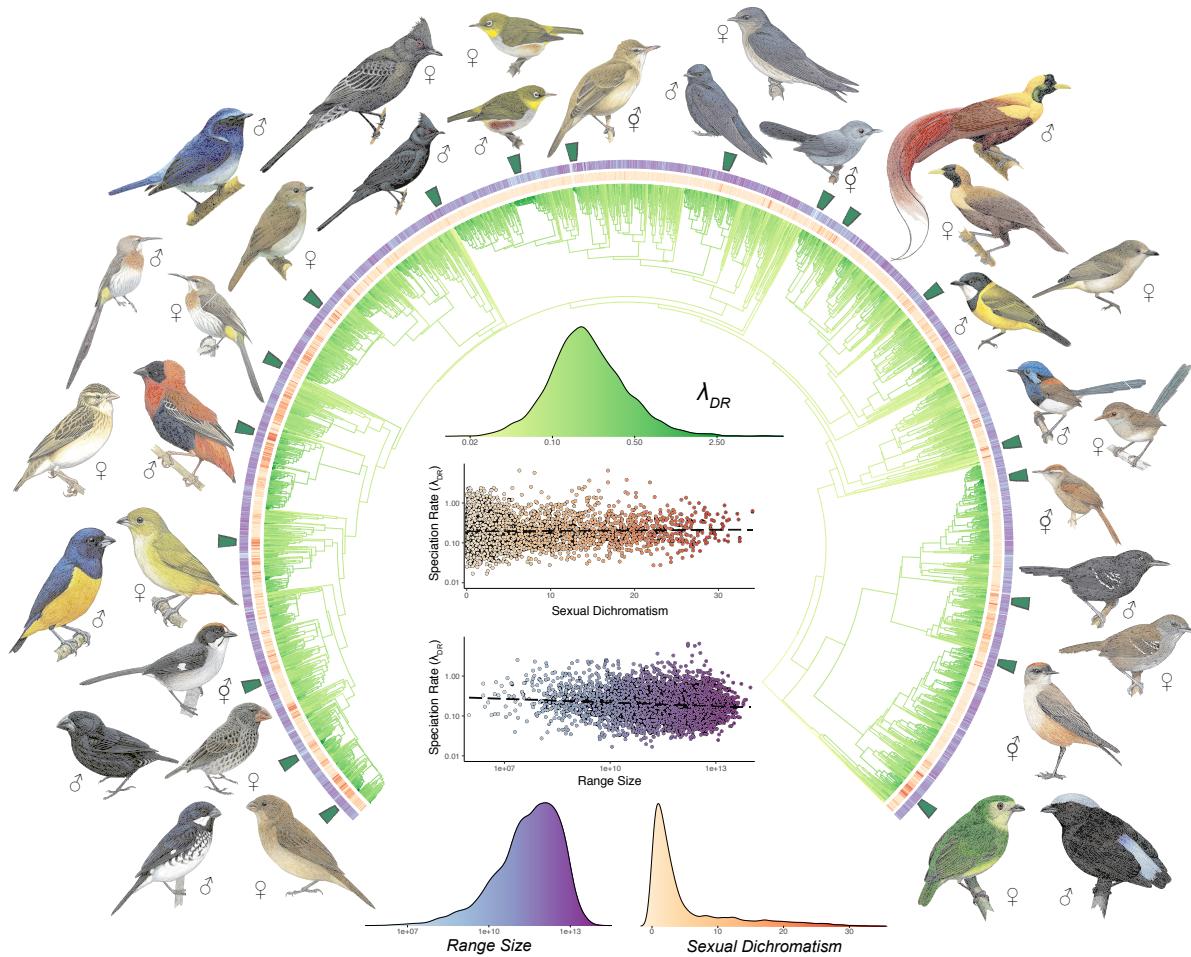


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism and range size available for 5,812 of them. Across these species there was a small but significant negative association between λ_{DR} and log-range size but no significant association between λ_{DR} and sexual dichromatism based on RGB. 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.

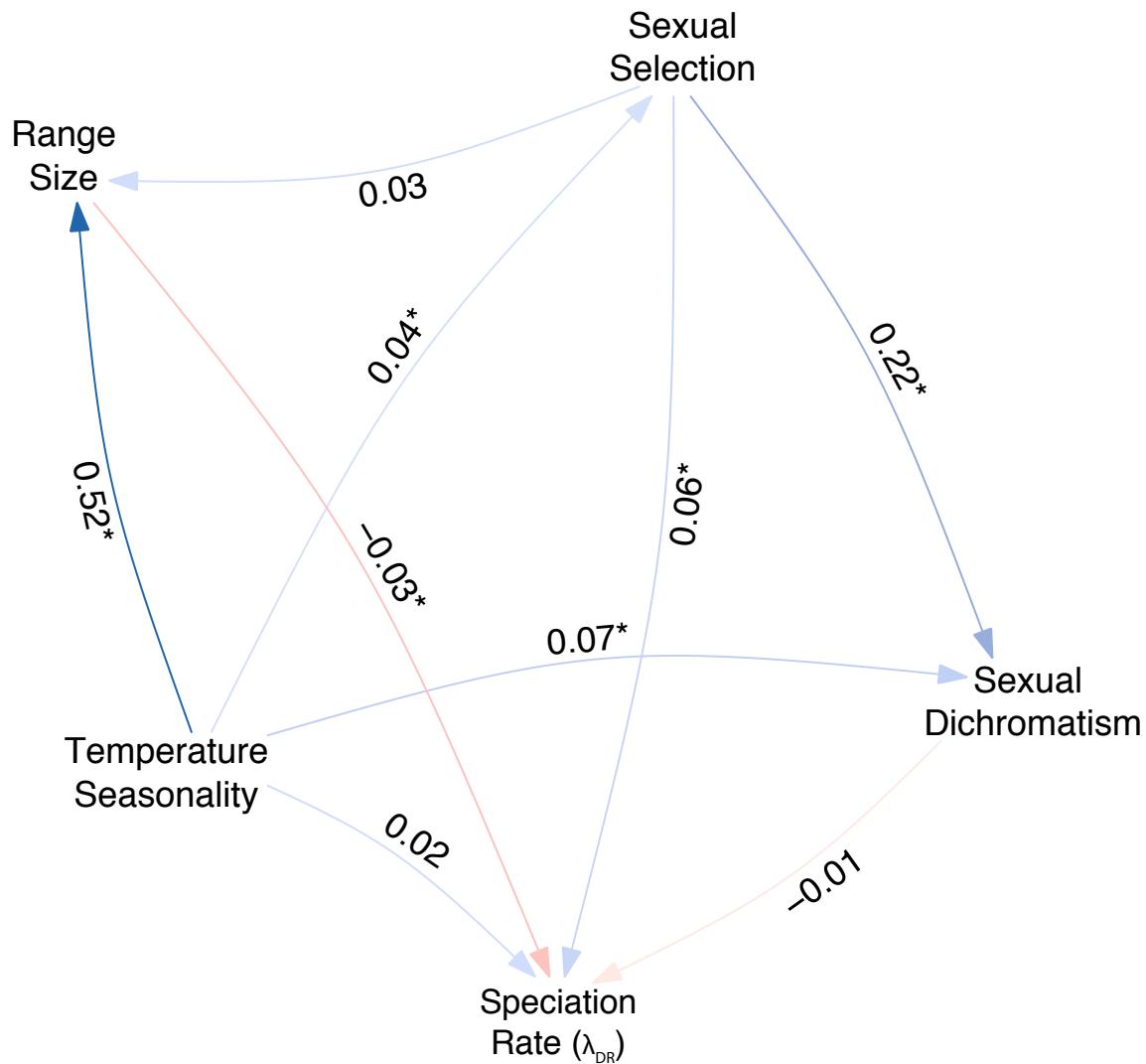


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with numeric values corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95 % confidence intervals of this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

323 Discussion

324 We found no evidence that sexual dichromatism alters the rate of speciation in passerine birds independently
325 or via interactions with environmental variability. This result is consistent across different measures of
326 speciation (λ_{DR} , λ_{ND} and λ_{BAMM}) and two measures of dichromatism (spectral and RGB). The results
327 are also consistent with previous studies performed at a smaller scale (Huang and Rabosky 2014; Cooney
328 et al. 2017). However, we found that when using a measure of male-biased sexual selection — instead
329 of sexual dichromatism — there was a positive association with speciation, though the strength of this
330 relationship varied across different rate estimates. Our findings suggest that the components of the composite
331 measure of male-biased sexual selection (sexual size dimorphism, social polygyny and [lack of] paternal care)
332 are better predictors of speciation than sexual dichromatism. No bioclimatic measures of environmental
333 variability (temperature seasonality, long-term temperature variation and spatial temperature variation)
334 predicted speciation, but range size was negatively associated with two measures of speciation (λ_{DR} , λ_{ND}).
335 This suggests that species with smaller range sizes have increased speciation rate, however, small range size
336 may be a cause or effect of elevated speciation rate and potentially even an artifact of taxonomic classification.
337 Interestingly we found a discrepancy in the model results obtained from tip-rate statistics (λ_{DR} , λ_{ND}) and
338 those using tip-rate estimates from a model-based approach (λ_{BAMM}); whereby BAMM produced precisely
339 null results for most associations between predictors and speciation as well as extinction.

340 The association between sexual selection and sexual dichromatism in birds is a Darwinian trope (Darwin
341 1871) that allows it to be commonly used as a proxy for the strength of sexual selection in comparative
342 studies (e.g., Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and
343 Rabosky 2014). Despite the association between sexual selection and sexual dichromatism in passerine birds
344 (Dale et al. 2015) we find that sexual dichromatism does not predict speciation rate, whereas male-biased
345 sexual selection does. Given our results, we suggest that sexual dichromatism may not be a robust proxy
346 for sexual selection, and that variance in the association between dichromatism and the strength of sexual
347 selection may obscure any relationship with speciation rate, despite the high power of our comparative study.
348 There are several reasons why the use of sexual dichromatism as a proxy for sexual selection is problematic.
349 Firstly, ecological pressures could drive sexual dichromatism in the absence of mate choice if sex-specific
350 niches provide opportunity for the evolution of sex-limited traits (Wallace 1889; Kottler 1980; Slatkin 1984;
351 Shine 1989). Specifically, natural selection on females may be important in explaining patterns of sexual
352 dichromatism in birds (Price and Eaton 2014). In fairy-wrens (*Malurus cyaneus*), female colouration has
353 evolved in response to environmental pressures, leading to increased sexual dichromatism in regions where
354 females are under stronger selection from predation (Medina et al. 2017). Ecological impacts on sexual
355 dichromatism are supported by our path analysis, which reveals that sexual dichromatism is positively affected
356 by temperature seasonality (a measure of environmental variation), albeit relatively weakly. Secondly, colour
357 is but one trait and sexual selection may drive the evolution of sex differences in a wide variety of traits
358 used in mate choice or intrasexual competition (Miles and Fuxjager 2018). And lastly, not all plumage
359 colouration honestly reflects mate quality. A recent meta-analysis found that converted carotenoids (but *not*
360 those sourced from diet) predict mate quality through improvements in parasite resistance and reproductive
361 success (Weaver et al. 2018). Given the importance of honest signaling in sexual selection and the variability
362 in colour production across birds, sexual dichromatism in many species may be an unreliable measure of
363 mate quality for female birds and sexual selection for researchers.

364 In-line with predictions and a previous meta-analysis (Kraaijeveld et al. 2011) we found that male-biased
365 sexual selection increases speciation rate — at least for λ_{DR} and λ_{ND} estimates — but this association was
366 not dependent on variable or stressful environments. When evolving under stressful conditions, sexually
367 antagonistic selection is hypothesised to be weakened relative to selection that is concordant between the
368 sexes (Connallon 2015; Connallon and Hall 2016). While these predictions are supported in several lab
369 (experimental evolution) studies (Long et al. 2012; Punzalan et al. 2013; Berger et al. 2014), other studies
370 have not found the association (Delcourt et al. 2009; Martinossi-Allibert et al. 2017; Holman and Jacomb
371 2017). The environmental variability predictors used here often reflected changes in climate across space and
372 time, whereby high environmental variation would likely increase the strength of natural selection on a given
373 species. Given that we did not detect an effect of environmental variability (by itself or as an interaction
374 with sexual selection) we are left with several possible explanations. Firstly, the effects of sexual selection on
375 adaptation and thus speciation may depend on the type of environmental variability the species is evolving
376 under. Specifically, sexual antagonism may be more easily purged in environments where cyclic pressures
377 (*e.g.* seasonality) are perpetuated; whereas when environmental variability is directional (*e.g.* long-term
378 climatic change) sexual antagonism can remain indefinitely as a fitness burden (Connallon and Hall 2016).
379 Secondly, the environmental predictors used here may not account for the key ecological forces/natural
380 selection pressures that interact with sexual selection to drive speciation. Specifically, access to dietary
381 resources, and the impacts of predation or parasitism are unaccounted for here, these are likely key processes
382 affecting sexual selection and speciation (*reviewed in* Maan and Seehausen 2011). Thirdly, it is also possible
383 that there is no effect of environmental variability on speciation rates; at least not in the species investigated
384 here.

385 The most consistent finding uncovered in this comparative analysis is that smaller range sizes are associated
386 with increased speciation rates; however reduced range size can be a cause or consequence of speciation.
387 Intuitively, large range size should promote speciation by creating greater opportunities for geographic barriers
388 to form (Rosenzweig 1995). However, birds with smaller range sizes are predicted to have lower dispersal
389 ability. This ensues that individuals might not be able to overcome geographical barriers and maintain gene
390 flow; which would promote reproductive isolation and speciation (Birand et al. 2012; Claramunt et al. 2012).
391 Several studies have used morphological measures of wing shape (Hand-wing index/ Kipp's distance) — a
392 proxy for dispersal ability — as predictors of speciation and coexistence (*e.g.*, Kennedy et al. 2016; Pigot et
393 al. 2016). But currently, published datasets of these measurements are not available for many passerines.
394 Alternatively, reduced range size may be a consequence of speciation. Under this view, high speciation rate
395 may lead to smaller range sizes as niche filling by recently diverged species will suppress the expansion of
396 newly speciated relatives. Within Himalayan songbirds, range expansions are prevented by the competition
397 for resources by related species (Price and Eaton 2014); this suppression on range expansion is consequently
398 expected to prevent future speciation events (Rosenzweig 1995; Weir and Price 2011). Unlike Himalayan
399 songbirds, species undergoing adaptive radiation in new niches are unlikely to be limited by competition for
400 resources from existing taxa. Across islands we expect to see a correlation between speciation and small range
401 size because they reflect newly formed environments with empty niches. Thus, our findings may be heavily
402 dependent on species whose range size is restricted to a single island within an archipelago (*e.g.* *Geospiza*
403 sp.; a.k.a. Darwin's finches). One further explanation for the negative association between range size and
404 sexual dichromatism/sexual selection is the potential bias of taxonomic classification, whereby over-splitting
405 of species in clades with large ranges leads to increased recent phylogenetic branching as well as smaller
406 ranges. Given the problems of determining causality and mode of speciation the reason for the negative

407 association found here remains obscured.

408 In addition to speciation, sexual selection has frequently been invoked as a driver of extinction. Sexual
409 selection may increase extinction risk as it often leads individuals (usually males) to invest in exaggerated
410 mating signals as opposed to traits — such as parental care — that elevate offspring fitness (*reviewed in* Kokko
411 and Brooks 2003). Using BAMM, we found no association between extinction rate and sexual dichromatism,
412 male-biased sexual selection or measures of environmental variability. Extinction is notoriously hard to
413 estimate accurately (*see* Rabosky 2016). It can be estimated from phylogenetic inference, fossil record, records
414 of recent extinctions and IUCN extinction threat status. Phylogenetic methods — like BAMM — allow for
415 speciation and extinction rates to be measured using moderately sized phylogenies. However, BAMM has
416 been subject to controversy in its ability to model rate shifts and extinction rates (*see*, Beaulieu and O'Meara
417 2015; Rabosky 2016; Moore et al. 2016; Rabosky et al. 2017), and while several tip-rate estimates exist for
418 speciation (*e.g.*, λ_{DR} and λ_{ND}) extinction estimates are not as easily obtained. Here, we found that BAMM
419 often produced homogeneous speciation and extinction rates for clades with few rate shifts; arguably this
420 could reduce our power to detect small differences in extinction rates among closely related taxa (Rabosky
421 et al. 2017; Rabosky and others 2018). The ability to detect extinction rates rarely improves when fossil
422 records are used, as many clades (*e.g.* birds) lack the stratigraphic sampling across time to statistically
423 calculate extinction rates. But, there are exceptions: ostracods — a group of marine invertebrates — have
424 extensive fossil records and show identifiable sexual dimorphism. Across 93 species of ostracods, Martins et
425 al. (2018) found that ostracod taxa with larger sexual dimorphism (representing exaggerated investment by
426 males in reproductive organs) had higher extinction rates; implying that sexual selection increases extinction
427 risk. Alternatively, when comparative studies have assessed the relationship between sexual selection and
428 extinction in extant birds (Mitra et al. 1996; Doherty et al. 2003; Morrow and Pitcher 2003) and mammals
429 (Morrow and Fricke 2004; Bro-Jorgensen 2014) there has been no consensus. Unfortunately, these methods
430 often rely on extinction threat status from the International Union for Conservation of Nature (IUCN) Red
431 List (*e.g.*, Morrow and Pitcher 2003; Morrow and Fricke 2004; Bro-Jorgensen 2014) and may be biased to
432 species under greater anthropogenic threat, culturally valued or well researched.

433 Improvements in estimating tip-rates of speciation has allowed us to revisit the association between sexual
434 selection and speciation. With high power and alongside extensive ecological predictors we find support that
435 male-biased sexual selection predicts speciation. If sexual selection promotes speciation through improvements
436 in fitness and adaptation the implications are manifold with sexual selection a potentially valuable utility in
437 conservation (*reviewed in*, Holman and Kokko 2013) and captive breeding programs for threatened species
438 (*reviewed in*, Charge et al. 2014). Furthermore, our finding that high speciation rate is associated with
439 smaller range size has pronounced significance to the future survival of these rapidly speciating species in a
440 world with increased habitat loss and anthropogenic stress. Range size is the best predictor of extinction risk
441 (Harris and Pimm 2008) and the association found here ensues that many newly speciated clades may be at
442 greater risk of extinction due to their reduced range being impacted by anthropogenic effects.

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Critical analysis

[On Darwinism]... But it by no means follows that slight differences in the shape, pattern, or colours of the ornamental plumes are what lead a female to give the preference to one male over another; still less that all the females of a species, or the great majority of them, over a wide area of country, and for many successive generations, prefer exactly the same modification of the colour or ornament.

— ALFRED RUSSEL WALLACE

Strengths and limitations

Perhaps one of the biggest unravelings of this project was the decoupling of male-biased sexual selection from sexual dichromatism, remarkably this same controversy engrossed Wallace and Darwin 130 years ago (Kottler 1980). The widespread use of sexual dichromatism as a proxy for sexual selection often goes unchallenged as our instinctive Darwinian minds reminisce of peacocks and birds of paradise; my thoughts were such when I began this scientific inquiry. Although, sexual dichromatism measurements from illustrations were always going to be an imperfect estimate of sexual selection, across 5,831 species I anticipated a signal would permeate through the noise. Alas — this was not so — and male-biased sexual selection and sexual dichromatism had different effects on speciation. With this in mind, the practical use of sexual dichromatism in macroevolutionary research is severely weakened. This finding is pertinent as efficient proxy measurements are invaluable for comparative analyses, proxies of sexual selection increase the accessibility, available sample size and transferability of research, making a study more conducive to research synthesis. But, as Wallace remarks, the matter is inevitably more complex, despite the irresistibility of the Darwinian argument¹ (Kottler 1980; Caro 2017). On the bright side, the multivariate measure of male-biased sexual selection (sexual dimorphism, social polygyny and [lack of] paternal care) is a dataset that would benefit from being expanded across birds. Future research may also benefit from expanding this multivariate measure to account for ornamentation, often overlooked by sexual dimorphism and dichromatism measures [see Gomes_2016].

Not only are the measurements of sexual selection under a cloud of uncertainty, the estimates of speciation and extinction are another point of controversy. Macroevolutionary research is a field plagued by methodological uncertainty and conflicts. Originally, I had planned to continue my meta-analysis by investigating extinction rate across a large taxonomic group. There were signs that extinction rate could be measured from phylogenetic methods with relative confidence (Pyron and Burbrink 2016). However, these hopes soon dissipated, and with them the seeming *raison d'être* of the study. Extinction rate is arguably the best measure of population fitness as it tracks survival over multiple generations. And while a high profile study has measured extinction rate in experimental evolution (Lumley et al. 2015), it has been rarely measured accurately over evolutionarily meaningful timescales (*but see* Martins et al. 2018). We included measurements of extinction rate in this study, however the findings were played-down. The movement away from extinction and towards speciation is because of the controversy surrounding extinction rate measures as well as phylogenetic uncertainty. Measuring extinction rates from the Jetz et al. (2012) bird phylogeny is problematic because of the nature of phylogenetic

¹Wallace was initially supportive of the evolution of sexual dichromatism as a result of mate choice but later took the position where natural selection on predator-prone nesting females led to females losing their plumage colouration.

construction: a birth-only model of tree construction and incomplete genetic taxon sampling are large barriers that limit the ability to use model-based methods to detect extinction rate (Beaulieu and O'Meara 2015). Furthermore, the very detection of absence of data — which is what such methods attempt to do — is a hard sell, both conceptually and methodologically come peer review: see Rabosky (2016) for a cautionary tale on measuring extinction rate with BAMM. The mechanisms and rates at which speciation and extinction occur are an active area of research. In a recent pre-print Henao Diaz et al. (2018) used BAMM across 104 time-calibrated molecular phylogenies and found that despite variation in ecology, biogeography and taxonomy, younger clades consistently had higher rates of speciation and extinction. This finding of time-dependency in rates of diversification makes comparative analyses between clades challenging and calls into question countless studies. Similar to Wallace's view of sexual dichromatism we are left with a view of diversification rate measures where we cannot yet account for the underlying true variation; which is vastly more complex than we can currently measure.

As with sexual dichromatism and macroevolutionary rates, the most severe limitation for environmental variation was the coarseness of the measures. In total, for 5,831 species we extracted 338,203,831 point measures² of environmental variability, but these measures may not account for important variation in biotic components such as nutritional resources or predation. Arguably, the methods used here are much better than simply using the range mid-point to obtain a measure of temperature, precipitation or seasonality or where only one bioclimatic variable is used. I would argue that reducing the multivariate data into several biologically meaningful predictors is a conceptually challenging exercise, but researchers should not feel limited by the amount of raw data that they can access³. In fact, previous to our study on birds the same methodology was applied to ~ 100 species of bovids with speciation, extinction and environmental variability estimates obtained. This study was prematurely halted as there was homogeneity in the response variable (speciation and extinction rates) across the smaller bovid phylogeny. However, this workflow was easily transferred over to passerine birds with similar methods used for extracting environmental predictors. The use of extensive bioclimatic predictors and spatial data in macroevolutionary research is imperative as we scale up studies. At very least, if bioclimatic variables do not encapsulate key ecological parameters (*e.g.*, resources, predation, habitat structure) these predictors may account for some of the noise in the dataset and may help isolate the effect of the key moderator variables of interest.

Future Directions

I had initially envisaged that this comparative study would allow for the reliable measure of extinction rate, use multiple taxonomic groups and more robust measures of sexual selection (*see* Anthes et al. 2016). As such, many questions regarding this topic remain unanswered. Here I discuss the broader directions that we may follow in order to consolidate our understanding of sexual selection and its effects on fitness and diversification. I will draw heavily on the discussions from a Royal Society meeting on '*Sexual selection: patterns in the history of life*'⁴ in the UK this year. This meeting spurred further inquiry into the subject and how interdisciplinary approaches can be harnessed to liberate ourselves from conventional comparative

²5,831 species x 1000 samples per range x 59 environmental variability measures including bioclimatic predictors now, in the last inter-glacial and the last glacial maximum as well as NPP.

³This statement applies to species with documented range sizes, which varies across clades but is comprehensive for birds, mammals, amphibians and many marine groups. The [IUCN](#) has a large and accessible database for research use. Details of how we extracted data from these ranges is provided as a potentially useful resource in the [ESM](#).

⁴Specifically, the following two sections are spurred from dialogue with [Dr Gene Hunt](#) and [Associate Professor Erin E. Saupe](#)

methodologies.

The study by Martins et al. (2018) has already been referred to in the main text of both papers and for good reason. This elegant study was able to do what no one else has; reliably measure extinction rate over meaningful time scales. Using fossil ostracods with various levels of sexual dimorphism, Martins et al. (2018) found that species with high levels of sexual dimorphism were quickly swept to extinction. From stratigraphic occurrence data a capture–mark–recapture model was used to determine the rate of extinction for 93 species. Their finding challenges the results from experimental evolution studies (Jarzebowska and Radwan 2010; Plesnar-Bielak et al. 2012; Lumley et al. 2015) and our meta-analysis that suggest sexual selection mitigates extinction. In future, it would be incredibly valuable to see whether other groups of marine invertebrates have the fossil data and recognisable sexual dimorphism to conduct such a study. In the interim I would be eager to see how BAMM performs on an ostracod phylogeny and whether the same positive association between extinction rate and sexual dimorphism could be detected from the phylogeny. For me, this will be a true test of the applicability of BAMM and a key step in the effort to reliably measure extinction rates across a wider variety of species.

One aspect and only foreseeable shortcoming of the ostracod study is that it did not account for environmental variability; a challenging proposal for extinct species nevertheless. However, the use of paleoclimate models in evolution is now a reality; with recent studies incorporating averaged values across multiple paleoclimate models as predictors of speciation (see Quintero and Jetz 2018). While the uncertainty surrounding paleoclimates was beyond the scope of the study, future studies should remain vigilant of the everlasting need to use key ecological processes in macroevolutionary research (*reviewed in* Weber et al. 2017). In our study on passerine birds we found that range size is negatively associated with speciation, yet range size encapsulates multiple aspects of ecology and evolution so it is unclear what the finding truly means. The role of range size in speciation may be further investigated through ancestral geographic range reconstruction (Quintero et al. 2015), as ancestral ranges may be beneficial in understanding modes of speciation and the causality of range size expansions and contractions (Losos and Glor 2003). Within Palaeobiology the role of range size and niche breadth on diversification patterns has been the subject of recent interest (e.g. Saupe et al. 2015; Qiao et al. 2016). Across 92 bivalve species that lived during a mid-Pliocene warming period, Saupe et al. (2015) used environmental niche modelling to assess the impact of ecological processes on extinction. Harnessing ecological niche modelling in macroevolutionary studies across extant taxa such as passerine birds is a daunting challenge but offers an *eco-evo* synthesis that may be pertinent in questions relating to extinction; especially if the taxonomic group under inquiry is of high conservation value, for which the songbirds certainly are.