

1 Sexual selection, environmental variation, range size and speciation
2 in passerine birds

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4 **Abstract**

5 Sexual selection may influence patterns of diversification; yet controversy remains on whether sexual
6 selection leads to a net increase or decrease in speciation rate, or even elevates extinction. Sexual selection
7 is predicted to increase speciation rate as it can facilitate adaptation to new environments, and work
8 alongside divergent natural selection to swiftly promote reproductive isolation. However, sexual selection
9 frequently favours investment in costly or harmful traits that may reduce adaptation affect diversification.
10 Here, we investigate the association of sexual selection with speciation and extinction in passerine birds.
11 We use two measures of sexual selection: sexual dichromatism ($n = 5,812$ species) and a multivariate
12 measure of male-biased sexual selection (sexual dimorphism, polygyny and paternal care; $n = 2,465$),
13 three distinct measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one measure of extinction (μ_{BAMM}).
14 Importantly, we test whether the effects of sexual selection on speciation are dependent upon ecological
15 pressures such as temperature variability across time and space, primary productivity and range size. We
16 find that male-biased sexual selection but not sexual dichromatism predicts speciation. Additionally, we
17 find that birds with smaller ranges have higher speciation rates; although the direction of causality is
18 unclear.

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19 Introduction

20 Selection pressures drive speciation. As populations diverge they accumulate genetic and phenotypic changes
21 that ultimately erect barriers against gene flow (Presgraves 2010; *but see* Shaw and Mullen 2011). In this view,
22 populations will speciate and adapt more readily to new divergent environments if selection is strong and/or
23 persistant. Hence, the rate at which speciation occurs is likely dependent on both the populations response to
24 selection (adaptation) and the potential for divergent phenotypic traits to evolve (*e.g.* morphology or colour
25 Hugall and Stuart-Fox 2012; Rabosky et al. 2013). Sexual selection is an evolutionary force likely to affect
26 fitness components, such as reproductive success or viability, as well as the evolution of ornaments involved
27 in mating displays or weapons used in male-male competition. Sexual selection is therefore hypothesised to
28 be a key driver of diversification through shifting the rates of adaptation, speciation and extinction.

29 Sexual selection is applied by one sex on the other — more often by females on males (Kokko and Jennions
30 2008; Fromhage and Jennions 2016; Janicke et al. 2016) and the strength of sexual selection can increase or
31 decrease the average fitness of a population; often termed population fitness (*reviewed in* Kokko and Brooks
32 2003; Whitlock and Agrawal 2009; Holman and Kokko 2013). Specifically, in line with the ‘good genes’
33 perspective, sexual selection may purge deleterious mutations (Agrawal 2001; Siller 2001) and fix beneficial
34 mutations in a population (Whitlock 2000). Thus, sexual selection is thought to be a key process in mitigating
35 extinction risk and facilitating adaptation. Sexual selection can also increase the fitness of a population
36 when the genotypes under sexual selection (*e.g.* those that increase male mating/fertilisation success) are
37 genetically positively correlated with traits affecting fitness (*e.g.* female fecundity or survival). However,
38 this positive correlation is not ubiquitous; indeed sexual selection frequently favours traits having negative
39 pleiotropic effects on female fitness (Pischedda and Chippindale 2006; Bonduriansky and Chenoweth 2009;
40 Pennell and Morrow 2013; Berger et al. 2014). For instance, in species with high levels of sexual selection,
41 mating success becomes more variable and uncertain; thus individuals must invest heavily to increase their
42 chances of successfully reproducing. High investment into costly weaponry and sexual signals, may trade off
43 against strategies that would improve offspring fitness (*e.g.* parental care). This is a costly consequence of
44 sexual selection that affects persistence, adaptation and extinction (Kokko and Brooks 2003).

45 Alongside changes to fitness, sexual selection has been proposed to facilitate speciation through the evolution
46 of divergent signals/ornaments associated with improved mating success (Lande 1981, 1982). For instance,
47 in antbirds (Thamnophilidae), genera with complex songs and striking dichromatism, are more species rich
48 (Seddon et al. 2008). Under this model of speciation, divergent sexual signals in one sex (usually males)
49 co-evolve with divergent preferences for those signals in the opposite sex, leading to behavioural reproductive
50 isolation (Safran et al. 2013). Concurrently, sexual selection can promote the extent to which populations
51 diverge by enlarging the phenotypic space diverging species can evolve into. These predictions emerge as
52 sexual selection may increase genetic diversity as a result of trade-offs between naturally- and sexually-selected
53 traits or trade-offs under intra-locus sexual conflict between male and female trait expressions (Lorch et
54 al. 2003; Bonduriansky 2011; Radwan et al. 2016). However, the genetic architecture (*per se* heritability)
55 of fitness and sexually selected traits may vary due to different sex determination systems across taxa. In
56 male homogametic species (ZZ/ZW or ZZ/ZO) — such as birds — males are predicted to have increased
57 heritability of male-specific genotypes on the Z chromosome associated with mating success: such as elaborate
58 ornamentation or plumage colouration (Hastings 1994; Reeve and Pfennig 2003). We might therefore expect
59 bird populations experiencing stronger sexual selection to have increased adaptation and speciation rates.

Importantly, the effects of sexual selection on adaptation and speciation may depend on environmental conditions. Both theoretical and empirical studies suggest that under stressful/changing environments, sexual selection may have greater fitness benefits than under benign environments. Stressful environments strengthen the positive correlation between male mating success and female fitness, reducing the burden of negative pleiotropic effects (Long et al. 2012; Berger et al. 2014; Connallon and Hall 2016; Martinossi-Allibert et al. 2017). Conversely, benign or stable environments ensure consistent selection, preferentially eroding genetic variation at sexually concordant loci (*i.e.* loci where the optimum genotype is equivalent for both sexes). In this situation, genetic variation remains disproportionately at sexually antagonistic loci; causing displacement of male and female traits from their optimum. It follows from these predictions that populations with stronger sexual selection would have increased fitness and adaptive benefits, allowing them to adapt to novel environments (*reviewed in* Candolin and Heuschele 2008). In certain circumstances, sexual selection will reinforce locally adapted phenotypes through mate choice on phenotypes that effectively advertise quality in a specific ecological context (Boughman 2002; Maan and Seehausen 2011). Additionally, if mate choice operates on both sexes — or there is a correlation in trait values between a pair — assortative mating is likely to speed-up the evolution of divergent mating signals (Lande 1981). In several bird taxa, beak morphology is a trait that arose under natural selection and is now a trait under sexual selection (a.k.a. “magic traits”; Servedio et al. 2011). In Darwin’s finches (*Geospiza fortis*) divergent beak morphology is an adaptation to local food availability that has been maintained through assortative mating (Huber et al. 2007). Sexual selection may also interact with natural selection in opposing directions when environmental conditions modify the sexually selected signal, such as turbid waters that reduce the signal efficacy in sticklebacks (Candolin et al. 2007; Wong et al. 2007). In this conflicting view, changing environments may limit the divergence of sexually selected traits and consequently reduce speciation rate.

The association between sexual selection and speciation has been investigated using many macroevolutionary approaches applied to various taxa. A meta-analysis of 64 effect sizes from 20 studies found a small, but significant positive association between sexual selection and speciation (Kraaijeveld et al. 2011). However, there was large variation in effect sizes due to variation in the measures of sexual selection used and other methodological choices (*e.g.* species richness *vs* rate estimates). Given that species richness and speciation rate can be inversely correlated (*e.g.* Rabosky et al. 2018) and the recent refinement of methods to obtain tip-rate diversification estimates (Jetz et al. 2012; Rabosky 2014; Rabosky and others 2018) the association between sexual selection and speciation rate is worth revisiting. Firstly, the strength of sexual selection strength in macroevolutionary studies is often estimated using measures of sexual dimorphism or dichromatism; but these are often partial measures of sexual selection and may not account for the true variation in sexual selection across taxa. Secondlly, many studies use incomplete taxon sampling, with family-level analysis restricted to well sampled avian clades (Seddon et al. 2008; Huang and Rabosky 2014). Thirdly, until recently, studies on the association between sexual selection and speciation have largely ignored the contribution and interaction with environmental variables to explain variation in speciation rates. Fourthly, phylogenetic uncertainty in the avian tree (Jetz et al. 2012; *but see* Rubolini et al. 2015) and uncertainty in tip-rate measures of speciation such as the diversification rate statistic (λ_{DR}) or node density (λ_{ND}) (Rabosky and others 2018) as well as speciation and extinction tip-rates from models using BAMM (Bayesian Analysis of Macroevolutionary Mixtures) (*see*, Beaulieu and O’Meara 2015; Moore et al. 2016; Rabosky 2016; Rabosky et al. 2017) continue to plague efforts to identify drivers of speciation and extinction.

Here, we perform a comprehensive analysis of the relationship between sexual selection and speciation or

extinction in passerine birds (Order: Passeriformes), arguably the largest group for which there exists comprehensive data. Recently, Huang and Rabosky (2014) found no association between sexual dichromatism and speciation using tip-rate estimates from a genetic-only phylogeny (Jetz et al. 2012) and sexual dichromatism data from a limited spectrophotometry dataset ($n = 918$; Armenta et al. 2008). We build on these previous studies by using published datasets of sexual dichromatism measured from images ($n = 5,812$; Dale et al. 2015) alongside smaller datasets of sexual dichromatism measured from spectrophotometry ($n = 581$; Armenta et al. 2008) and a composite measure of male-biased sexual selection ($n = 2,465$; Dale et al. 2015). We assess the relationship between sexual selection, environmental variability and their interaction with three tip-rate measures of speciation and one measure of extinction (λ_{DR} , λ_{ND} , λ_{BAMM} and μ_{BAMM}). Using expert range maps and bioclimatic variables we are able to investigate whether the effect of sexual selection on speciation is dependent on range size, seasonal variation in temperature, spatial temperature variation (across a species' range), long-term variation in temperature between now and the last inter-glacial (LIG) as well net primary productivity (NPP).

Materials and methods

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

Compiling data for sexual selection and environmental stress

Sexual dichromatism

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

135 Male-biased sexual selection

136 Sexual dichromatism is a widely used indicator of sexual selection in birds (*e.g.*, Barraclough et al. 1995;
137 Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014), but only partially
138 captures variation in the strength of sexual selection across taxa. Therefore, we also use an existing dataset
139 (Dale et al. 2015) of male-biased sexual selection based on the first component of a phylogenetic principle
140 component analysis (PPCA) of three characteristics associated with sexual selection (sexual size dimorphism,
141 social polygyny and [lack of] paternal care). This measure of male-biased sexual selection is available for only
142 2,465 species and is weakly correlated with the absolute values of sexual dichromatism using RGB measures
143 ($r = 0.34$; **Figure S10**).

144 Environmental variables

145 We obtained estimates of species range size using expert range maps (BirdLife International and Handbook
146 of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the *Birdlife* database
147 (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual dichromatism
148 dataset (Dale et al. 2015). From these distributions we obtained estimates of climatic conditions that
149 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19
150 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature
151 and precipitation) with 30 seconds ($\sim 1 \text{ km}^2$) spatial resolution (Fick and Hijmans 2017). From these values
152 we obtained means and standard deviations for each species. Using the same spatial sampling we extracted
153 means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial
154 (LIG; 120,000 - 140,000 years ago) (Otto-Bliesner et al. 2006). Furthermore, to estimate variability in the
155 energy available to species we obtained the mean and standard deviation of net primary productivity (NPP)
156 values between 2000 - 2015 across each species distribution. Estimates of NPP had 30 second resolution
157 and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production
158 products stage 3 (MOD17A3) (Zhao et al. 2005). Using this data, which we provide as a potentially useful
159 data resource (see ESM), we generated five predictors of speciation associated with different patterns in
160 environmental variability (see below).

161 Generating biologically relevant predictors for environmental variation

162 Using the extracted environmental variables from each species range size we developed biologically meaningful
163 predictors of environmental variation/stress relating to (*i*) seasonal climate variation, (*ii*) spatial climate
164 variation and (*iii*) long-term climate variation. To obtain seasonal climate variation we used mean values
165 of temperature seasonality (BIO4) for each range. To estimate levels of spatial environmental variation
166 a species may endure we used the first principle component (PC1) from a PCA on standard deviations
167 from all bioclimatic variables, excluding temperature (BIO4) and precipitation seasonality (BIO15). PC1
168 was heavily loaded towards bioclimatic variables relating to temperature, thus PC1 reflects the variation
169 in temperature across a species' range (**Table S1**). Given that species range is a potentially informative
170 predictor of speciation and extinction we controlled for the correlation between spatial variation and range
171 size — where larger ranges have larger variation in PC1 — by taking the residuals of a fitted general additive
172 model (GAM; **Figure S1**). To obtain long-term variation in climates for each species range we take the first

173 principal component of the absolute difference in the bioclimatic variables between the LIG and current values.
174 Similarly to spatial variation, the long-term climate variation is primarily loaded to temperature differences
175 between the LIG and current climates (**Table S2**, **Figure S2**). The five predictors of environmental variability
176 are not strongly correlated (**Figure S3**). Details and code to generate these predictors can be found within
177 the ESM.

178 **Estimating extinction and speciation.**

179 Phylogenetic information was obtained from www.birdtree.org (Jetz et al. 2012). We used a maximum clade
180 credibility (MCC) tree from 2,500 samples of the posterior distribution that were subset to the passerine bird
181 order ($n = 5,965$) as the main phylogenetic tree in our comparative analysis. Additionally, a random draw of
182 100 full trees (including species without genetic data) from the posterior distribution of phylogenetic trees
183 was used for diversification analyses using tip-rate measures and BAMM (Rabosky 2014). These trees used
184 a ‘Hackett backbone’ (Hackett et al. 2008) and were constructed using the a pure birth (Yule) model. We
185 calculated three different tip-rate metrics of speciation and one of extinction across all trees.

186 Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes
187 and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating
188 the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES),
189 also known as diversification rate (DR) (e.g., Jetz et al. 2012; Quintero and Jetz 2018; Rabosky et al. 2018),
190 is derived from the sum of edge lengths branching from a node, with each more basal node having the sum of
191 lengths down-weighted. Studies have suggested that DR and ND (henceforth referred to as λ_{DR} and λ_{ND})
192 are more reflective estimates of speciation than diversification (Belmaker and Jetz 2015; Rabosky and others
193 2018). Therefore, λ_{DR} is a measure of speciation rate more heavily weighted to recent speciation events
194 and λ_{ND} is a measure of speciation across the root to tip path. These tip-rate measures are alternatives to
195 state-dependent diversification models such as Quantitative State Speciation-Extinction (QuaSSE) models.
196 Based on previous simulation studies λ_{DR} and λ_{ND} are robust and intuitive measures that provide high
197 power and low false discovery rate with large phylogenies when incorporated into Phylogenetic Generalized
198 Least Squares (PGLS) models (Harvey Michael et al. 2017).

199 Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic
200 trees (Rabosky 2014). This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo)
201 to generate a probability distribution of evolutionary rate-shift configurations with variable speciation and
202 extinction rates. Importantly, these models provide tip-rate estimates of speciation and extinction rate. The
203 parameters of the 100 BAMM runs are detailed in full in the ESM; briefly we used a time-variable model
204 with 100 expected number of shifts and prior rates set from the initial speciation and extinction values using
205 the **BAMMtools** R package (Rabosky et al. 2014). Each BAMM model (one MCC and 100 random draws of
206 the posterior) was run for 100 million generations, and given the computationally intensive nature of BAMM,
207 runs were conducted across multiple CPU’s. Each run of BAMM reached convergence with effective sample
208 size (ESS) of MCMC (Markov Chain Monte Carlo) samples surpassing 200 (an arbitrary value, above which
209 phylogeneticists believe posterior tree distributions can be accurately inferred) for the key model parameters
210 of log-likelihood and number of rate shifts (**Table S3**, **Table S4**). Further details of BAMM parameters
211 and output are available in the ESM, with tip-rate means and variances provided. Additionally, given the
212 variability in BAMM estimates, we also provide some analysis of BAMM shift configurations and tip-rate

213 estimates from our run on the MCC tree and within a BAMM run on the MCC tree from a genetic-only
214 phylogeny across all birds (Harvey et al. 2017). All analyses were conducted on log-rates.

215 **Statistical analysis**

216 **Phylogenetic comparative analysis**

217 To test the association between speciation/extinction and sexual selection, environmental variability and
218 their interaction, we used phylogenetic least squares (PGLS) models in the `nlme` package (Pinheiro et al.
219 2018). We began by estimating the phylogenetic signal — Pagel's λ (Pagel 1999) — using `corPagel` in the
220 `ape` package (Paradis et al. 2004) on the MCC tree. The estimate of λ was then fixed for model selection,
221 which was conducted on the same MCC tree derived from 2,500 draws of the posterior distribution (Jetz et
222 al. 2012). Model selection used either λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} tip-rate estimates from the MCC tree
223 as the response variable. For λ_{BAMM} and μ_{BAMM} we were also able to use model weights sourced from the
224 inverse of the variance of tip-rates for a given species from the posterior distribution ($n = 1,000$). Using model
225 selection we only compared interaction terms between a measure of sexual selection (sexual dichromatism
226 or male-biased sexual selection) and environmental measures. That is, we fixed the individual predictors
227 of: dichromatism/male-biased sexual selection measures, log-transformed range size, seasonal temperature
228 variation, spatial temperature variation, long-term temperature variation and NPP while comparing 32
229 models with different combinations of interactions (including none). Model selection was done in `MuMIn` using
230 the `dredge` function (Bartoń 2017). Using the terms from the top-ranking model (lowest AICc), we ran the
231 equivalent model for each of the 100 phylogenetic trees used to derive λ_{DR} , λ_{ND} , λ_{BAMM} and μ_{BAMM} , using
232 the unique response variables and phylogenetic tree correlation structure in each model. This method enabled
233 us to present model estimates for an MCC tree alongside 100 trees from the posterior distribution of trees to
234 account for phylogenetic uncertainty. This approach was repeated on three datasets corresponding to each
235 measure of sexual selection: dichromatism derived from RGB values of images ($n = 5,812$); dichromatism
236 from spectrophotometry ($n = 581$) and the multivariate measure of male-biased sexual selection ($n = 2,465$).
237 Finally, using data subsetted for species with measurements of male-biased sexual selection, we conducted
238 a phylogenetic path analysis using the `phylopath` R package (Bijl 2018). The phylogenetic path analysis
239 was used to assess causal paths between variables not able to be modelled within the univariate response of
240 PGLS. That is, a phylogenetic path analysis allowed us to model relationships between the predictor variables
241 used in our PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection and
242 range size to have effects on each other and not just on speciation rate. To minimise path complexity we use
243 temperature seasonality (BIO4) as the single measure for environmental variability and use λ_{DR} as the single
244 measure of speciation. The phylogenetic path analysis used tip-rates and correlation structure from the MCC
245 tree. Further details of the path analysis including reasons for path directions can be found within the ESM
246 along with all other analyses and the relevant R code to reproduce results.

247 Results

248 Effects of sexual dichromatism/selection on speciation are not dependent on 249 environmental variability

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

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} ($\beta = -1.279e-03$, $p = 0.147$; [Figure 1a](#),
265 [Figure 2a](#)) or λ_{ND} ($\beta = -5.745e-05$, $p = 0.078$; [Figure 1a](#)). Furthermore, speciation rates from BAMM
266 (λ_{BAMM}) were also unaffected by sexual dichromatism ($\beta = -1.430e-05$, $p = 0.872$; [Figure 1a](#)). PGLS analyses
267 using subsetted data ($n = 581$), where sexual dichromatism was measured using spectrophotometry (Armenta
268 et al. 2008) yielded results concordant to the full data set; that is, no association between sexual dichromatism
269 and speciation or extinction ([Figure S10](#)). Our results from MCC models are largely corroborated by model
270 estimates from PGLS analyses of the rates and correlation structures from 100 random trees. Model estimates
271 are normally distributed around zero when using complete taxon sampling models and RGB measures of
272 sexual dichromatism ([Figure 1a](#), see HPD (highest posterior density) intervals in **Table S8**). For PGLS
273 models using spectrophotometry-based measures of sexual dichromatism, the estimates from the 100 trees in
274 the λ_{DR} models are positively skewed (-1.781e-02, 3.488e-02) but normally distributed around zero for λ_{ND}
275 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} (β
278 = 3.887e-02, $p = 0.012$; [Figure 1b](#)). However, this associate was not significant for the other two measures
279 of speciation rate (λ_{ND} : $\beta = 4.381e-04$, $p = 0.351$; λ_{BAMM} : $\beta = 9.422e-04$, $p = 0.764$; [Figure 1b](#)). The
280 distribution of estimates from PGLS models on 100 random trees was similar to the estimate from an MCC
281 tree: among the 100 trees there was a positive association between sexual selection and λ_{DR} (HPD Interval =
282 9.115e-03, 6.085e-02), and a smaller positive association between sexual selection and λ_{ND} (HPD Interval =

²⁸³ -3.104e-04, 1.536e-03;) as well as λ_{BAMM} (HPD Interval = -1.297e-02, 3.089e-02). Complete HPD intervals
²⁸⁴ for models using male-bias sexual selection PPCA as a predictor can be found within **Table S15**.

²⁸⁵ Species with smaller ranges have increased rates of speciation

²⁸⁶ Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation we found a negative association between range size and
²⁸⁷ speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This negative
²⁸⁸ association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.578e-03$, $p = 0.001$; λ_{ND} :
²⁸⁹ $\beta = -1.462e-04$, $p = 0.034$; [Figure 1a](#), [Figure 2](#)). This association was also evident across the estimates from
²⁹⁰ models using the 100 trees (λ_{DR} : HPD Interval = -8.438e-03, -1.823e-03; λ_{ND} : HPD Interval = -1.899e-04,
²⁹¹ 9.112e-06; [Figure 1a](#)). Subsetted models with reduced sample size and different measures of sexual selection —
²⁹² but the same measure of range size — showed variable evidence that range size is negatively associated with
²⁹³ speciation. Range size significantly predicted λ_{DR} ([Figure 1b](#)) using data subsetted for male-biased sexual
²⁹⁴ selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} . Model using data subsetted for spectrophotometry-based
²⁹⁵ dichromatism ($n = 581$) gave non-significant estimates for the effect of range size on all measures of speciation
²⁹⁶ ([Figure S10](#), [Table S11](#), [Table S2](#)). Because the range size dataset is the same across the three data
²⁹⁷ subsets we draw our conclusions from the models with highest power using near-complete taxon sampling (n
²⁹⁸ = 5,812).

²⁹⁹ Phylogenetic path analysis

³⁰⁰ Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
³⁰¹ ([Figure 3](#); [Figure S13](#)). Notably, environmental variability (temperature seasonality) directly affected sexual
³⁰² dichromatism ($\beta = 0.07$) and the path from male-biased sexual selection to sexual dichromatism was relatively
³⁰³ weak, ($\beta = 0.22$), despite dichromatism being widely used as an indicator of the strength of sexual selection.
³⁰⁴ Additionally, the large direct effect of temperature seasonality on range size ($\beta = 0.52$) suggests an indirect
³⁰⁵ effect of temperature seasonality on λ_{DR} ($\beta = -0.02$; [Figure 3](#)), given the negative we identified between λ_{DR}
³⁰⁶ and range size in PGLS models.

³⁰⁷ Extinction rate

³⁰⁸ We found no evidence that extinction (μ_{BAMM}) was impacted by the extent of sexual dichromatism for
³⁰⁹ full-taxon sampling ($\beta = 2.390e-05$, $p = 0.93$; [Figure 1a](#)), nor spectrophotometry-based measures of sexual
³¹⁰ dichromatism ([Figure S10](#), [Table S11](#), [Table S12](#)) or male-biased sexual selection ([Figure 1b](#), [Table S14](#),
³¹¹ [Table S15](#)).

³¹² Variability across trees and methods

³¹³ We tested our hypothesis that sexual selection is associated with speciation using several methods and across
³¹⁴ 100 trees drawn from the post burn-in posterior (Jetz et al. 2012). We used a range of methods to overcome
³¹⁵ uncertainty in the power and precision of various tip-rate estimates as well as the variation between trees.
³¹⁶ We found that that the tip-rate estimates across the 100 trees were quite variable for both λ_{DR} and λ_{BAMM}

317 (Figure S14). Despite this, tip-rate estimates of speciation from the two methods were moderately correlated
318 across the 100 trees ($r = 0.75$) and for the MCC tree ($r = 0.68$; Figure S15). However, in comparison
319 to λ_{DR} , the value of λ_{BAMM} was the *mean* drawn from a posterior distribution ($n = 1,000$) of BAMM
320 generations, thus estimates of λ_{BAMM} (and μ_{BAMM}) have an added level of variation. To account for this
321 variation, weights (using the inverse of the variance) were used for the PGLS models. From 1000 posterior
322 samples of the MCC BAMM run the coefficient of variation (CV) for all log-rates of λ_{BAMM} was relatively
323 low (*mean CV* = 21.49, *median CV* = 15.76 ; see Figures S5 and S7). Despite the convergence of the
324 BAMM model in all runs — where effective sample sizes of the number of shifts and log-likelihood were all
325 greater than 200 (Table S3 and S4) — we found that the unique combinations of rate shifts across the
326 large phylogenetic tree ($n = 5,966$ species) was high. This means that although the number of rate shifts
327 reached convergence (*median* = 59; Figure S6), the locations of the rate shifts (*i.e.* the credible shift set)
328 across the tree are highly heterogeneous. The variability in the locations for the shift configurations is a
329 likely source of uncertainty in downstream tip-rates used as the response variable in PGLS models. Notably,
330 the 95 % HPD interval for model estimates using BAMM rates from 100 trees was about 20-fold the 95 %
331 confidence intervals of the estimate from the MCC tree; whereas for λ_{DR} and λ_{ND} the HPD 95 % interval
332 width was equal to or less than the MCC 95 % CI (Figure 1, Table S9).

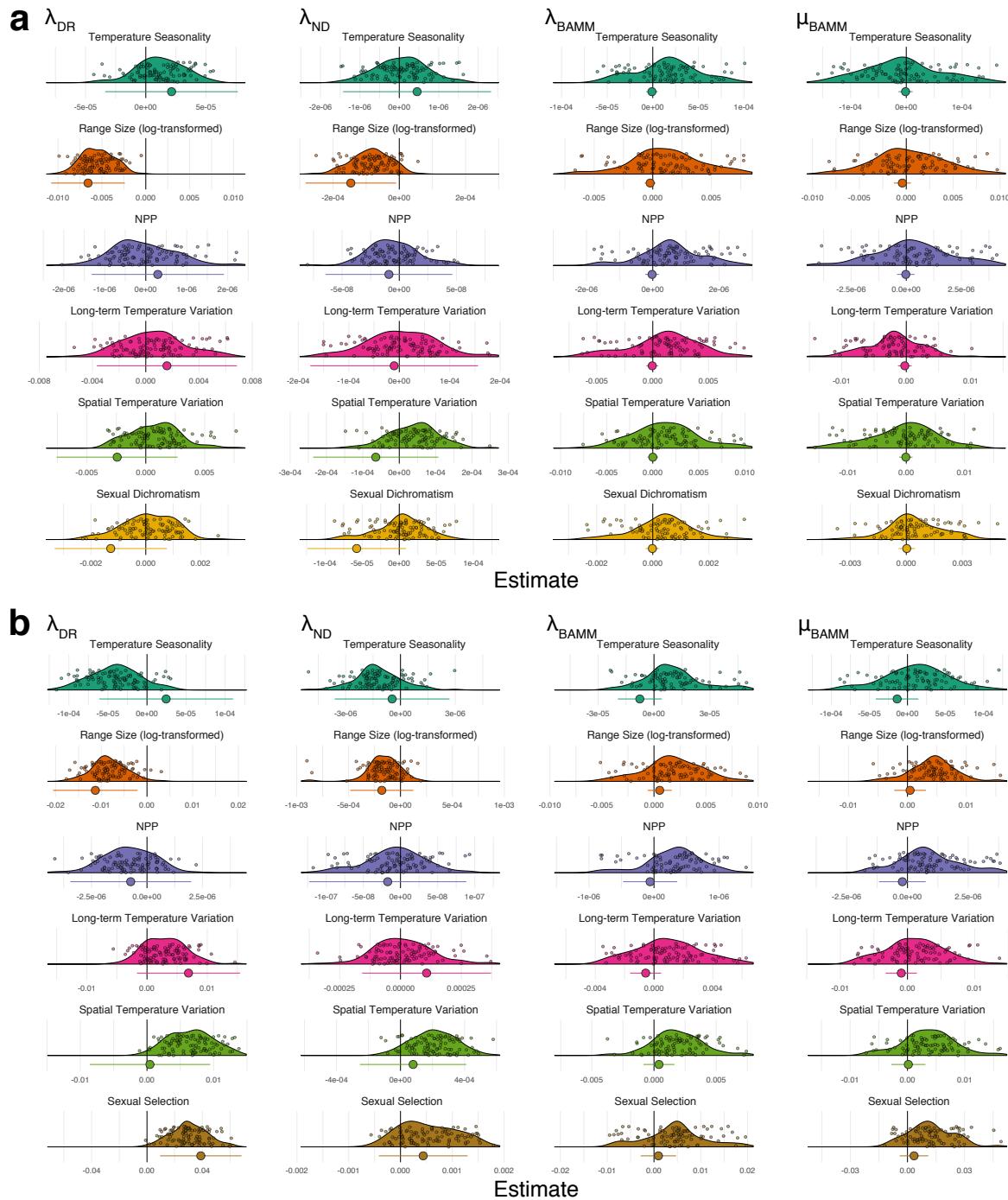


Figure 1: Model estimates for (a) PGLS analyses using sexual dichromatism ($n = 5,812$) and (b) PGLS analyses using measures of male-biased sexual selection ($n = 2,465$). Both datasets were used for analyses with three measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one measure of extinction (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 within 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.

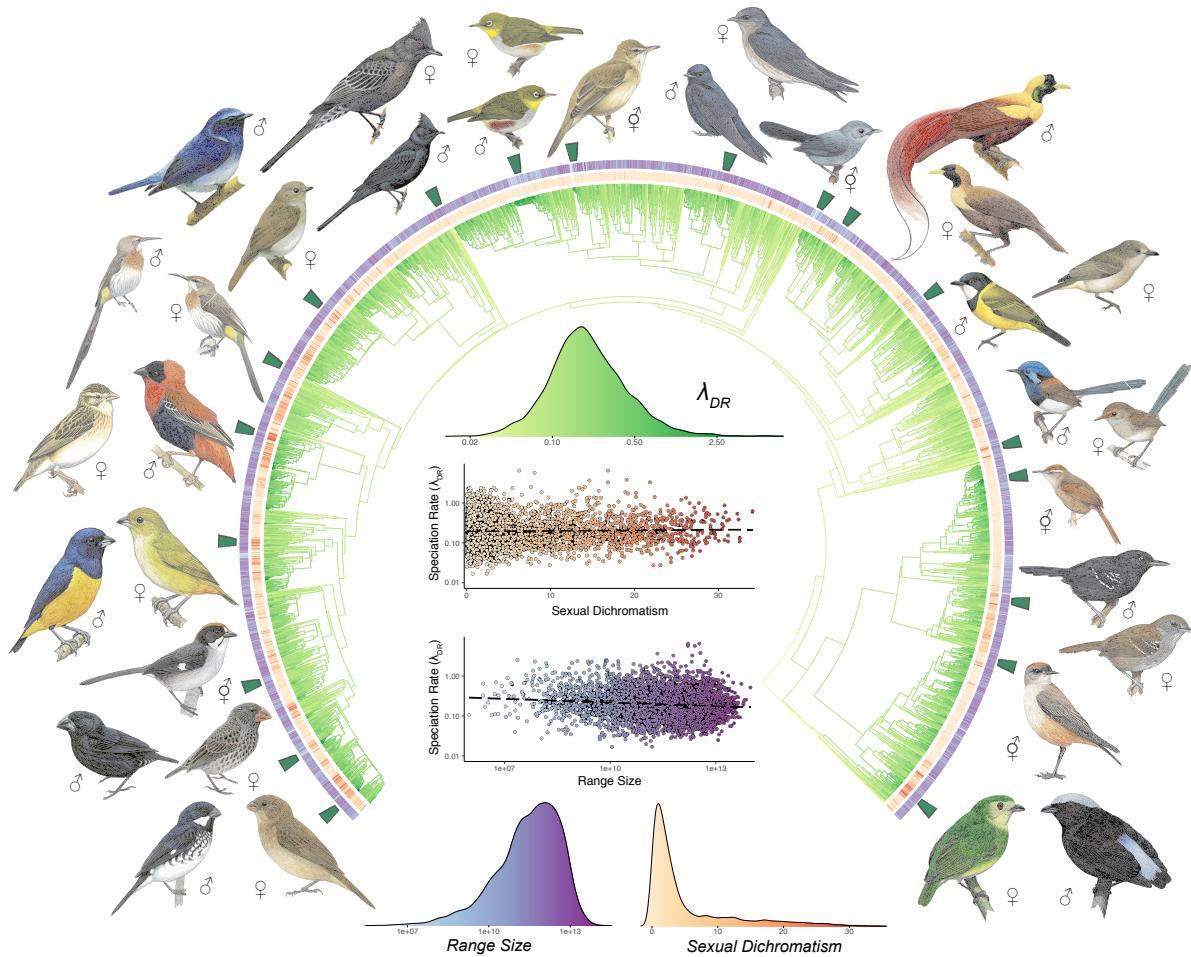


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism and range size available for 5,812 of them. Across these species there was a small but significant negative association between λ_{DR} and log-range size but no significant association between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

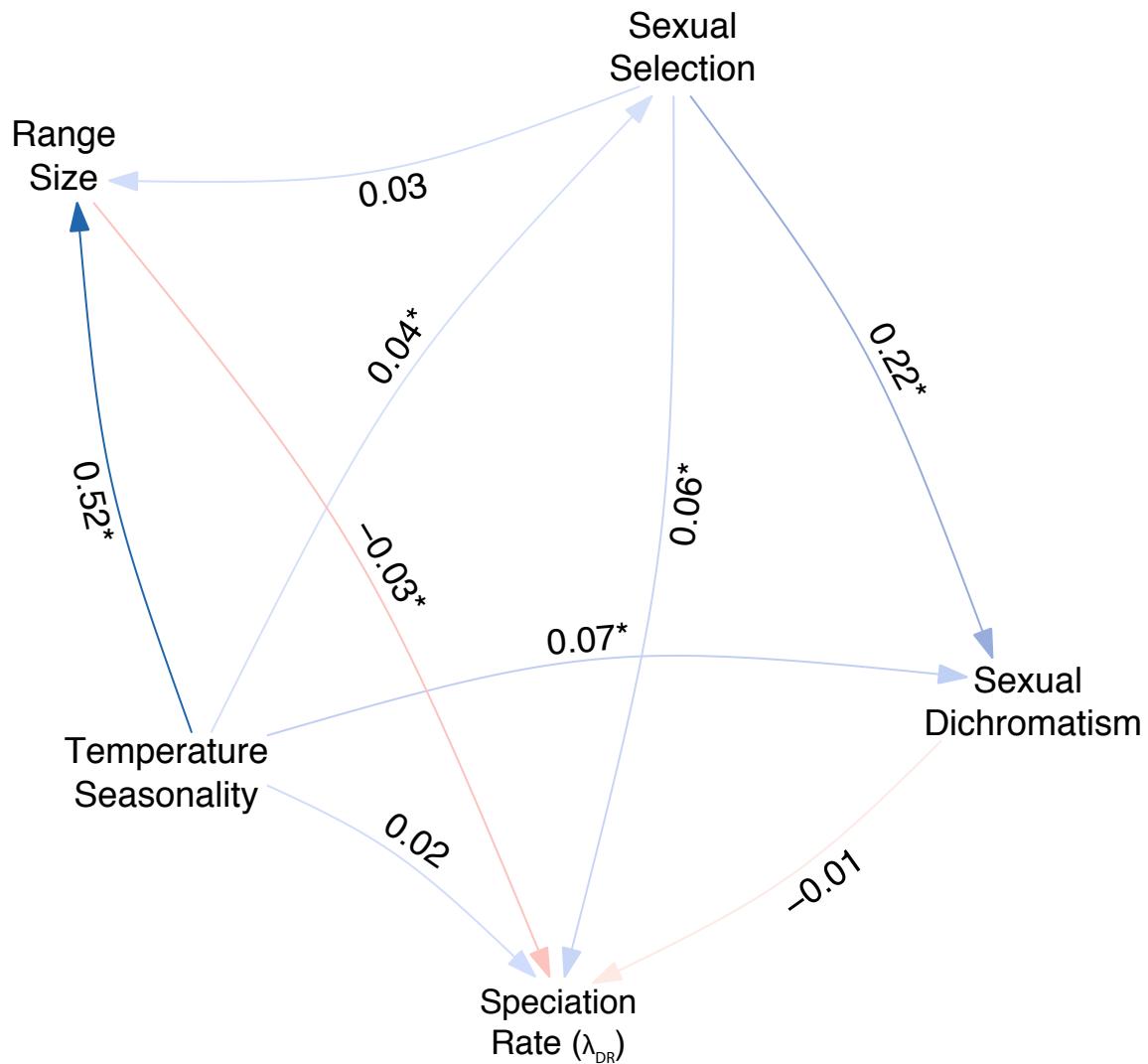


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with numeric values corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95 % confidence intervals of this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

333 Discussion

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

349 The association between sexual selection and sexual dichromatism in birds is a Darwinian trope (Darwin
350 1871) that allows it to be commonly used as a proxy for the strength of sexual selection in comparative
351 studies (e.g., Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and
352 Rabosky 2014). Despite the association between sexual selection and sexual dichromatism in passerine birds
353 (Dale et al. 2015) we find that sexual dichromatism does not predict speciation rate, whereas male-biased
354 sexual selection does. Given our results, we suggest that sexual dichromatism may not be a robust proxy
355 for sexual selection, and that variance in the association between dichromatism and the strength of sexual
356 selection may obscure any relationship with speciation rate, despite the high power of our comparative study.
357 There are several reasons why the use of sexual dichromatism as a proxy for sexual selection is enigmatic.
358 Firstly, ecological pressures could drive sexual dichromatism in the absence of mate choice if sex-specific niches
359 provide opportunity for the evolution of sex-limited traits (Wallace 1889; Kottler 1980; Slatkin 1984; Shine
360 1989). In damselflies, differences between the sexes in their exposure to UV radiation drives dichromatism
361 between the sexes (Cooper 2010; Punzalan and Hosken 2010). Ecological impacts on sexual dichromatism are
362 supported by our path analysis, which reveals that sexual dichromatism is positively affected by temperature
363 seasonality (a measure of environmental variation) albeit relatively weakly. Secondly, colour is but one
364 trait and sexual selection may drive the evolution of sex differences in a wide variety of traits used in mate
365 choice or intrasexual competition. And thirdly, not all plumage colouration honestly reflects mate quality.
366 A recent meta-analysis found that converted carotenoids (but not those sourced from diet) predict mate
367 quality through improvements in parasite resistance and reproductive success (Weaver et al. 2018). Given
368 the importance of honest signaling in sexual selection and the variability in colour production across birds,
369 sexual dichromatism in many species may be an unreliable measure of mate quality for female birds and
370 sexual selection for researchers.

371 In-line with predictions and a previous meta-analysis (Kraaijeveld et al. 2011) we find that male-biased sexual
372 selection increases speciation rate — at least for λ_{DR} and λ_{ND} — but this association was not dependent on
373 variable or stressful environments. When evolving under stressful conditions, sexually antagonistic selection

is hypothesised to be weakened relative to selection that is concordant between the sexes (Connallon 2015; Connallon and Hall 2016). While these predictions are supported in several lab (experimental evolution) studies (Long et al. 2012; Punzalan et al. 2013; Berger et al. 2014), other studies have not found the association (Delcourt et al. 2009; Holman and Jacomb 2017; Martinossi-Allibert et al. 2017). Given that we did not detect an effect of environmental variability (by itself or as an interaction with sexual selection) we are left with several possible explanations. Firstly, the effects of sexual selection on adaptation and thus speciation may depend on the type of environmental variability the species is evolving under. Specifically, sexual antagonism may be more easily purged in environments where cyclic pressures (e.g. seasonality) are perpetuated; whereas when environmental variability is directional (e.g. long-term climatic change) sexual antagonism can remain indefinitely as a fitness burden (Connallon and Hall 2016). Secondly, the environmental predictors used here may not account for the key ecological forces/natural selection pressures that interact with sexual selection to drive speciation. Specifically, access to dietary resources, and the impacts of predation or parasitism are unaccounted for here: arguably these are key processes affecting sexual selection and speciation (*reviewed in* Maan and Seehausen 2011). Thirdly, it is also possible that there is no effect of environmental variability on speciation rates; at least not in the species investigated here.

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

In addition to speciation, sexual selection has frequently been invoked as a driver of extinction. Sexual selection may increase extinction risk as it often leads individuals (usually males) to invest in exaggerated mating signals as opposed to traits — such as parental care — that elevate offspring fitness (*reviewed in* Kokko and Brooks 2003). Using BAMM, we found no association between extinction rate and sexual dichromatism, male-biased sexual selection or measures of environmental variability. Extinction is notoriously hard to

416 estimate accurately (see Rabosky 2016). It can be estimated from phylogenetic inference, fossil record, records
417 of recent extinctions and IUCN extinction threat status. Phylogenetic methods — like BAMM — allow
418 for speciation and extinction rates to be measured using moderately sized phylogenies. However, BAMM
419 has been subject to controversy in its ability to model rate shifts and extinction rates (see, Beaulieu and
420 O'Meara 2015; Moore et al. 2016; Rabosky 2016; Rabosky et al. 2017), and while several tip-rate estimates
421 exist for speciation (*e.g.*, λ_{DR} and λ_{ND}) extinction estimates are not as easily obtained. Here, we found
422 that BAMM often produced homogeneous λ_{BAMM} and μ_{BAMM} for clades with few rate shifts; arguably this
423 could reduce our power to detect extinction rates (Rabosky et al. 2017; Rabosky and others 2018). The
424 ability to detect extinction rates rarely improves when fossil records are used, as many clades (*e.g.* birds) lack
425 the stratigraphic sampling across time to statistically calculate extinction rates. But, there are exceptions,
426 ostracods — a group of marine invertebratesone — have extensive fossil records and show identifiable sexual
427 dimorphism. Across 93 species of ostracods, Martins et al. (2018) found that ostracod taxa with larger sexual
428 dimorphism (representing exaggerated investment by males in reproductive organs) had higher extinction
429 rates; implying that sexual selection increases extinction risk. Alternatively, when comparative studies have
430 assessed the relationship between sexual selection and extinction in extant birds (Mitra et al. 1996; Doherty
431 et al. 2003; Morrow and Pitcher 2003) and mammals (Morrow and Fricke 2004; Bro-Jorgensen 2014) there has
432 been no consensus. Unfortunately, these methods often rely on extinction threat status from the International
433 Union for Conservation of Nature (IUCN) Red List (*e.g.*, Morrow and Pitcher 2003; Morrow and Fricke 2004;
434 Bro-Jorgensen 2014) and may be biased to species under greater anthropogenic threat, culturally valued or
435 well researched.

436 Improvements in estimating tip-rates of speciation has allowed us to revisit the association between sexual
437 selection and speciation. With high power and alongside extensive ecological predictors we find that male-
438 biased sexual selection predicts speciation but sexual dichromatism does not. If sexual selection promotes
439 speciation through improvements in fitness and adaptation the implications are manifold with sexual selection
440 a potentially valuable utility in conservation (*reviewed in*, Holman and Kokko 2013) and captive breeding
441 programs for threatened species (*reviewed in*, Charge et al. 2014). Furthermore, our finding that high
442 speciation rate is associated with smaller range size has pronounced significance to the future survival of
443 these rapidly speciating species in a world with increased habitat loss and anthropogenic stress. Range size
444 is the best predictor of extinction risk (Harris and Pimm 2008) and the association found here ensues that
445 many newly speciated clades may be at greater risk of extinction due to their reduced range being impacted
446 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-bias sexual selection from sexual dichromatism. Despite the complex statistical models, monsterous sample size and modern sexual conflict theory the most fascinating finding was one that Wallace and Darwin were at odds over 130 years prior (Kottler 1980). The widespread use of sexual dichromatism largely goes unchallenged as our instinctive Darwinian mind reminisces of peacocks and birds of paradise. My thoughts were such when I began this scientific inquiry, but am now skeptical and somewhat disheartened. Of course, I was expecting sexual dichromatism from RGB measures to be a noisy measure of sexual selection, but across 5,831 species I anticipated a signal would permeate through the noise. And despite the correlation between sexual dichromatism and male-bias sexual selection is present, the relationship is surprisingly weak (see Figure 3 in main text). With this in mind, the practical use of sexual dichromatism in macroevolutionary research is severely weakened. This finding is particularly pertinent as efficient proxy measurements are incredibly valuable in comparative analyses: that's because they increase the accessibility, available sample size and transfer-ability of a study making it 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 sexual selection that is the PPCA of sexual dimorphism, social polygyny and [lack of] paternal care is a dataset that better predicts speciation and would benefit from being expanded across birds.

Not only are the measurement 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. And during the second part of this MSc I jumped head-first into the controversy. 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 project. Extinction rate is arguably the best measure of population fitness. And while a high profile study has measured extinction rate in experimental evolution (Lumley et al. 2015), it has been rarely measured over long, evolutionarily meaningful timescales (*but see* Martins et al. 2018). We included measurements of extinction rate within the paper, however these findings were played down. The reason for this movement away from extinction and towards speciation is the controversy surrounding

¹Wallace was initially supportive of the evolution of sexual dichromatism as a result of mate choice but later took more interest in a view where natural selection on predator-prone nesting females generated dullness in females but not males.

extinction rate measures. Measuring extinction rates within the bird phylogeny are problematic because of the nature of phylogenetic construction; for passerine birds 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. Furthermore, the very detection of an absence of data — which is what such methods attempt to do — is a hard sell both conceptually and methodically come peer review: see Rabosky (2010) 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 novel finding of time-dependency in rates of macroevolutionary diversification makes comparative analyses between clades challenging and calls into question countless studies (Henao Diaz et al. 2018). 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 our measures may not account for variation in biotic components such as nutritional resources or predation. However, the methods employed here are arguably much better than those implemented by other studies; where the range mid-point is used to obtain a single 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 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 will 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, utilise multiple taxonomic groups and use more robust measures of sexual selection (*see* Anthes et al. 2016). As such, many questions regarding this topic remain unanswered. Here I discuss the 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

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 taxa 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 Supplementary Material.

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

and how interdisciplinary approaches can be harnessed to liberate ourselves from conventional comparative methodologies.

The study by Martins et al. (2018) has already been referred to several times 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 higher levels of dimorphism were swept to extinction more quickly. From stratigraphic occurrence data a capture–mark–recapture model was used to determine the rate of extinction of different 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 find a positive effect of sexual selection in mitigating extinction. Importantly the time-scale used by Martins et al. (2018) is a key advantage of their study. Moving forward, it would be incredibly valuable to see whether other groups of marine invertebrates have the fossil data and recognisable sexual metamorphosis to conduct such a study. In the interim I would be eager to see how BAMM would perform on a ostracod phylogeny and whether the same positive association between extinction rate and sexual dimorphism could be detected among extant taxa. For me, this will be a true test of the applicability of BAMM and a key step in the effort to reliably measure extinction from phylogenetic inference.

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 incorporate 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. 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 macroevolutionary patterns of extinction. Harnessing ecological niche modelling in macroevolutionary studies across expansive extant taxa such as passerine birds is a daunting challenge but offers an Eco-evo synthesis that may be particularly pertinent in questions relating to extinction, especially if the taxonomic group under inquiry are of high conservation and cultural value, for which the songbirds certainly are.

Importantly, macroevolutionary comparative studies can examine the association between sexual selection and speciation across taxa, over evolutionary time-scales and in natural environments.