

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 their relationship remains unclear with
6 controversy on whether sexual selection leads to a net increase or decrease in speciation rate. Sexual
7 selection is predicted to increase speciation rate as it can facilitate adaptation to new environments by
8 elevating the average fitness of a population. Additionally, sexual selection may work alongside divergent
9 natural selection and swiftly promote reproductive isolation. Here we use sexual dichromatism as a
10 proxy for sexual selection across 5,812 species of passerine birds and a multivariate male-bias measure of
11 sexual selection (sexual dimorphism, polygyny and paternal care) across 2,465 species to investigate the
12 association of sexual selection with speciation and extinction. Importantly, we test whether the effects of
13 sexual selection on speciation are dependent upon ecological pressures such as temperature variability
14 across time and space, primary productivity and range size. Our results from three distinct measures
15 of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one measure of extinction (μ_{BAMM}) find that male-bias sexual
16 selection but not sexual dichromatism predicts speciation. Additionally, we find that birds with smaller
17 ranges have higher speciation rates; however the causality of this finding remains inconclusive.

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18 Introduction

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

28 **Sexual selection and fitness:** Sexual selection is applied by one sex on the other - more often by females
29 on males (Kokko and Jennions 2008; Fromhage and Jennions 2016; Janicke et al. 2016) and the strength of
30 sexual selection can increase or decrease the average fitness of a population; often termed population fitness
31 (*reviewed in*, Kokko and Brooks 2003; Whitlock and Agrawal 2009; Holman and Kokko 2013). Specifically,
32 in line with the ‘good genes’ perspective, sexual selection may purge deleterious mutations (Agrawal 2001;
33 Siller 2001) and fixate beneficial mutations in a population (Whitlock 2000). Thus, sexual selection is
34 thought to be a key process in mitigating extinction risk and facilitating adaptation. However, sexual
35 selection can increase the fitness of a population when the genotypes under sexual selection (*e.g.* those that
36 increase male mating/fertilisation success) are genetically positively correlated with traits affecting fitness
37 (*e.g.* female fecundity or survival). This positive correlation is unlikely to always be the case; regularly, sexual
38 selection favours traits having negative pleiotropic effects on female fitness (Pischedda and Chippindale 2006;
39 Bonduriansky and Chenoweth 2009; Pennell and Morrow 2013; Berger et al. 2014). For instance, in species
40 with high levels of sexual selection mating success becomes more variable and uncertain, thus individuals
41 must heavily invest to increase their chances of successfully reproducing. Through prioritising mating success
42 a sex may invest in costly weaponry and sexual signals, while forgoing strategies that would improve offspring
43 fitness (parental care). This is a costly consequence of sexual selection that affects persistence, adaptation
44 and extinction (Kokko and Brooks 2003).

45 **Sexual selection, heritability and mechanisms of speciation:** Alongside changes to fitness, sexual
46 selection has been proposed to facilitate speciation through the evolution of divergent signals/ornaments
47 associated with improved mating success (Lande 1981, 1982). For instance, in antbirds (Thamnophilidae),
48 genera with complex songs and stark dichromatism were more species rich (Seddon et al. 2008). Under this
49 model of speciation, divergent sexual signals in one sex (usually males) co-evolve with divergent preferences
50 for those signals in the opposite sex, and by itself sexual selection could lead to behavioural reproductive
51 isolation (Safran et al. 2013). Concurrently, sexual selection can promote the extent to which populations
52 diverge by enlarging the phenotypic space diverging species can evolve into. This prediction emanates from
53 increased genetic diversity as a result of sexual conflict: a consequence of sexual selection (Lorch et al.
54 2003; Bonduriansky 2011; Radwan et al. 2016). However, the genetic architecture (*per se* heritability) of
55 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 anticipated 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 birds with magnified sexual selection to have increased adaptation and speciation rates.

60 **Environmental interaction:** Importantly, the effects of sexual selection on adaptation and speciation may
61 depend on environmental conditions. Studies suggest that under stressful/changing environments sexual
62 selection may have greater fitness benefits than under benign environments. In stressful environments, the
63 positive correlation between male mating success and female fitness components improves, reducing the
64 burden of negative pleiotropic effects (Long et al. 2012; Berger et al. 2014; Connallon and Hall 2016;
65 Martinossi-Alibert et al. 2017). Conversely, under benign environments environmental stability ensures
66 consistent selection, preferentially eroding genetic variation at sexually concordant loci (*i.e.* loci where
67 the optimum genotype is equivalent for both sexes). In these cases genetic variation preferentially remains
68 at sexually antagonistic loci; causing displacement of male and female traits from their optimum. These
69 predictions would ensue that populations with stronger sexual selection would have increased fitness and
70 adaptive benefits, allowing them to adapt to novel environments (*reviewed in* Candolin and Heuschele 2008).
71 In certain circumstances sexual selection will reinforce diverging locally adapted phenotypes through mate
72 choice on phenotypes that advertise quality in a specific ecological context (Maan and Seehausen 2011). If
73 mate choice operates on both sexes — or there is a correlation in trait values between a pair — assortative
74 mating is likely to strengthen this positive feedback loop and promote population divergence (Lande 1981).
75 In several birds, beak morphology is a trait that arose under natural selection and is now a trait under
76 sexual selection (a.k.a. “magic traits”). In Darwin’s finches (*Geospiza fortis*) divergent beak morphology is
77 an adaptation to local food availability that has been maintained through assortative mating (Huber et al.
78 2007). Sexual selection may also interact with natural selection in opposing directions when environmental
79 conditions modify the sexually selected signal, such as turbid waters that reduce the signalling strength in
80 sticklebacks (Candolin et al. 2007; Wong et al. 2007). In this opposing view, changing environments may
81 limit the divergence of sexually selected traits and consequently reduce speciation rate.

82 **Previous limitations:** The association between sexual selection and speciation has been investigated using
83 many macroevolutionary approaches across various taxa. Importantly, macroevolutionary comparative studies
84 can examine the association between sexual selection and speciation in more diverse taxon, over longer
85 evolutionary time-scales and in more natural environments. A meta-analysis of 64 effect sizes from 20 papers
86 found a small, but positively significant association between sexual selection and speciation (Kraaijeveld
87 et al. 2011). However, variation in sexual selection proxies used and other methodological choices (species
88 richness vs rate estimates) led to heterogeneity in effect sizes for the correlation between sexual selection
89 and speciation. Given that species richness and speciation rate are not necessarily correlated (*e.g.* Rabosky
90 et al. 2018) and the recent development and refinement of methodologies in obtaining tip-rate estimates
91 of speciation and extinction (Jetz et al. 2012; Rabosky 2014; Rabosky and others 2018) the association
92 between sexual selection and speciation rate is worth revisiting with methods that address several issues
93 that have previously limited macroevolutionary comparative studies. Firstly, sexual selection strength in
94 macroevolutionary studies are often estimated using measures of dimorphism or dichromatism; but these
95 are often partial measures of sexual selection and may not account for the true variation in sexual selection
96 across taxa; which arguably decreases the power to detect an association, especially if phylogenetic signal is
97 strong. Secondlly, many studies use incomplete taxon sampling, with family-level analysis restricted to well
98 sampled avian clades (Seddon et al. 2008; Huang and Rabosky 2014). Thirdly, until recently studies on the
99 association between sexual selection and speciation have largely ignored the contribution of environmental
100 variables to explain variation in speciation rates. Furthermore, these studies haven’t taken into account either

the potential interaction between natural and sexual selection in the generation of new species. 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 our ability to draw widely accepted findings.

Our study: We chose to do our study on passerine birds because of the wealth of data available for these (Order: Passeriformes). 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). But, here we assess the effects of sexual dichromatism measures based on RGB values ($n = 5,812$) alongside smaller datasets of sexual dichromatism from spectrophotometry measures ($n = 581$) and male-bias sexual selection measures ($n = 2,465$). Specifically, we assess the relationship between sexual dichromatism, 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. Many of the processes undertaken in this study are documented with reproducible code in the electronic supplementary material (ESM).

Compiling data for sexual selection and environmental stress

Sexual dichromatism

We used sexual dichromatism as proxy of sexual selection strength. Male and female plumage scores have previously been measured across 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 mean RGB values were calculated and provided male and female plumage scores. Here we use the absolute difference between males and female RGB scores as an estimate of sexual dichromatism. Additionally, we compiled a colour discriminability measure of sexual dichromatism from spectrophotometer measures (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

¹³⁷ species available for this analysis. While there is a correlation between these two measures, there is residual
¹³⁸ variation ($r = 0.79$; **Figure S9**).

¹³⁹ **Male-biased sexual selection**

¹⁴⁰ Sexual dichromatism has long been associated with levels of sexual selection (Darwin 1871), with sexual
¹⁴¹ dichromatism often used as a measure of sexual selection in avian taxa (e.g., Barraclough et al. 1995; Owens et
¹⁴² al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014). However, sexual dichromatism
¹⁴³ is likely to account for only partial variation in sexual selection across taxa. Here we use an existing dataset
¹⁴⁴ (Dale et al. 2015) of male-bias sexual selection based on the first component of a phylogenetic principle
¹⁴⁵ component analysis (ppca) of three characteristics associated with sexual selection (sexual size dimorphism,
¹⁴⁶ social polygyny and [lack of] paternal care). This measure of male-bias sexual selection is present for only
¹⁴⁷ 2,465 species and is weakly correlated with the absolute values for sexual dichromatism using RGB measures
¹⁴⁸ ($r = 0.34$; **Figure S10**).

¹⁴⁹ **Environmental variables**

¹⁵⁰ Using expert range maps (BirdLife International and Handbook of the Birds of the World 2017) we obtained
¹⁵¹ estimates of species range size. From these distributions we were able to obtain estimates for extensive
¹⁵² climatic conditions that each species is exposed to. Because of taxonomic changes to 1,230 species in the
¹⁵³ *Birdlife* database (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual
¹⁵⁴ dichromatism dataset (Dale et al. 2015). From 1,000 random point samples in each range we extracted 19
¹⁵⁵ present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature
¹⁵⁶ and precipitation) with 30 seconds (~1 km²) spatial resolution (Fick and Hijmans 2017). From these values
¹⁵⁷ we obtained means and standard deviations for each species. Using the same spatial sampling we extracted
¹⁵⁸ means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial
¹⁵⁹ (LIG; 120,000 - 140,000 years ago) (Otto-Bliesner et al. 2006). Furthermore, to estimate variability in the
¹⁶⁰ energy available to species we obtained the mean and standard deviation of net primary productivity (NPP)
¹⁶¹ values between 2000 - 2015 across each species distribution. Estimates of NPP had 30 second resolution
¹⁶² and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production
¹⁶³ products stage 3 (MOD17A3) (Zhao et al. 2005). Using this data, which we provide as a potentially useful
¹⁶⁴ data resource (see ESM), we generated five predictors of speciation associated with different patterns in
¹⁶⁵ environmental variability (see below).

¹⁶⁶ **Estimating extinction and speciation.**

¹⁶⁷ Phylogenetic information was obtained from www.birdtree.org (Jetz et al. 2012). We used a maximum clade
¹⁶⁸ credibility tree (MCC) from 2,500 samples of the posterior distribution that were subset to the passerine
¹⁶⁹ bird order ($n = 5,965$) as the main phylogenetic tree in our comparative analysis. Additionally, a random
¹⁷⁰ draw of 100 full trees (including species without genetic data) from the posterior distribution of phylogenetic
¹⁷¹ trees was used for diversification analyses using BAMM. These trees used a ‘Hackett backbone’ and were
¹⁷² constructed using the a pure birth (Yule) model. We calculated three different tip-rate metrics of speciation
¹⁷³ and one of extinction across all trees.

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

187 Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic
 188 trees (Rabosky 2014). This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo)
 189 to generate a probability distribution of evolutionary regimes with variable speciation and extinction rates.
 190 Importantly, these models provide tip-rate estimates of speciation and extinction rate. The parameters of the
 191 100 BAMM runs are detailed in full in the ESM; briefly we used a time-variable model with 100 expected
 192 number of shifts and prior rates set from the initial speciation and extinction values using the **BAMMtools**
 193 R package (Rabosky et al. 2014). Each BAMM model (one MCC and 100 random draws of the posterior)
 194 was run for 100 million generations, and given the computationally intensive nature of BAMM, runs were
 195 conducted across multiple CPU's. We obtained effective sample sizes for log-likelihood and number of rate
 196 shifts over 200 for each run (**Table S3**, **Table S4**). Further details of BAMM parameters and output are
 197 available through ESM, with tip-rate means and variances included in the ESM. Additionally, given the
 198 variability in BAMM estimates we also provide some analysis of BAMM shift configurations and tip-rate
 199 estimates from our run on the MCC tree and within a BAMM run on an MCC from a genetic-only phylogeny
 200 across all birds (Harvey et al. 2017). All analyses were conducted on log-rates.

201 Statistical analysis

202 Generating biologically relevant predictors for environmental variation

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

214 principal component of the absolute difference in the bioclimatic variables between the LIG and current values.
215 Similarly to spatial variation, the long-term climate variation is primarily loaded to temperature differences
216 between the LIG and current climates (**Table S2**, **Figure S2**). Despite similar theoretical underpinnings
217 the predictors of environmental variability used in PGLS analyses are not strongly correlated (**Figure S3**).
218 Details and code to generate these predictors can be found within the ESM.

219 **Phylogenetic comparative analysis**

220 To test the association between speciation/extinction and sexual selection, environmental variability and its
221 interaction we used phylogenetic least squares (PGLS) models in the `nlme` package (Pinheiro et al. 2018).
222 We began by estimating the phylogenetic signal — Pagel's λ (Pagel 1999) — using `corPagel` in the `ape`
223 package (Paradis et al. 2004) on a MCC tree. The estimate of λ was then fixed for model selection, which
224 was conducted on the same MCC tree derived from 2,500 draws of the posterior distribution (Jetz et al.
225 2012). Model selection used either λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} tip-rate estimates from the MCC as the
226 response variable and only compared interaction terms. That is, we fixed the individual predictors of: sexual
227 dichromatism/selection, log-transformed range size, seasonal temperature variation, spatial temperature
228 variation, long-term temperature variation and NPP while comparing 32 models with different combinations
229 of interactions (including none). Model selection was done in `MuMIn` using the `dredge` function (Bartoń 2017).
230 Using the terms from the top-ranking model (lowest AICc) we ran the equivalent model in each of the 100
231 phylogenetic trees, using the unique response variables and phylogenetic tree correlation structure in each
232 model. This method gave us the ability to present model estimates for an MCC alongside 100 random draws;
233 acknowledging the potential role phylogenetic uncertainty has in tapering conclusions drawn from a random
234 sample of the data. This method was conducted on models that used data from all available passerine species
235 ($n = 5,812$). The same procedure described above was applied to a subset dataset of passerine birds ($n =$
236 581), where sexual dichromatism measures were sourced from spectrophotometry measures (Armenta et al.
237 2008) and where male-bias sexual selection pPCA was used as a predictor instead of sexual dichromatism ($n =$
238 2,465). Finally, using this data subsetted for species with measurements of male-bias sexual selection we
239 conducted a phylogenetic path analysis using the `phylopath` R package (Bijl 2018). The phylogenetic path
240 analysis was used to assess causal paths between variables not able to be modelled within the univariate
241 response of PGLS. To minimise path complexity we use temperature seasonality (BIO4) as the single measure
242 for environmental variability and use λ_{DR} as the single measure of speciation. The phylogenetic path analysis
243 used tip-rates and correlation structure from the MCC tree. Further details of the path analysis including
244 reasons for path directions can be found within the ESM along with all other analyses and the relevant R
245 code to reproduce results.

246 **Results**

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

249 PGLS models with interaction terms between the respective measure of sexual dichromatism/selection and
250 the five measures of environmental variability (seasonal temperature variation, log-range size, long-term

temperature variation, spatial temperature variation and NPP) were included in model selection. However, in all model selection phases for different measure of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and different measures of sexual selection (RGB values, spectrophotometry and male-biased sexual selection) no interaction terms were significant or present in the top models ($\delta AICc > 4$; **Table S5**, **Table S6**, **Table S10**, **Table S13**). Hence we find no evidence that the effect of sexual selection on speciation or extinction is dependent upon certain environmental conditions. Furthermore, we find no support that these individual bioclimatic factors (seasonal temperature variation, long-term temperature variation, spatial temperature variation and NPP) act as drivers of speciation independently from sexual dichromatism/selection ([Figure 1](#), [Figure S10](#)).

259 No evidence that sexual dichromatism affects speciation

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

275 Male-bias sexual selection increases speciation

When we conducted PGLS analysis using data subsetted for values of sexual selection estimated from a phylogenetic PCA of sexual dimorphism, social polygyny and paternal care ($n = 2,465$) there was a significant positive association between sexual selection and λ_{DR} ($\beta = 3.887e-02$, $p = 0.012$; [Figure 1b](#)). However, this positive finding was non-significant between sexual selection and λ_{ND} ($\beta = 4.381e-04$, $p = 0.351$; [Figure 1b](#)) as well as between sexual selection and λ_{BAMM} ($\beta = 9.422e-04$, $p = 0.764$; [Figure 1b](#)). For PGLS models on 100 random trees, we find the distribution to be similar to the estimates when an MCC tree is used. Among the 100 trees we find a positive association between sexual selection and λ_{DR} (HPD Interval = 9.115e-03, 6.085e-02), and a positive (but less so) association between sexual selection and λ_{ND} (HPD Interval = -3.104e-04, 1.536e-03;) as well as λ_{BAMM} (HPD Interval = -1.297e-02, 3.089e-02). Complete HPD intervals for models using male-bias sexual selection pPCA as a predictor can be found within **Table S15**.

286 Species with smaller ranges have increased rates of speciation

287 Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation we find a negative association between range size and
 288 speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . Model
 289 estimates from PGLS models using an MCC tree for determining tip-rates and correlation structures place
 290 this negative association as small but significant (λ_{DR} : $\beta = -6.578\text{e-}03$, $p = 0.001$; λ_{ND} : $\beta = -1.462\text{e-}04$, p
 291 = 0.034; [Figure 1a](#), [Figure 2a](#)). This association was also evident across the estimates from models using
 292 the 100 trees (λ_{DR} : HPD Interval = -8.438e-03, -1.823e-03; λ_{ND} : HPD Interval = -1.899e-04, 9.112e-06;
 293 [Figure 1a](#)). Subsetted models with reduced sample size and different measures of sexual selection — but the
 294 same measure of range size — show variable evidence that range size is negatively associated with speciation.
 295 Data subsetted based on the sexual selection pPCA ($n = 2,465$) show that smaller range size significantly
 296 predicted increased λ_{DR} ([Figure 1b](#)), yet this negative association was not significant for λ_{ND} and near-zero
 297 for λ_{BAMM} . Alternatively, models using subsetted data ($n = 581$), where sexual dichromatism was measured
 298 using spectrophotometry distance measures (Armenta et al. 2008) gave non-significant estimates for the
 299 effect of range size on all measures of speciation ([Figure S10](#), [Table S11](#), [Table S2](#)). Because the range
 300 size dataset is the same across the three data subsets we draw our conclusions from the models with highest
 301 power using near-complete taxon sampling ($n = 5,812$).

302 Phylogenetic path analysis

303 Using a phylogenetic path analysis we found there to be multiple significant paths between variables used in
 304 the PGLS ([Figure 3](#); [Figure S13](#)). Notably, environmental variability (temperature seasonality) directly
 305 affected sexual dichromatism ($\beta = 0.07$) and the path from sexual selection to sexual dichromatism was
 306 relatively weak given the expectations of dichromatism being a well utilised proxy of sexual selection ($\beta =$
 307 0.22). Additionally, because of the large direct effect of temperature seasonality on range size ($\beta = 0.52$) and
 308 our findings from the PGLS that range size is negatively associated with λ_{DR} , there is an indirect effect of
 309 temperature seasonality on λ_{DR} ($\beta = -0.02$; [Figure 3](#)).

310 Extinction rate

311 We found no evidence that extinction (μ_{BAMM}) was impacted by the extent of sexual dichromatism for
 312 full-taxon sampling ($\beta = 2.390\text{e-}05$, $p = 0.93$; [Figure 1a](#)). This null result was consistent for spectrophotometry
 313 measures of sexual dichromatism ([Figure S10](#), [Table S11](#), [Table S12](#)) and for the estimates of sexual
 314 selection using the sexual selection pPCA ([Figure 1b](#), [Table S14](#), [Table S15](#)).

315 Variability across trees and methods

316 We tested our hypothesis that sexual selection is associated with speciation using several methods and across
 317 100 samples of phylogenetic trees drawn from the post burn-in posterior (Jetz et al. 2012). The range of
 318 methods utilised were implemented to overcome uncertainty in the power and precision of various tip-rate
 319 estimates as well as the variation between trees. We found that the tip-rate estimates across the 100
 320 trees were quite variable for both λ_{DR} and λ_{BAMM} ([Figure S14](#)). Despite this variation, both methods

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

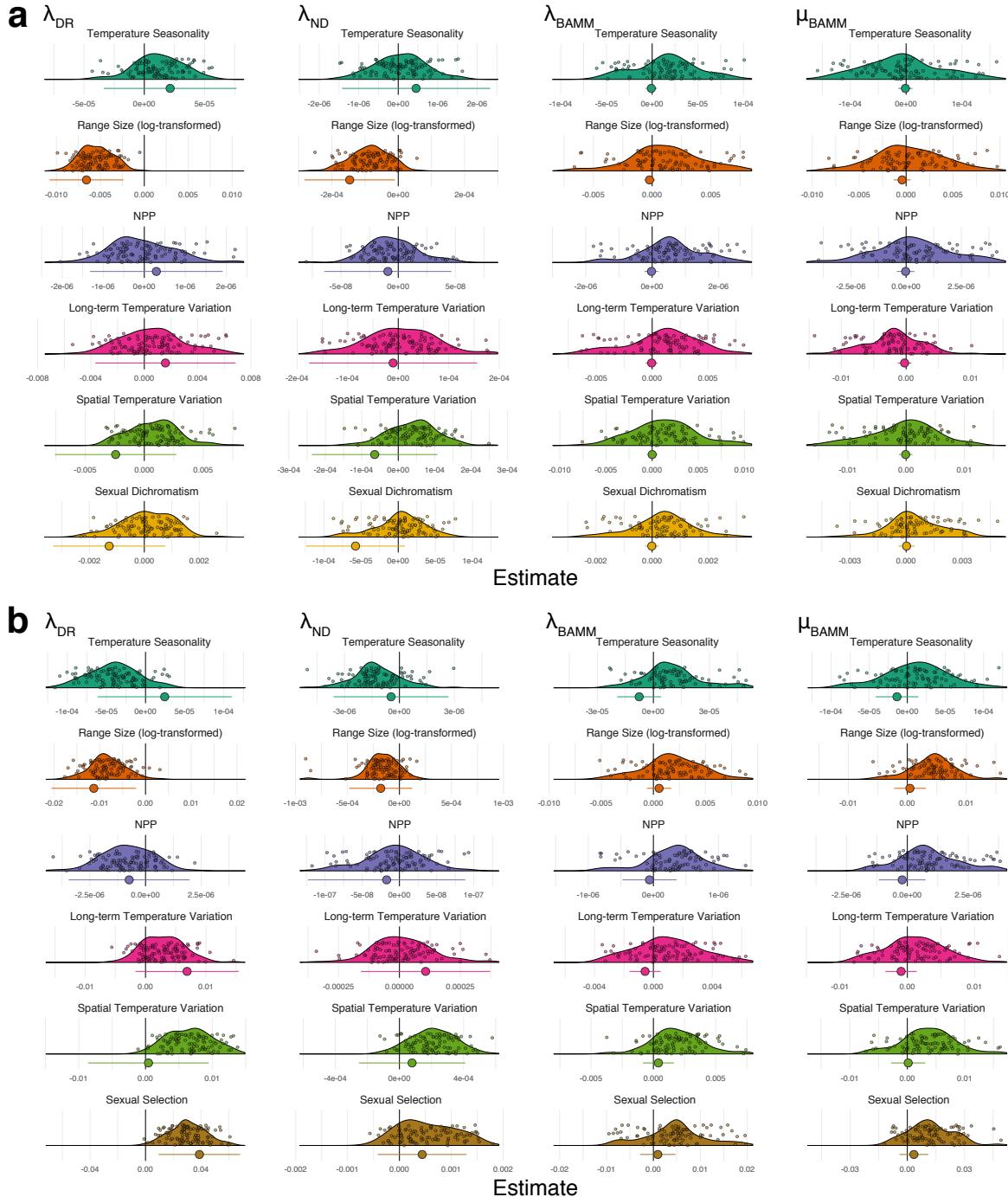


Figure 1: Model estimates for (a) PGLS analyses using sexual dichromatism measures ($n = 5,812$) and (b) PGLS analyses using a subsetted male-bias measure of sexual selection ($n = 2,465$). Both datasets were used for analyses with three measures of speciation λ_{DR} , λ_{ND} , λ_{BAMM} and one measure of extinction μ_{BAMM} as response variables. The numerical values for the model estimates using the MCC tree and hpd 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. 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.

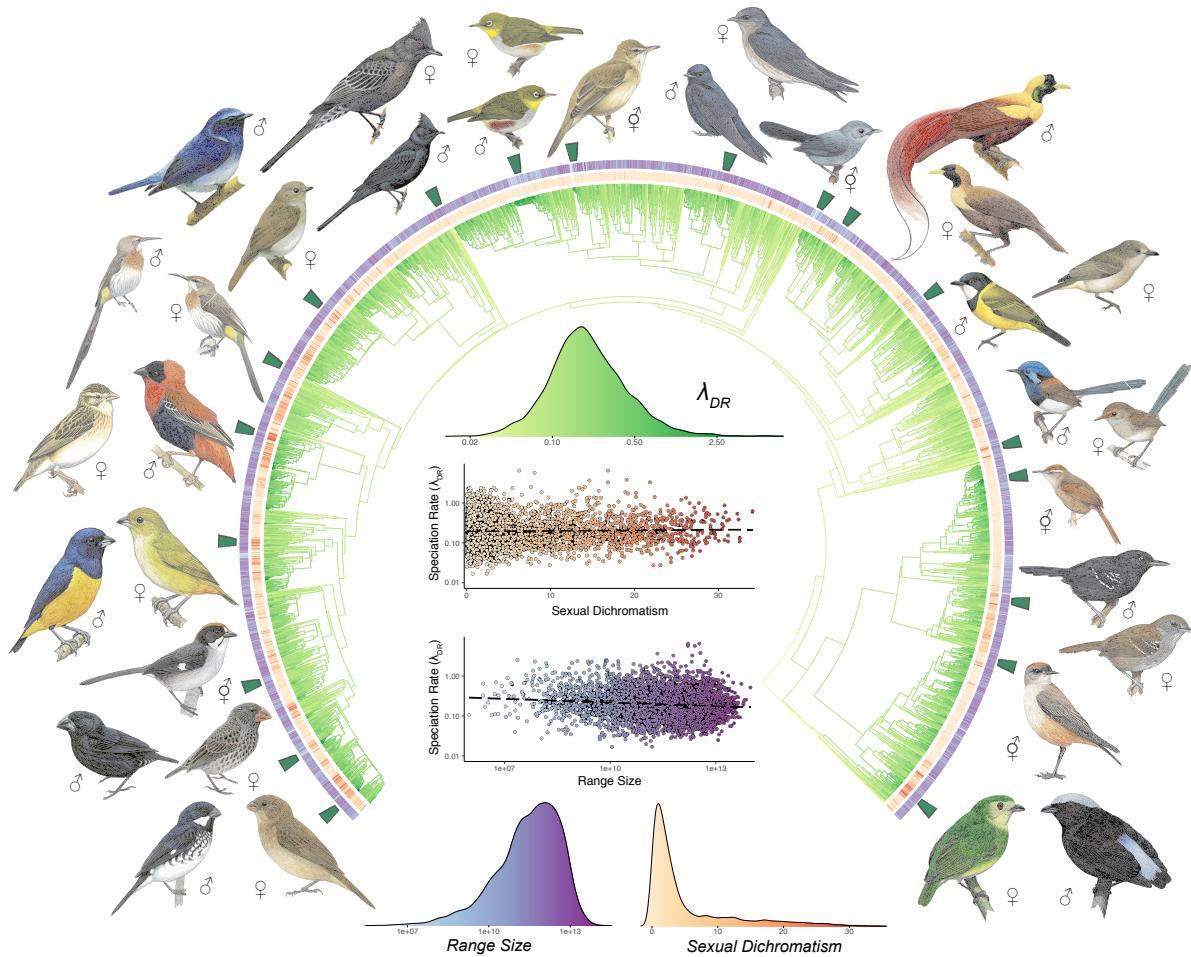


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism and range size available for 5,812 of them. Across these species there was a small but significant negative association between λ_{DR} and log-range size but no significant association between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

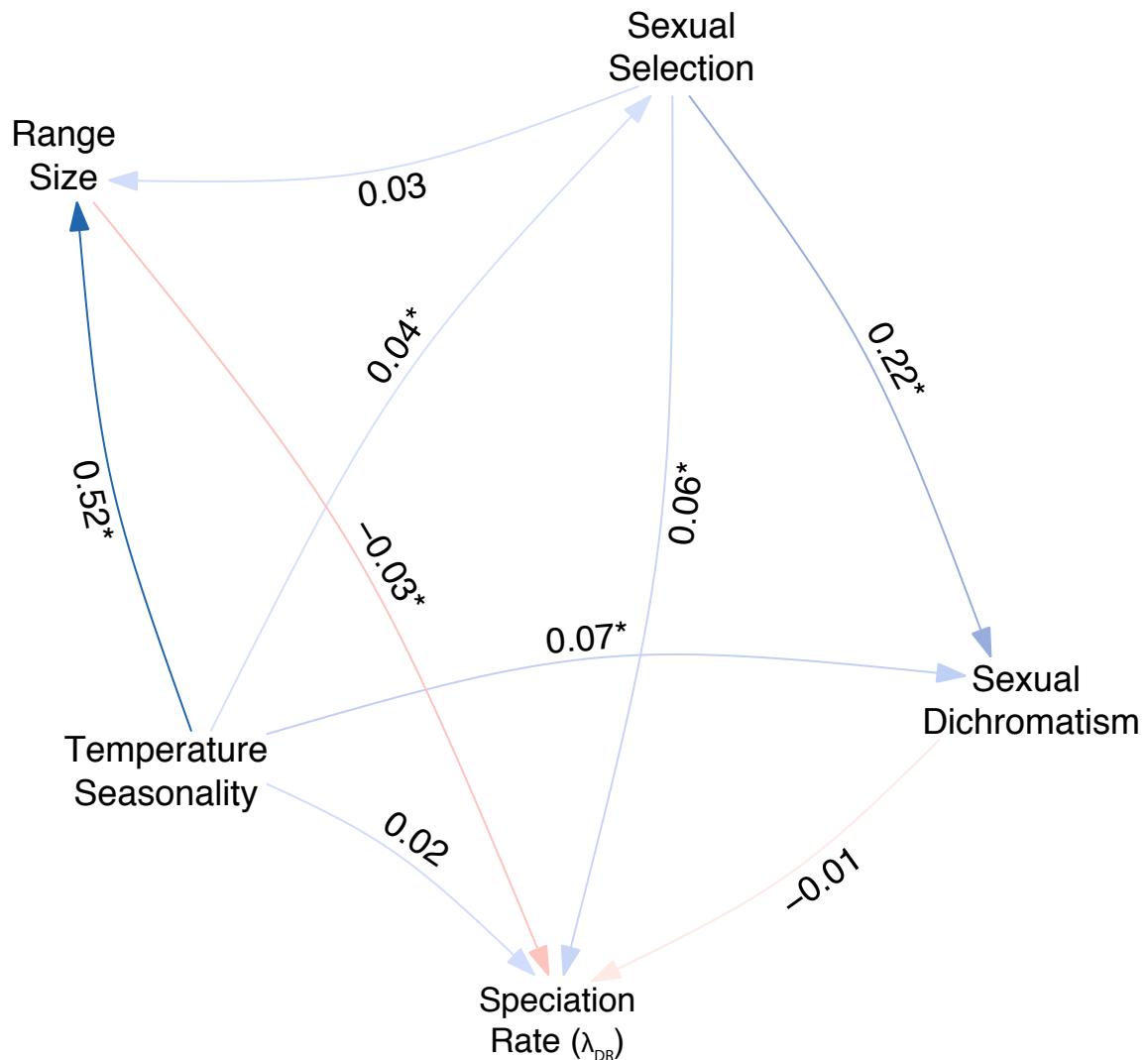


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with numeric values corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisk indicates that the 95 % confidence intervals of this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

338 Discussion

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

354 Despite the association between sexual selection and sexual dichromatism in passerine birds (Dale et al. 2015)
355 we find that sexual dichromatism does not predict speciation rate as sexual selection does. The association
356 between sexual selection and sexual dichromatism in birds is a Darwinian trope (Darwin 1871) that allows it
357 to be commonly used as a proxy for sexual selection in comparative studies (e.g., Barraclough et al. 1995;
358 Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014). However, the
359 presence of high sexual dichromatism in bird species may be also dependent on ecological selection pressures.
360 Ecological pressures could drive sexual dichromatism in the absence of mate choice if sex-specific niches
361 provide opportunity for the evolution of sex-limited traits (Kottler 1980; Slatkin 1984; Shine 1989). In
362 damselflies, differences between the sexes in their exposure to UV radiation drives dichromatism between the
363 sexes (Cooper 2010; Punzalan and Hosken 2010). Ecological impacts on sexual dichromatism are supported
364 by our path analysis; which reveals that sexual dichromatism is positively affected by temperature seasonality
365 (a measure of environmental variation) albeit by a relatively small amount. Given that our results show
366 that speciation rate increases with sexual selection strength, but not sexual dichromatism, we are led to
367 conclude that sexual dichromatism is a seemingly poor proxy of sexual selection and that the noise associated
368 with the proxy measurement of sexual selection cancels out the obtained signal; this is despite the high
369 power of our comparative study. The usefulness of sexual dichromatism as a proxy of sexual selection may
370 be dependent upon the metabolic pathways that give rise to plumage colouration; with not all plumage
371 colouration reflecting mate quality. A recent meta-analysis found that converted carotenoids (but not those
372 sourced from diet) predict mate quality through improvements in parasite resistance and reproductive success
373 (Weaver et al. 2018). Given the importance of honest signalling in sexual selection and the variability in
374 colour production across birds, sexual dichromatism in many species may be an unreliable measure of mate
375 quality for female birds and sexual selection for researchers.

376 In-line with predictions and a previous meta-analysis (Kraaijeveld et al. 2011) we find male-bias sexual
377 selection marginally increases speciation rate (at least for λ_{DR} and λ_{ND}) yet there is no direct evidence of this
378 association being dependent on variable or stressful environments; albeit a phylogenetic path analysis shows

379 an indirect effect of environmental variability (through range size). When evolving under stressful conditions,
380 sexually antagonistic selection is hypothesised to be weakened relative to selection that is concordant between
381 the sexes (Connallon 2015; Connallon and Hall 2016). While these predictions are supported in several lab
382 (experimental evolution) studies (Long et al. 2012; Punzalan et al. 2013; Berger et al. 2014), other studies
383 have not found the association (Delcourt et al. 2009; Holman and Jacomb 2017; Martinossi-Allibert et al.
384 2017). Given that we did not detect an effect of environmental variability (by itself or as an interaction with
385 sexual selection) we are left with several possible explanations. Firstly, the effects of sexual selection on
386 adaptation and thus speciation may depend on the type of environmental variability the species is evolving
387 under. Specifically, sexual antagonism may be more easily purged in environments where cyclic pressures
388 (e.g. seasonality) are perpetuated; whereas when environmental variability is directional (e.g. long-term
389 climatic change) sexual antagonism can remain indefinitely as a fitness burden (Connallon and Hall 2016).
390 Secondly, the environmental predictors used here may not account for the key ecological forces/natural
391 selection pressures that interact with sexual selection to drive speciation. Specifically, access to dietary
392 resources, and the impacts of predation or parasitism are unaccounted for here: arguably these are key
393 processes affecting sexual selection and speciation (*reviewed in*, Maan and Seehausen 2011). Thirdly, it is
394 also likely that there is no effect; at least not in the species investigated here.

395 The most consistent finding uncovered in this comparative analysis is that smaller range sizes are associated
396 with increased speciation rates. But drawing conclusions from this finding is fraught with challenges.
397 Challenges arise on determining the causality of range size and speciation; as arguably small range size could
398 either be a cause or effect of speciation. Intuitively, large range size should promote speciation by creating
399 greater opportunities for geographic barriers to form (Rosenzweig 1995). Birds with smaller range sizes
400 are also predicted to have lower dispersal ability; in these cases individuals might not be able to overcome
401 geographical barriers and maintain gene flow; thus promoting reproductive isolation and speciation (Birand
402 et al. 2012; Claramunt et al. 2012). Several studies have used morphological measures of wing shape, a
403 proxy for dispersal ability (Hand-wing index/ Kipp's distance), as a predictor of speciation and coexistence
404 (e.g., Kennedy et al. 2016; Pigot et al. 2016), but these measurements across passerines is not yet extensive.
405 Alternatively, reduced range size may be a consequence of speciation. Under this view, high speciation rate
406 may lead to smaller range sizes as niche filling by recently diverged species will suppress the expansion of
407 newly speciated relatives. Within Himalayan songbirds range expansions are prevented by the competition
408 for resources by related species (Price et al. 2014); however this limitation on range expansion is then
409 expected to prevent future speciation events (Rosenzweig 1995; Weir and Price 2011). Unlike Himalayan
410 songbirds, species undergoing adaptive radiation in new niches are unlikely to be limited by competition for
411 resources from pre-existing taxa. Across islands we expect to see a correlation between speciation and small
412 range size, not because of any inherent properties of the range size, rather that they reflect newly formed
413 islands with empty niches **This seems like a very established idea but not sure whose it is.** Thus
414 our findings may be heavily dependent on species whose range size is restricted to a single island within an
415 archipelago (e.g. *Geospiza* sp.; a.k.a. Darwin's finches). One further explanation for the negative association
416 between range size and sexual dichromatism/sexual selection is the potential bias of taxonomic classification
417 whereby splitting of subspecies into species in clades with large ranges leads to increased recent phylogenetic
418 branching as well as a more subdivided range **Has this argument been articulated? I can't remember**
419 **reading it, maybe is not true and I made it up haha. Makes sense to me but maybe good to**
420 **see what reviewers would think about it. I guess it would also depend on whether the taxa**
421 **with large ranges are considered the same species because there is actually no strong genetic**

422 **differentiation across the range and not because there isn't enough information (e.g.sampling)**
423 **to split a species with massive range into smaller ranges and more species**. The role of range
424 size in speciation may be further investigated through ancestral geographic range reconstruction (Quintero et
425 al. 2015), as ancestral ranges may be beneficial in understanding modes of speciation and the causality of
426 range size expansions and contractions (Losos and Glor 2003).

427 Here we used BAMM to calculate extinction rates and test whether these rates were associated with sexual
428 dichromatism/selection or various ecological variables. We found no associations in this respect despite the
429 wealth of theoretical predictions on the effects of sexual selection on fitness. Extinction is notoriously difficult
430 to obtain accurate estimates for in comparative studies (*see* Rabosky 2016), as it is a process that occurs
431 over millennia, leaving scant traces for use in high-power comparative studies. One exception to this comes
432 from fossil ostracods, a group of marine invertebrates. In these species there is an extensive fossil record
433 of extinct ostracod species from the Late Cretaceous epoch (84–66 million years ago) as well as identifiable
434 sexual dimorphism. Across 93 species, Martins et al. (2018) found that ostracod taxa with larger sexual
435 dimorphism (representing exaggerated investment by males in reproductive organs) had higher extinction
436 rates; insinuating that sexual selection increases extinction risk. Other comparative studies have assessed
437 the relationship between sexual selection and extinction in birds (Doherty et al. (2003); Mitra et al. (1996);
438 Morrow and Pitcher (2003)) and mammals (Morrow and Fricke 2004; Bro-Jorgensen 2014) without consensus.
439 Yet these methods often rely on extinction threat status from the International Union for Conservation of
440 Nature (IUCN) Red List (*e.g.*, Morrow and Pitcher 2003; Morrow and Fricke 2004; Bro-Jorgensen 2014) and
441 may be heavily biased to species under greater anthropogenic threat, culturally valued or well researched.
442 While estimating extinction risk from the phylogeny may not come with these biases, they are riddled with
443 others (*reviewed in*, Pyron and Burbrink 2016). BAMM has been subject to controversy in its ability to model
444 rate shifts and extinction rates (*see*, Beaulieu and O'Meara 2015; Moore et al. 2016; Rabosky 2016; Rabosky
445 et al. 2017), and while several tip-rate estimates exist for speciation (*e.g.*, λ_{DR} and λ_{ND}) extinction estimates
446 are not as easily obtained. Here we anticipated extinction rates would be underestimated because we used
447 a phylogeny constructed with a birth-only (Yule) model (Jetz et al. 2012). Given these underestimates of
448 μ_{BAMM} it is likely we failed to detect true associations between sexual dichromatism/selection and extinction.
449 The power of BAMM as a model based-approach in estimating λ and μ is dependent on the size of the rate
450 regimes. BAMM often produces homogeneous λ_{BAMM} and μ_{BAMM} for clades with few rate shifts, whereas
451 λ_{DR} produces higher heterogeneity in tip-rates; arguably this could reflect increased power or sampling
452 error (Rabosky et al. 2017; Rabosky and others 2018). Thus we are somewhat uncertain in the validity of
453 conclusions from μ_{BAMM} estimates as well as λ_{BAMM} and λ_{DR} given their discrepancy.
454 Improvements in estimating tip-rates of speciation recently has allowed us to revisit the association between
455 sexual selection and speciation. With high power and alongside extensive ecological predictors we find that
456 male-bias measures of sexual selection predict speciation but sexual dichromatism does not. If sexual selection
457 promotes speciation through improvements in fitness and adaptation the implications are manifold with
458 sexual selection a potentially valuable utility in conservation (*reviewed in*, Holman and Kokko 2013) and
459 captive breeding programs for threatened species (*reviewed in*, Charge et al. 2014). Furthermore, our finding
460 that high speciation rate is associated with smaller range size has pronounced significance to the future
461 survival of these rapidly speciating species in a world with increased habitat loss and anthropogenic stress.
462 Range size is the best predictor of extinction risk (Harris and Pimm 2008) and the association found here
463 ensues that many newly speciated clades may be at greater risk of extinction due to their reduced range

⁴⁶⁴ 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-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 unchallanged as our instinctive Darwinian mind reminisces of peacocks and birds of paradise. My thoughts were such when I began this scientific inquiry, but now I am sceptical 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 while the correlation between sexual dichromatism and male-bias sexual selection is present, it is surprisingly weak. With this in mind, the practical use of sexual dichromatism in macroevolutionary research is severely weakened, with these noisy sexual dichromatism measurements calling dozens of studies into question due to false negative associations. This finding is particularly pertinent as efficient proxy measurements are incredibly valuable in comparative analyses; they increase the accessibility, available sample size and transferability of a study making it more conducive to research synthesis. But, as Wallace remarks, the matter is inevitabley more complex despite the irresistability 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 dateset that has great value and would benefit from being expanded across birds.

Not only was the measurement of sexual selection under a cloud of uncertainty, the estimates of speciation and extinction are also a point of controversy to many. 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 **CITE**. However, these hopes soon dissapated, and with them the seeming *raison d'être* of the project. In measuring extinction rate one can obtain the most valid measures of population fitness in evolutionary biology. 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 did include 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

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.

the controversy surrounding 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 exvtinction 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 challanging 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 despite the advancements in the field we cannot yet account for the underlting true variation; which is vastly more complex than we can currently measuure.

As with sexual dichromatism and macroevolutionary rates, the most severe limitation for environmental variation was the courseness of the meausres. In total, for 5,831 species we extracted 338,203,831 point measures¹ of environmental variability, despite this our measures may not account for variation in biotic components such as food or predation. However, the methods employed here are arguably much better than those implemented by many studies; where the range mid-point is used to obtain a single measure of temperature, precipitation or seasonality. **CITE**. I would argue that while reducing the multivariate data into several biologically meaningful predictors is a conceptually challanging exercise researchers should not feel limited by the amount of raw data that they can access².

¹5,831 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

²This 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.