

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

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4 Abstract

5 Sexual selection can shape phylogenetic diversity by altering speciation or extinction rates. The predicted
6 effects on diversity are often contradictory; for example, sexual selection might promote speciation by
7 creating reproductive isolation, or hinder it by selecting for traits that facilitate gene flow. Similarly, sexual
8 selection might precipitate extinction by favouring competitive phenotypes with poor survival, or stave
9 it off by helping populations shed deleterious mutations. Here, we investigate the relationship between
10 sexual selection and rates of speciation and extinction in passerine birds. We use two measures of sexual
11 selection — sexual dichromatism ($n = 5,812$ species) and a multivariate measure of male-biased sexual
12 selection (sexual dimorphism, polygyny and paternal care; $n = 2,465$) — as well as three distinct measures
13 of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}), and one measure of extinction (μ_{BAMM}). We also tested whether
14 the effects of sexual selection is contingent on ecological variables such as spatiotemporal temperature
15 variation, primary productivity, and range size. We find that birds with smaller ranges have higher
16 speciation rates; although the direction of causality is unclear. Moreover, our results show that male-biased
17 sexual selection, but not sexual dichromatism, is an agent of adaptation and speciation. This finding
18 suggests that sexual selection is an evolutionary force shaping patterns of diversity amongst songbirds,
19 which has broad implications for ecology and conservation biology. dichromatism, Range size, Extinction
20 rate.

21 **Keywords:** Speciation rate, Comparative analysis, Plumage

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22 INTRODUCTION

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

31 Sexual selection results from competition for matings, fertilisations, or associated resources, and is typically
32 stronger in males than females (Kokko and Jennions 2008; Fromhage and Jennions 2016; Janicke et al. 2016).
33 This evolutionary force has been proposed to facilitate speciation through the evolution of divergent signals
34 associated with improved mating success (Lande 1981, 1982). For instance, in antbirds (Thamnophilidae),
35 genera with complex songs and striking dichromatism are more species rich (Seddon et al. 2008). Under this
36 model of speciation, divergent mating signals in one sex (usually males) co-evolve with divergent preferences for
37 those signals in the opposite sex, leading to behavioural reproductive isolation (Safran et al. 2013). Alongside
38 facilitating the evolution of divergent mating signals, sexual selection can increase the extent populations
39 diverge by enlarging the available phenotypic space for mating signals. These predictions emerge as sexual
40 selection may increase genetic diversity as a result of trade-offs between naturally- and sexually-selected traits
41 or trade-offs under *intra*-locus sexual conflict between male and female trait expressions (Lorch et al. 2003;
42 Bonduriansky 2011; Radwan et al. 2016). Additionally, sexual selection can have both positive and negative
43 consequences for adaptation (*e.g.*, Kokko and Brooks 2003; Whitlock and Agrawal 2009; Holman and Kokko
44 2013). For example, sexual selection can elevate average fitness by helping to purge deleterious mutations
45 (Agrawal 2001; Siller 2001) and fix beneficial ones (Whitlock 2000), which should mitigate extinction risk and
46 facilitate adaptation to environmental change. However, sexual selection might also promote extinction, by
47 selecting for male traits that have detrimental pleiotropic effects on female traits (Pischedda and Chippindale
48 2006; Bonduriansky and Chenoweth 2009; Pennell and Morrow 2013; Berger et al. 2014), or selecting for male
49 phenotypes with improved mating success but which harm population productivity, such as under-investing
50 in parental care (Kokko and Rankin 2006).

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

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

69 As a speciose and well-characterised group of organisms with remarkable and variable sexually-selected
70 traits such as song and colourful plumage, birds are a popular focus for macroevolutionary studies of sexual
71 selection and diversification (e.g. Baracalough et al. 1995; Morrow et al. 2003; Seddon et al. 2008, 2013;
72 Huang and Rabosky 2014). A 2011 meta-analysis, covering 20 studies of birds and other taxa, found a small
73 but significant positive association between sexual selection and speciation, with the average effect size in
74 birds stronger than in mammals but weaker than in insects and fish (Kraaijeveld et al. 2011). However,
75 Kraaijeveld et al. (2011) found large variation in effect sizes between studies, likely because of differences in
76 the metrics used as estimates of speciation and the strength of sexual selection. More recently, Huang and
77 Rabosky (2014) found no association between sexual dichromatism and speciation ($n = 918$ species) when
78 using spectrophotometry measures on taxonomic specimens (Armenta et al. 2008) and tip-rate estimates
79 from a molecular-only phylogeny (Jetz et al. 2012). Similarly, Cooney et al. (2017) found no effect of sexual
80 dichromatism on diversification across 1,306 pairs of species, using dichromatism scores from human observers.

81 Here, we investigate the association between sexual selection and diversification in birds while extending
82 previous work in multiple ways. Firstly, many macroevolutionary studies estimate the strength of sexual
83 selection using proxies such as sexual dimorphism or dichromatism, but these are imperfect correlates. We
84 used a very large ($n = 5,812$) dataset of sexual dichromatism (estimated from illustrated drawings; Dale et
85 al. 2015), as well as a smaller but still substantial dataset ($n = 2,465$) that gives a composite measure of
86 male-biased sexual selection, capturing variation in sexual dimorphism, social polygyny and [lack of] paternal
87 care. These datasets allow us to cover the great majority of bird genera, in contrast to previous work that
88 has often focused on particular clades (e.g. Seddon et al. 2008). Secondly, we use the latest methods for
89 estimating speciation and extinction rates at the tips of phylogenetic trees, including BAMM (Bayesian
90 Analysis of Macroevolutionary Mixtures) (see, Beaulieu and O'Meara 2015; Rabosky 2016; Moore et al. 2016;
91 Rabosky et al. 2017), as well as older but less controversial tip-rate statistics, such as diversification rate
92 (λ_{DR}) and node density (λ_{ND}). We also conduct analyses that allow phylogenetic uncertainty in the avian tree
93 (Jetz et al. 2012; but see Rubolini et al. 2015) to affect the precision of our estimates, rather than implicitly
94 assuming that the single best-supported phylogenetic tree, or consensus tree, is correct. Thirdly, our analysis
95 includes several potentially important environmental variables as predictors: range size, seasonal variation
96 in temperature, spatial temperature variation (across a species' range), long-term variation in temperature
97 between now and the last inter-glacial (LIG) as well net primary productivity (NPP). By including these
98 environmental variables in our models, we statistically account for their effects on variation in diversification
99 rates and thereby improve our estimates of the effects of sexual selection. We also test whether the effects
100 of sexual selection are contingent on the environment, as predicted by some theories (e.g. the theory that
101 sexual selection is more likely to elevate adaptation in changeable relative to static environments; Long et al.
102 2012; Connallon and Hall 2016).

¹⁰³ MATERIALS AND METHODS

¹⁰⁴ We examined the effect of sexual selection on speciation and extinction rate in 97 % of passerines ($n = 5,812$
¹⁰⁵ species; 58 % of all birds). Specifically, we (*i*) compiled datasets for sexual dichromatism/selection strength
¹⁰⁶ and environmental variability, (*ii*) obtained estimates of speciation and extinction rates across passerines,
¹⁰⁷ and (*iii*) conducted phylogenetic generalized least-squares (PGLS) regressions. Analyses are documented
¹⁰⁸ with reproducible code in the [Electronic Supplementary Material \(ESM\)](#).

¹⁰⁹ Compiling data for sexual selection and environmental stress

¹¹⁰ Sexual dichromatism

¹¹¹ We used a previously published measure of sexual dichromatism for 5,983 species of passerines (Dale et al.
¹¹² 2015). Briefly, Dale et al. (2015) obtained sex-specific RGB (red, green and blue) values across six body
¹¹³ patches (nape, crown, forehead, throat, upper breast and lower breast) from *Handbook of the Birds of the*
¹¹⁴ *World* (volumes 8–16) (Del Hoyo et al. 2011). The relative contribution of male and female RGB colour
¹¹⁵ values were averaged across body patches and provide ‘male-like’ and ‘female-like’ plumage scores. Here we
¹¹⁶ use the absolute difference between male and female plumage scores as an estimate of sexual dichromatism.
¹¹⁷ Additionally, we used a more accurate measure of dichromatism corresponding to colour distance in avian
¹¹⁸ colour space derived from spectral data (Armenta et al. 2008). These measurements include variation in the
¹¹⁹ ultraviolet and bird-visible range and — unlike the RGB measures — are sourced from taxonomic samples (as
¹²⁰ opposed to colour drawings). However, this spectrophotometry data is not as extensive as the RGB measures;
¹²¹ with only 581 passerine species available for this analysis. While there is a correlation between these two
¹²² measures, there is residual variation ($r = 0.79$; [Figure S10](#)).

¹²³ Male-biased sexual selection

¹²⁴ Sexual dichromatism is a widely used indicator of sexual selection in birds (e.g., Barraclough et al. 1995;
¹²⁵ Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang and Rabosky 2014), but only partially
¹²⁶ captures variation in the strength of sexual selection across taxa. Therefore, we also use an existing dataset
¹²⁷ (Dale et al. 2015) of male-biased sexual selection based on the first component of a phylogenetic principle
¹²⁸ component analysis (PPCA) of three characteristics associated with sexual selection (sexual size dimorphism,
¹²⁹ social polygyny and [lack of] paternal care). This measure of male-biased sexual selection is available for only
¹³⁰ 2,465 species and is weakly correlated with the absolute values of sexual dichromatism using RGB measures
¹³¹ ($r = 0.34$; [Figure S12](#)).

¹³² Environmental variables

¹³³ We obtained estimates of species range size using expert range maps (BirdLife International and Handbook
¹³⁴ of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the *Birdlife* database
¹³⁵ (Hoyo and Collar 2016) we manually matched these taxa with the names used in the sexual dichromatism

dataset (Dale et al. 2015). From these distributions we obtained estimates of climatic conditions that each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature and precipitation) with 30 seconds ($\sim 1 \text{ km}^2$) spatial resolution (Fick and Hijmans 2017). From these values we obtained means and standard deviations for each species. Using the same spatial sampling, we extracted means and standard deviations of bioclimatic variables from the paleoclimate during the last interglacial (LIG; 120,000 - 140,000 years ago) (Otto-Bliesner et al. 2006). Furthermore, to estimate variability in the energy available to species, we obtained the mean and standard deviation of net primary productivity (NPP) values between 2000 - 2015 across each species distribution. Estimates of NPP had 30 second resolution and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production products stage 3 (MOD17A3) (Zhao et al. 2005). Using these data, which we provide as a potentially useful data resource (see [ESM](#)), we generated five predictors of speciation associated with different patterns in environmental variability (see below).

Generating biologically relevant predictors for environmental variation

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

Estimating extinction and speciation

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

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

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

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

Phylogenetic comparative analysis

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we used phylogenetic least squares (PGLS) models in the **nlme** package (Pinheiro et al. 2018). We began by estimating the phylogenetic signal — Pagel’s λ (Pagel 1999) — using the **corPagel** function in the **ape** package (Paradis et al. 2004) on the MCC tree. The estimate of λ was then fixed for model selection, which was conducted on the same MCC tree derived from 2,500 draws of the posterior distribution (Jetz et al. 2012). Model selection used either λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} tip-rate estimates from the MCC tree as the response variable. For λ_{BAMM} and μ_{BAMM} we were also able to use model weights sourced from the inverse of the variance of tip-rates for a given species from the posterior distribution ($n = 1,000$). Model weights thus reflect the degree of precision to which each species tip-rate is measured in BAMM. Using model selection we only compared interaction terms between a measure of sexual selection (sexual dichromatism or male-biased sexual selection) and environmental measures. That is, we fixed the

214 individual predictors of: dichromatism/male-biased sexual selection measures, log-transformed range size,
215 seasonal temperature variation, spatial temperature variation, long-term temperature variation and NPP
216 while comparing 32 models with different combinations of interactions (including none). Model selection was
217 done in MuMIn using the `dredge` function (Bartoń 2017). Using the terms from the top-ranking model (lowest
218 AICc), we ran the equivalent model for each of the 100 phylogenetic trees used to derive λ_{DR} , λ_{ND} , λ_{BAMM}
219 and μ_{BAMM} , using the unique response variables and phylogenetic tree correlation structure in each model.
220 This method enabled us to present model estimates for an MCC tree alongside 100 trees from the posterior
221 distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three datasets
222 corresponding to each measure of sexual selection: dichromatism derived from RGB values of images ($n =$
223 5,812); dichromatism from spectrophotometry ($n = 581$) and the multivariate measure of male-biased sexual
224 selection ($n = 2,465$).

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

235 RESULTS

236 Effects of sexual dichromatism/selection on speciation are not dependent on
237 environmental variability

238 PGLS models with interaction terms between each measure of sexual dichromatism/selection and the five
239 measures of environmental variability (seasonal temperature variation, log-range size, long-term temperature
240 variation, spatial temperature variation and NPP) were included in model selection. However, no interaction
241 terms were significant or present in the top models ($\delta \text{ AICc} > 4$) for any measure of speciation (λ_{DR} , λ_{ND} ,
242 λ_{BAMM}) or sexual selection (RGB values, spectrophotometry and male-biased sexual selection; $\delta \text{ AICc}$
243 > 4 ; [Table S5](#), [Table S6](#), [Table S10](#), [Table S13](#)). Thus we found no evidence that the effect of sexual
244 selection on speciation is dependent on our measures of environmental variation. Furthermore, we found no
245 evidence that these environmental factors (seasonal temperature variation, long-term temperature variation,
246 spatial temperature variation and NPP) predict speciation independently from sexual dichromatism/selection
247 ([Figure 1](#), [Figure S11](#)).

²⁴⁸ No evidence that sexual dichromatism affects speciation

²⁴⁹ We found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation.
²⁵⁰ Using three response measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}), the effect of sexual dichromatism was not
²⁵¹ significant in any PGLS model based on tip-rate estimates and correlation structures from the MCC tree.
²⁵² Specifically, sexual dichromatism showed no association with λ_{DR} ($\beta = -1.279e-03$, $p = 0.147$; [Figure 1a](#),
²⁵³ [Figure 2a](#)) or λ_{ND} ($\beta = -5.745e-05$, $p = 0.078$; [Figure 1a](#)). Furthermore, speciation rates from BAMM
²⁵⁴ (λ_{BAMM}) were also unaffected by sexual dichromatism ($\beta = -1.430e-05$, $p = 0.872$; [Figure 1a](#)). PGLS
²⁵⁵ analyses using sexual dichromatism ($n = 581$) measured by spectrophotometry (Armenta et al. 2008) yielded
²⁵⁶ results concordant with the full dataset; *i.e.* no association between sexual dichromatism and speciation
²⁵⁷ ([Figure S11](#)). Our results from models based on the MCC tree are largely corroborated by model estimates
²⁵⁸ from PGLS analyses of the rates and correlation structures from 100 random trees. The HPD (highest
²⁵⁹ posterior density) intervals show model estimates are distributed around zero when using complete taxon
²⁶⁰ sampling models and RGB measures of sexual dichromatism ([Figure 1a](#), [Table S8](#)). For PGLS models using
²⁶¹ spectrophotometry-based measures of sexual dichromatism, the estimates from the 100 trees in the λ_{DR}
²⁶² models are positively skewed (HPD Interval = $-1.781e-02$, $3.488e-02$) but normally distributed around zero
²⁶³ for λ_{ND} and λ_{BAMM} ([Table S12](#)).

²⁶⁴ Male-biased sexual selection increases speciation

²⁶⁵ We found a significant positive association between male-biased sexual selection ($n = 2,465$) and λ_{DR} ($\beta =$
²⁶⁶ $3.887e-02$, $p = 0.012$; [Figure 1b](#)). However, this association was not significant for the other two measures
²⁶⁷ of speciation rate (λ_{ND} : $\beta = 4.381e-04$, $p = 0.351$; λ_{BAMM} : $\beta = 9.422e-04$, $p = 0.764$; [Figure 1b](#)). The
²⁶⁸ distribution of estimates from PGLS models on 100 random trees was similar to the estimate from the MCC
²⁶⁹ tree: among the 100 trees there was a positive association between sexual selection and λ_{DR} (HPD Interval =
²⁷⁰ $9.115e-03$, $6.085e-02$), and a smaller positive association between sexual selection and λ_{ND} (HPD Interval =
²⁷¹ $-3.104e-04$, $1.536e-03$;) as well as λ_{BAMM} (HPD Interval = $-1.297e-02$, $3.089e-02$). Complete HPD intervals
²⁷² for models using male-biased sexual selection PPCA as a predictor can be found within [Table S15](#).

²⁷³ Species with smaller ranges have increased rates of speciation

²⁷⁴ Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation, we found a negative association between range size and
²⁷⁵ speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This negative
²⁷⁶ association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.578e-03$, $p = 0.001$; λ_{ND} :
²⁷⁷ $\beta = -1.462e-04$, $p = 0.034$; [Figure 1a](#), [Figure 2](#)). This association was also evident across the estimates from
²⁷⁸ models using the 100 trees (λ_{DR} : HPD Interval = $-8.438e-03$, $-1.823e-03$; λ_{ND} : HPD Interval = $-1.899e-04$,
²⁷⁹ $9.112e-06$; [Figure 1a](#)). Subset models with reduced sample size and different measures of sexual selection
²⁸⁰ — but the same measure of range size — showed variable evidence that range size is negatively associated
²⁸¹ with speciation. Range size significantly predicted λ_{DR} ([Figure 1b](#)) using data subset for male-biased sexual
²⁸² selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} . Models using data subsetted for spectrophotometry-based
²⁸³ dichromatism ($n = 581$) gave non-significant estimates for the effect of range size on all measures of speciation
²⁸⁴ ([Figure S11](#), [Table S11](#), [Table S12](#)). Because the range size dataset is the same across the three data subsets

285 we draw our conclusions from the models with highest power using near-complete taxon sampling ($n = 5,812$).

286

287 Phylogenetic path analysis

288 Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
289 (Figure 3; Figure S14). Notably, environmental variability (temperature seasonality) directly affected sexual
290 dichromatism ($\beta = 0.07$) and the path from male-biased sexual selection to sexual dichromatism was relatively
291 weak, ($\beta = 0.22$). Additionally, the large direct effect of temperature seasonality on range size ($\beta = 0.52$)
292 suggests an indirect effect of temperature seasonality on λ_{DR} ($\beta_{indirect} = -0.02$; Figure 3), given the negative
293 association we identified between λ_{DR} and range size in PGLS models.

294 Extinction rate

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

299 Variability across trees and methods

300 We tested our hypothesis that sexual selection is associated with speciation using several methods and across
301 100 trees drawn from the post burn-in posterior (Jetz et al. 2012). We used a range of methods to overcome
302 uncertainty in the power and precision of various tip-rate estimates as well as the variation between trees.
303 We found that the tip-rate estimates across the 100 trees were quite variable for both λ_{DR} and λ_{BAMM}
304 (Figure S15). Despite this, tip-rate estimates of speciation from the two methods were moderately correlated
305 across the 100 trees ($r = 0.75$) and for the MCC tree ($r = 0.68$; Figure S16). However, in comparison to λ_{DR} ,
306 the value of λ_{BAMM} was the *mean* drawn from a posterior distribution ($n = 1,000$) of BAMM generations,
307 thus estimates of λ_{BAMM} (and μ_{BAMM}) have an added level of variation. To account for this variation,
308 weights (using the inverse of the variance) were used for the PGLS models. From 1,000 posterior samples
309 of the MCC BAMM run, the coefficient of variation (CV) for all log-rates of λ_{BAMM} was relatively low
310 (*mean CV* = 21.49, *median CV* = 15.76 ; see Figures S6 and Figure S8). Despite the convergence of the
311 BAMM model in all runs — where effective sample sizes of the number of shifts and log-likelihood were all
312 greater than 200 (Table S3, Table S4) — we found that the unique combinations of rate shifts across the
313 large phylogenetic tree ($n = 5,966$ species) was high. This means that although the number of rate shifts
314 reached convergence (*median* = 59; Figure S7), the locations of the rate shifts (*i.e.* the credible shift set)
315 across the tree are highly heterogeneous. The variability in the locations for the shift configurations is a
316 likely source of uncertainty in downstream tip-rates used as the response variable in PGLS models. Notably,
317 the 95 % HPD interval for model estimates using BAMM rates from 100 trees was about 20-fold the 95 %
318 confidence intervals of the estimate from the MCC tree; whereas for λ_{DR} and λ_{ND} the HPD 95 % interval
319 width was equal to or less than the MCC 95 % CI (Figure 1, Table S9).

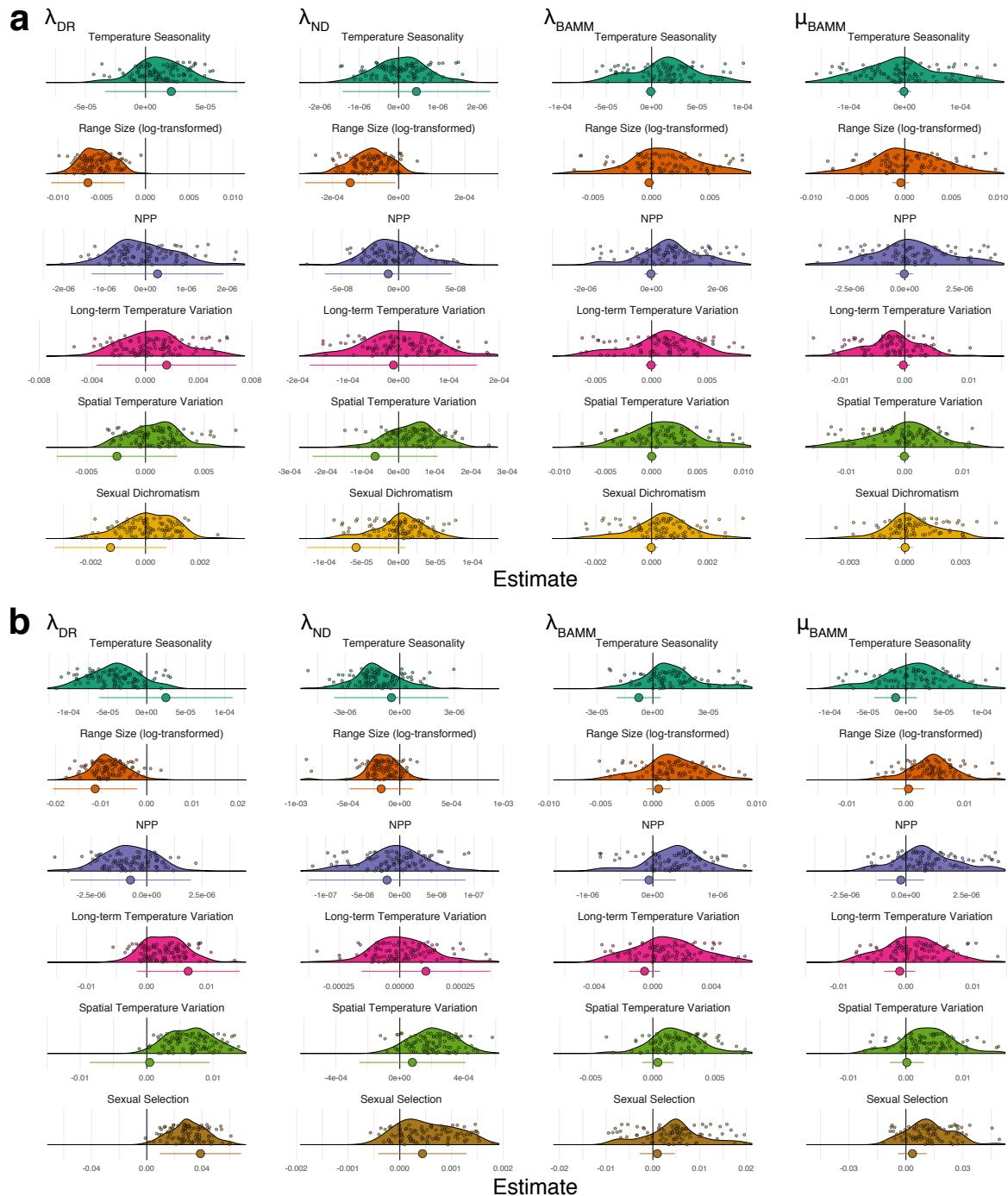


Figure 1: Model estimates for (a) PGLS analyses using sexual dichromatism ($n = 5,812$) and (b) PGLS analyses using measures of male-biased sexual selection ($n = 2,465$). Both datasets were used for analyses with three measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one measure of extinction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

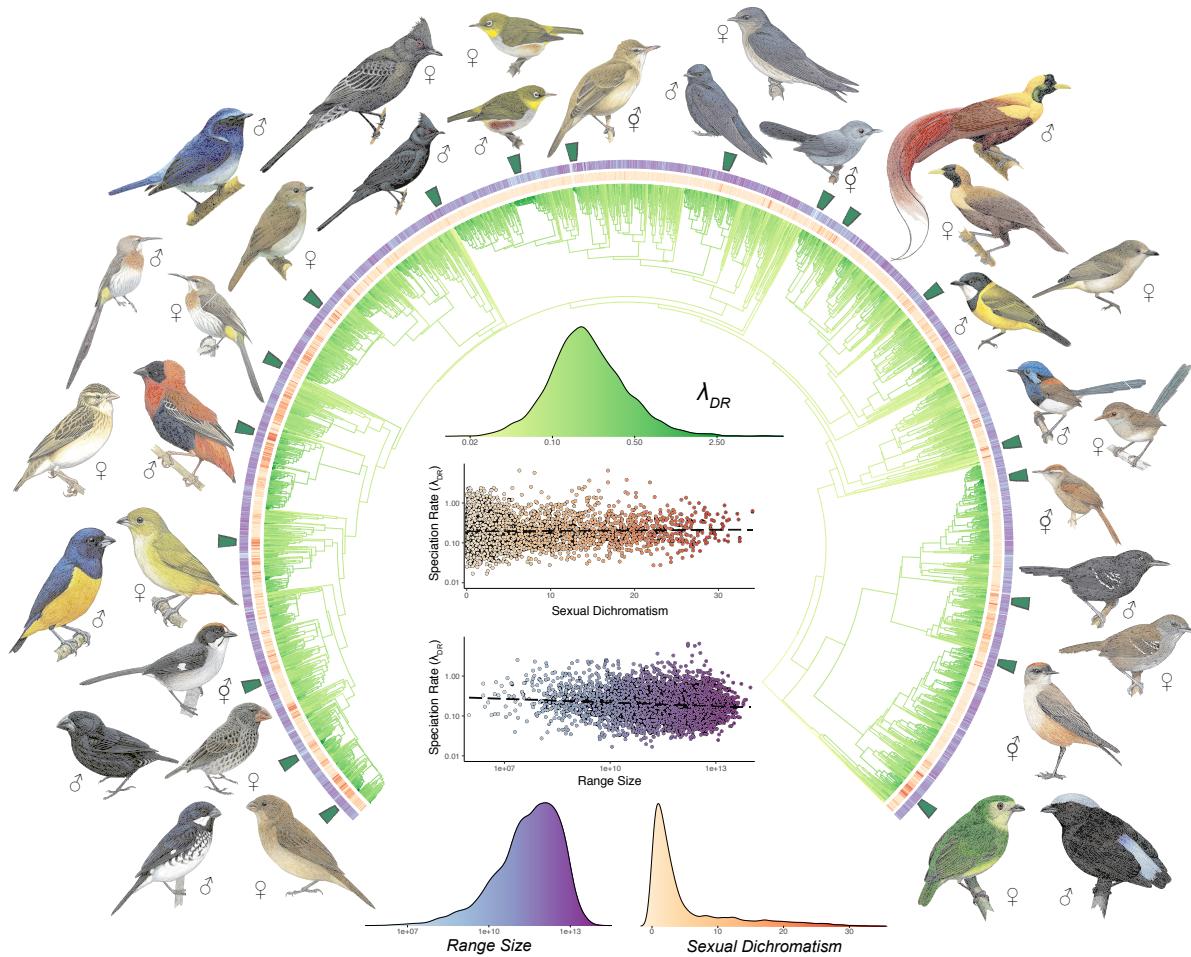


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism and range size available for 5,812 of them. Across these species there was a small but significant negative association between λ_{DR} and log-range size but no significant association between λ_{DR} and sexual dichromatism based on RGB. λ_{DR} are those from the MCC tree and images of birds are from the *Handbook of the Birds of the World*. Clockwise the species are: *Sporophila bouvronides*, *Geospiza magnirostris*, *Atlapetes leucopterus*, *Euphonia rufiventris*, *Euplectes franciscanus*, *Promerops gurneyi*, *Phainopepla nitens*, *Zosterops erythropleurus*, *Acrocephalus australis*, *Progne cryptoleuca*, *Mayrornis schistaceus*, *Paradisaea rubra*, *Pachycephala pectoralis*, *Malurus pulcherrimus*, *Cranioleuca curtata*, *Cercomacra manu*, *Muscisaxicola capistratus*, *Lepidothrix coeruleocapilla*. Edge colours for the terminal branch correspond to λ_{DR} but all precluding branches have been generated for graphical purposes using ancestral character state estimation and should not be interpreted.

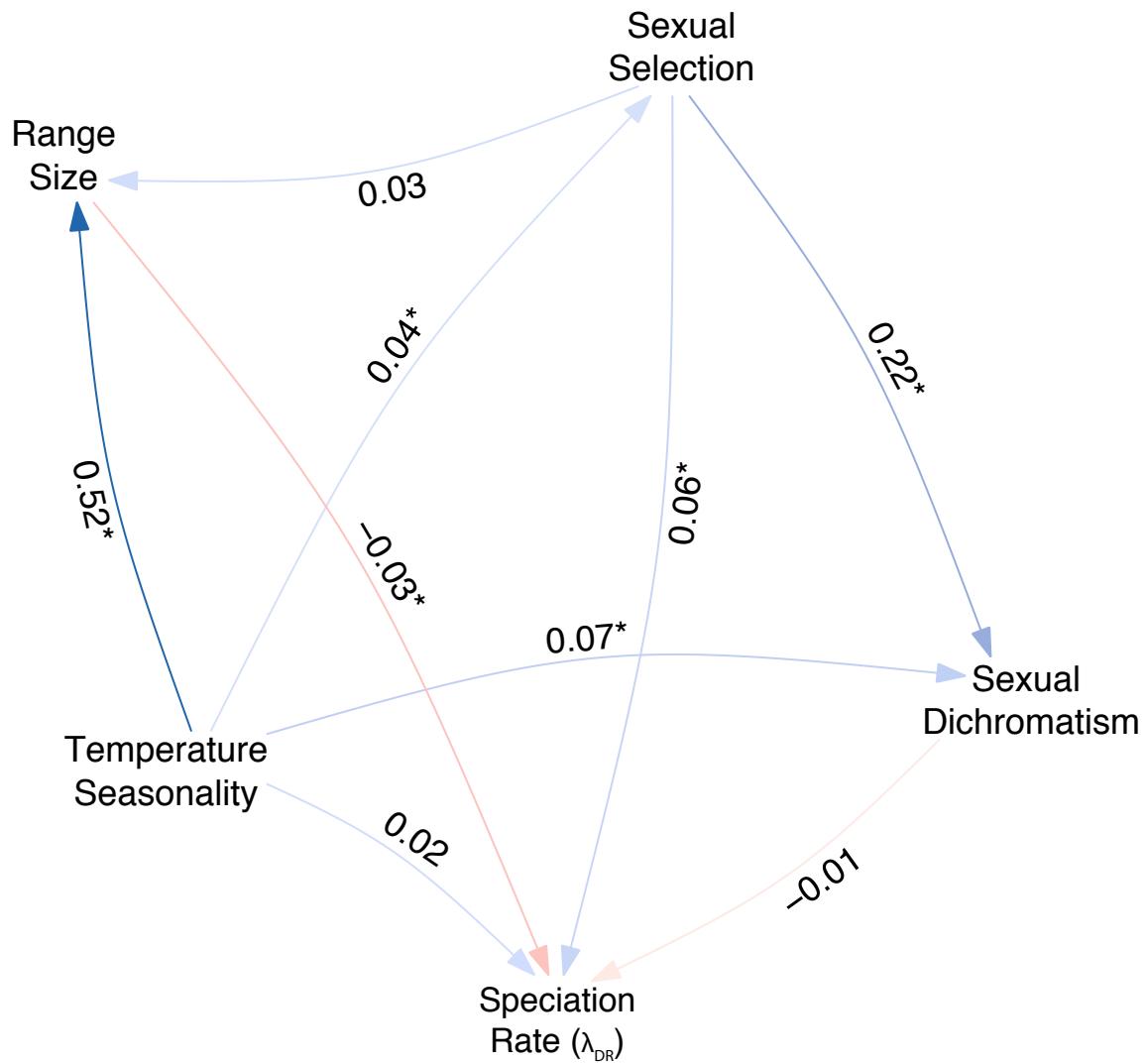


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with numeric values corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95 % confidence intervals of this estimate do not overlap with zero. The confidence intervals were obtained from 500 bootstrapped iterations and the data used in this analysis was subset to species with both sexual dichromatism and male-biased sexual selection measures ($n = 2,465$).

320 DISCUSSION

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

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

361 In-line with predictions and a previous meta-analysis (Kraaijeveld et al. 2011) we found that male-biased
362 sexual selection increases speciation rate — at least for λ_{DR} and λ_{ND} estimates — but this association
363 was not dependent on environmental variability. The environmental variability predictors used here often
364 reflected changes in climate across space and time, whereby high environmental variation would likely
365 increase the strength of natural selection on a given species. Given that we did not detect an effect of
366 environmental variability (by itself or as an interaction with sexual selection) we are left with several possible
367 explanations. Firstly, the effects of sexual selection on adaptation and thus speciation may depend on the
368 type of environmental variability the species is evolving under. Specifically, sexual antagonism may be more
369 easily purged in environments where pressures are cyclic (*e.g.* seasonality); whereas when environmental
370 variability is directional (*e.g.* long-term climate change) sexual antagonism can remain indefinitely as a fitness
371 burden (Connallon and Hall 2016). Secondly, the environmental predictors used here may not account for
372 the key ecological forces/natural selection pressures that interact with sexual selection to drive speciation.
373 Specifically, access to dietary resources, and the impacts of predation or parasitism are unaccounted for here.
374 These are likely key processes affecting sexual selection and speciation (*reviewed in* Maan and Seehausen
375 2011). Thirdly, it is also possible that there is no effect of environmental variability on speciation rates; at
376 least not in the species investigated here.

377 The most consistent finding uncovered in this comparative analysis is that smaller range sizes are associated
378 with increased speciation rates; however reduced range size can be a cause or consequence of speciation.
379 Intuitively, large range size should promote speciation by creating greater opportunities for geographic
380 barriers to form (Rosenzweig 1995). However, birds with smaller range sizes are predicted to have lower
381 dispersal ability, which would promote reproductive isolation and speciation (Birand et al. 2012; Claramunt
382 et al. 2012). Alternatively, reduced range size may be a consequence of speciation. Under this view, high
383 speciation rate may lead to smaller range sizes as niche filling by recently diverged species will suppress
384 the expansion of newly speciated relatives (Rosenzweig 1995; Weir and Price 2011; Price and Eaton 2014).
385 However, species undergoing adaptive radiation in new niches are unlikely to be limited by competition for
386 resources from existing taxa. Across islands we expect to see a correlation between speciation and small
387 range size because they reflect newly formed environments with empty niches. Thus, our findings may be
388 heavily dependent on island radiations (*e.g.* *Geospiza* sp.; a.k.a. Darwin's finches). One further explanation
389 for the negative association between range size and sexual dichromatism/sexual selection is the potential bias
390 of taxonomic classification, whereby over-splitting of species in clades with large ranges leads to increased
391 recent phylogenetic branching as well as smaller ranges. Given the problems of determining causality and
392 mode of speciation, the reason for the negative association found here remains unclear.

393 In addition to speciation, sexual selection has frequently been invoked as a driver of extinction. Sexual
394 selection may increase extinction risk as it often leads individuals (usually males) to invest in exaggerated
395 mating signals as opposed to traits — such as parental care — that elevate offspring fitness (*reviewed in* Kokko
396 and Brooks 2003). Using BAMM, we found no association between extinction rate and sexual dichromatism,
397 male-biased sexual selection or measures of environmental variability. Extinction is notoriously hard to
398 estimate accurately (*see* Rabosky 2016). It can be estimated from phylogenies, the fossil record, documented
399 recent extinctions and IUCN extinction threat status, but each approach has limitations. Phylogenetic
400 methods — like BAMM — allow for speciation and extinction rates to be measured using moderately sized
401 phylogenies. However, BAMM has been the subject of controversy over its ability to model evolutionary rate
402 shifts and extinction rates (*see*, Beaulieu and O'Meara 2015; Rabosky 2016; Moore et al. 2016; Rabosky et al.

403 2017), and while several tip-rate estimates exist for speciation (*e.g.*, λ_{DR} and λ_{ND}) extinction estimates are
404 not as easily obtained. Here, we found that BAMM often produced homogeneous speciation and extinction
405 rates for clades with few rate shifts which could arguably reduce our power to detect small differences in
406 extinction rates among closely related taxa (Rabosky et al. 2017; Rabosky and others 2018).

407 We have shown that in passerines, male-biased sexual selection, but not sexual dichromatism, predicts
408 speciation, independent of several measures of environmental variability. If sexual selection promotes
409 speciation through improvements in fitness and adaptation the implications are manifold, including for
410 conservation (*reviewed in*, Holman and Kokko 2013) and captive breeding programs for threatened species
411 (*reviewed in*, Charge et al. 2014). Furthermore, our finding that high speciation rate is associated with smaller
412 range size highlights the threat to the persistence of rapidly speciating lineages in a world with increased
413 habitat loss and anthropogenic stress. Range size is the best predictor of extinction risk (Harris and Pimm
414 2008) and the association found here implies that many newly speciated clades may be at greater risk of
415 extinction due to their small range being impacted by anthropogenic effects.

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CRITICAL ANALYSIS

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

— ALFRED RUSSEL WALLACE

Strengths and limitations

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

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

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

extinction rates from the Jetz et al. (2012) bird phylogeny is problematic because of the nature of phylogenetic construction: a birth-only model of tree construction and incomplete genetic taxon sampling are large barriers that limit the ability to use model-based methods to detect extinction rate (Beaulieu and O'Meara 2015). Furthermore, the very detection of absence of data — which is what such methods attempt to do — is a hard sell, both conceptually and methodologically come peer review: see Rabosky (2016) for a cautionary tale on measuring extinction rate with BAMM. The mechanisms and rates at which speciation and extinction occur are an active area of research. In a recent pre-print Henao Diaz et al. (2018) used BAMM across 104 time-calibrated molecular phylogenies and found that despite variation in ecology, biogeography and taxonomy, younger clades consistently had higher rates of speciation and extinction. This finding of time-dependency in rates of diversification makes comparative analyses between clades challenging and calls into question countless studies. Similar to Wallace's view of sexual dichromatism we are left with a view of diversification rate measures where we cannot yet account for the underlying true variation; which is vastly more complex than we can currently measure.

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

Future directions

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

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

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

⁴Specifically, the following two sections are spurred from dialogue with **Dr Gene Hunt** and **Associate Professor Erin E. Saupe**

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

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