

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

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4 Abstract

5 Sexual selection can shape phylogenetic diversity by affecting speciation or extinction rates. The predicted
6 effects on diversity are often contradictory; for example, sexual selection might promote speciation by
7 creating reproductive isolation, or hinder it by selecting for traits that facilitate gene flow. Here, we
8 investigate the relationship between sexual selection and diversification in passerine birds. Multiple studies
9 use sexual dichromatism as a proxy for sexual selection, however, this relationship can be weak in many
10 clades. Thus, we use two measures of sexual selection — sexual dichromatism and a multivariate measure
11 of male-biased sexual selection — to test the link between sexual selection and diversification. We also
12 test whether the effect of sexual selection on diversification is contingent on ecological variables. Our
13 results show that male-biased sexual selection, but not sexual dichromatism, can explain speciation rates
14 (λ_{DR}) in passerines. We also find that birds with smaller ranges have higher speciation rates, but there
15 is no interaction between environmental variables and sexual selection. Our findings show that sexual
16 dichromatism is a poor proxy for sexual selection at least a a broad-scale, and support the view that
17 sexual selection is an evolutionary force shaping patterns of diversity amongst songbirds.

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

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19 INTRODUCTION

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

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

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

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

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

91 MATERIALS AND METHODS

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

97 Compiling data for sexual selection and environmental stress

98 Sexual dichromatism

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

111 Male-biased sexual selection

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

120 Environmental variables

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

Given that stressful environments are expected to interact with sexual selection and have a positive effect on adaptation (Cally et al. 2019), we used the extracted environmental variables from each species range size to develop biologically meaningful predictors of environmental variation/stress. Firstly we used (*i*) the average NPP in each species' range and (*v*) the log-transformed range size as potentially informative predictors of speciation rates. We also used three environmental predictors derived from bioclimatic data. These predictors relate to seasonal climate variation, spatial climate variation and long-term climate variation. To obtain seasonal climate variation we used (*iii*) mean values of temperature seasonality (BIO4) for each range. (*IV*) 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 and precipitation seasonality (BIO 4 and BIO15). PC1 was heavily loaded towards bioclimatic variables relating to temperature, thus PC1 reflects the variation in temperature across a species' range ([Table S1](#)). Species range is a potentially informative predictor of speciation and extinction, so we controlled for the correlation between environmental spatial variation and range size — where larger ranges have larger variation in PC1 — by using the residuals of a fitted general additive model (GAM; [Figure S1](#)) as a predictor. To obtain long-term variation in climates for each species range we take (*v*) 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 R 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 ($n = 5,965$) as the main phylogenetic hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using tip-rate measures (1000 trees) and BAMM (100 trees)(Rabosky 2014). These trees used a 'Hackett backbone' (Hackett et al. 2008) and were constructed using 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 edge towards the root having the length down-weighted. Studies have suggested that DR and ND (henceforth referred to as λ_{DR} and λ_{ND})

are more reflective estimates of speciation than diversification (Belmaker and Jetz 2015; Title and Rabosky 2018). Therefore, λ_{DR} is a measure of speciation rate more heavily weighted to recent speciation events and λ_{ND} is a measure of speciation across the root-to-tip path. These tip-rate measures are alternatives to state-dependent diversification models such as Quantitative State Speciation-Extinction (QuaSSE). But, based on previous simulation studies, λ_{DR} and λ_{ND} are robust and intuitive measures that provide high power and low false discovery rate with large phylogenies when incorporated into Phylogenetic Generalized Least Squares (PGLS) models (Harvey Michael et al. 2017).

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

Phylogenetic comparative analysis

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we used phylogenetic least squares (PGLS) models in the [nlme](#) package (Pinheiro et al. 2018). Firstly we conducted model selection using λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} tip-rate estimates from the same MCC tree, which was derived from 2,500 draws of the posterior distribution (Jetz et al. 2012). For λ_{BAMM} and μ_{BAMM} we were also able to use model weights sourced from the inverse of the variance of tip-rates for a given species from the posterior distribution ($n = 1,000$). Model weights thus reflect the degree of precision to which each species' tip-rate is measured in BAMM. Using model selection we only compared interaction terms between a measure of sexual selection (sexual dichromatism or male-biased sexual selection) and environmental measures. That is, we fixed the individual predictors of dichromatism/male-biased sexual selection measures, log-transformed range size, seasonal temperature variation, spatial temperature variation, long-term temperature variation, and NPP while comparing 32 models with different combinations of interactions (including none). Model selection was done in [MuMIn](#) using the [dredge](#) function (Bartoń 2017). Using the terms from the top-ranking model (lowest AICc), we ran the equivalent model for each of the 1,000 phylogenetic trees used to derive λ_{DR} , λ_{ND} and each of the 100 used to derive λ_{BAMM} and μ_{BAMM} . In each model we used the unique response variables and phylogenetic tree correlation structure. Specifically, for models using tip-rate metrics (λ_{DR} , λ_{ND}) we estimated the phylogenetic signal — Pagel's λ

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

RESULTS

Variability across phylogenetic hypotheses and measures of speciation and sexual selection

Estimates of speciation rates varied across phylogenetic trees, especially in the BAMM rates (λ_{BAMM} and μ_{BAMM}), where the 95 % highest posterior density (HPD) interval across 100 trees was more than 20 times larger than the 95 % confidence interval calculated for the MCC tree. This contrasts with variation across trees for the other rate estimates (λ_{DR} and λ_{ND}), where the 95 % HPD interval across 1,000 trees was near-equivalent to the 95 % confidence interval calculated for the MCC tree ([Table S9](#)). Mean measures of speciation across 100 trees were positively correlated between measures (DR - BAMM: $r=0.75$, DR - ND: $r=0.65$, ND- BAMM: $r=0.51$; [Figure S15](#)). Given that the calculation of BAMM rates can be affected by the settings of the run and the use of different priors, we compared the estimate of our MCC tree with that of previous published analyses on birds, and found a high correlation ($r=0.81$, [Figure S8](#)). Details of the BAMM results are presented in the supplementary materials.

There was a strong correlation between spectral measures of colour dichromatism and RGB values ($r = 0.79$; [Figure S10](#)) and a weaker correlation between sexual dichromatism and the sexual selection index ($r = 0.34$, [Figure S12](#)).

²⁴⁵ Effects of sexual dichromatism/selection on speciation are not dependent on
²⁴⁶ environmental variability

²⁴⁷ PGLS models with interaction terms between each measure of sexual dichromatism/selection and the five
²⁴⁸ measures of environmental variability (seasonal temperature variation, log-range size, long-term temperature
²⁴⁹ variation, spatial temperature variation, and NPP) were included in model selection. However, no interaction
²⁵⁰ terms were significant or present in the top models ($\delta \text{ AICc} > 4$) for any measure of speciation (λ_{DR} , λ_{ND} ,
²⁵¹ λ_{BAMM}) or sexual selection (RGB values, spectrophotometry and male-biased sexual selection; $\delta \text{ AICc}$
²⁵² > 4 ; [Table S5](#), [Table S6](#), [Table S10](#), [Table S13](#)). Thus we found no evidence that the effect of sexual
²⁵³ selection on speciation is dependent on our measures of environmental variation. Furthermore, we found no
²⁵⁴ evidence that these environmental factors (seasonal temperature variation, long-term temperature variation,
²⁵⁵ spatial temperature variation, and NPP) predict speciation independently from sexual dichromatism/selection
²⁵⁶ ([Figure 1](#), [Figure S11](#)).

²⁵⁷

²⁵⁸ No evidence that sexual dichromatism affects speciation

²⁵⁹ We found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation.
²⁶⁰ Using three response measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}), the effect of sexual dichromatism was not
²⁶¹ significant in any PGLS model based on tip-rate estimates and correlation structures from the MCC tree.
²⁶² Specifically, sexual dichromatism showed no association with λ_{DR} ($\beta = -1.279\text{e-}03$, $p = 0.147$; [Figure 1a](#),
²⁶³ [Figure 2a](#)) or λ_{ND} ($\beta = -5.745\text{e-}05$, $p = 0.078$; [Figure 1a](#)). Furthermore, speciation rates from BAMM
²⁶⁴ (λ_{BAMM}) were also unaffected by sexual dichromatism ($\beta = -1.429\text{e-}05$, $p = 0.872$; [Figure 1a](#)). PGLS analyses
²⁶⁵ using sexual dichromatism ($n = 581$) measured by spectrophotometry (Armenta et al. 2008) yielded results
²⁶⁶ concordant with the full dataset; *i.e.* no association between sexual dichromatism and speciation ([Figure S11](#)).
²⁶⁷ Our results from models based on the MCC tree are largely corroborated by model estimates from PGLS
²⁶⁸ analyses of the rates and correlation structures from 1,000 random trees (for λ_{DR} , λ_{ND}) and 100 random
²⁶⁹ trees for λ_{BAMM} . The HPD (highest posterior density) intervals show model estimates are distributed around
²⁷⁰ zero when using complete taxon sampling models and RGB measures of sexual dichromatism ([Figure 1a](#),
²⁷¹ [Table S8](#)). For PGLS models using spectrophotometry-based measures of sexual dichromatism, the estimates
²⁷² from the 100 trees in the λ_{DR} models are positively skewed (HPD Interval = $-1.780\text{e-}02$, $3.489\text{e-}02$) but
²⁷³ normally distributed around zero for λ_{ND} and λ_{BAMM} ([Table S12](#)).

²⁷⁴ Male-biased sexual selection increases speciation

²⁷⁵ We found a significant positive association between male-biased sexual selection ($n = 2,465$) and λ_{DR} ($\beta =$
²⁷⁶ $3.887\text{e-}02$, $p = 0.012$; [Figure 1b](#)). However, this association was not significant for the other two measures
²⁷⁷ of speciation rate (λ_{ND} : $\beta = 4.383\text{e-}04$, $p = 0.351$; λ_{BAMM} : $\beta = 9.423\text{e-}04$, $p = 0.764$; [Figure 1b](#)). The
²⁷⁸ distribution of estimates from PGLS models on 1,000 random trees was similar to the estimate from the
²⁷⁹ MCC tree: among the 1,000 trees there was a positive association between sexual selection and λ_{DR} (HPD
²⁸⁰ Interval = $4.513\text{e-}03$, $5.718\text{e-}02$), and a smaller positive association between sexual selection and λ_{ND} (HPD

281 Interval = -5.044e-04, 1.585e-03;) as well as the 100 models using λ_{BAMM} (HPD Interval = -1.295e-02,
282 3.088e-02). Complete HPD intervals for models using male-bias sexual selection PPCA as a predictor can be
283 found within [Table S15](#).

284 Species with smaller ranges have increased rates of speciation

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

298 Phylogenetic path analysis

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

305 Extinction rate

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

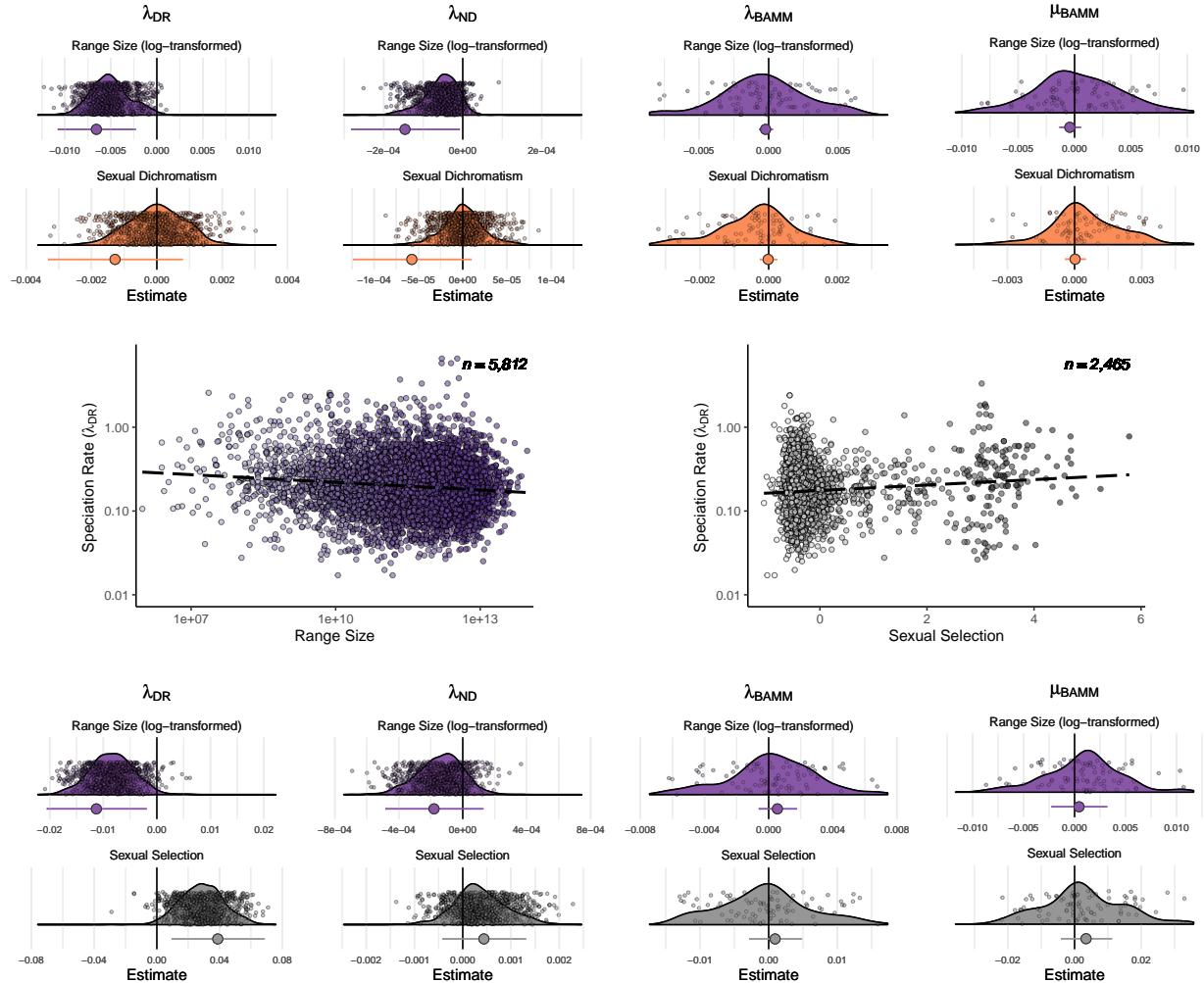


Figure 1: Model estimates (a) for the effect of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset ($n = 5,812$). (b) depicts the scatter plot of speciation rate (λ_{DR}) and log-range size with the model estimate presented as a dashed line. (c) shows the scatter plot of speciation rate (λ_{DR}) and male-biased sexual selection PPCA for a subsetted dataset ($n = 2,465$). Similar to (a), (d) presents Model estimates for PGLS analyses using a restricted dataset with measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one measure of extinction (μ_{BAMM}) as response variables. The numerical values for the model estimates using the MCC tree and HPD intervals of estimates from 1,000 random trees (for λ_{DR} and λ_{ND}) or 100 random trees for λ_{BAMM} and μ_{BAMM} can be found in the ESM. Density curves are based on model estimates from 1,000/100 trees and the circle below with error bars is the estimate and 95 % CIs from the MCC tree. For this figure we removed outliers from estimates coming from the 100 random trees for BAMM models in order to be able to visualise the MCC 95 % CIs.

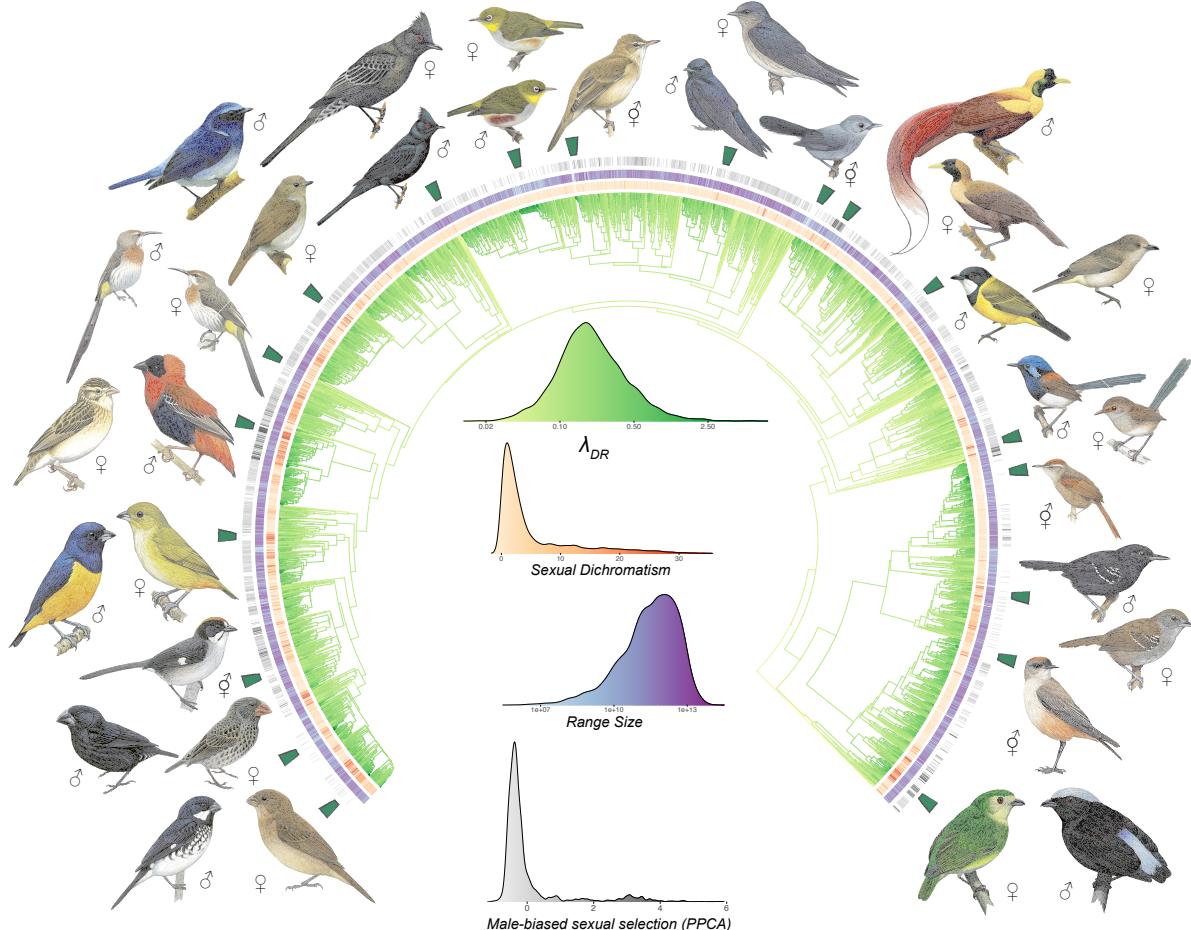


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism, range size available for 5,812 species and male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative association between λ_{DR} and log-range size as well as a significant positive association between λ_{DR} and male-biased sexual selection but no significant association between λ_{DR} and sexual dichromatism based on RGB measures. λ_{DR} are those from the MCC tree and images of birds are from the *Handbook of the Birds of the World*. Clockwise the species are: *Sporophila bouvronides*, *Geospiza magnirostris*, *Atlapetes leucopterus*, *Euphonia rufiventris*, *Euplectes franciscanus*, *Promerops gurneyi*, *Phainopepla nitens*, *Zosterops erythropleurus*, *Acrocephalus australis*, *Progne cryptoleuca*, *Mayrornis schistaceus*, *Paradisaea rubra*, *Pachycephala pectoralis*, *Malurus pulcherrimus*, *Cranioleuca curtata*, *Cercomacra manu*, *Muscisaxicola capistratus*, *Lepidothrix coeruleocapilla*. Edge colours for the terminal branch correspond to λ_{DR} but all precluding branches have been generated for graphical purposes using ancestral character state estimation and should not be interpreted.

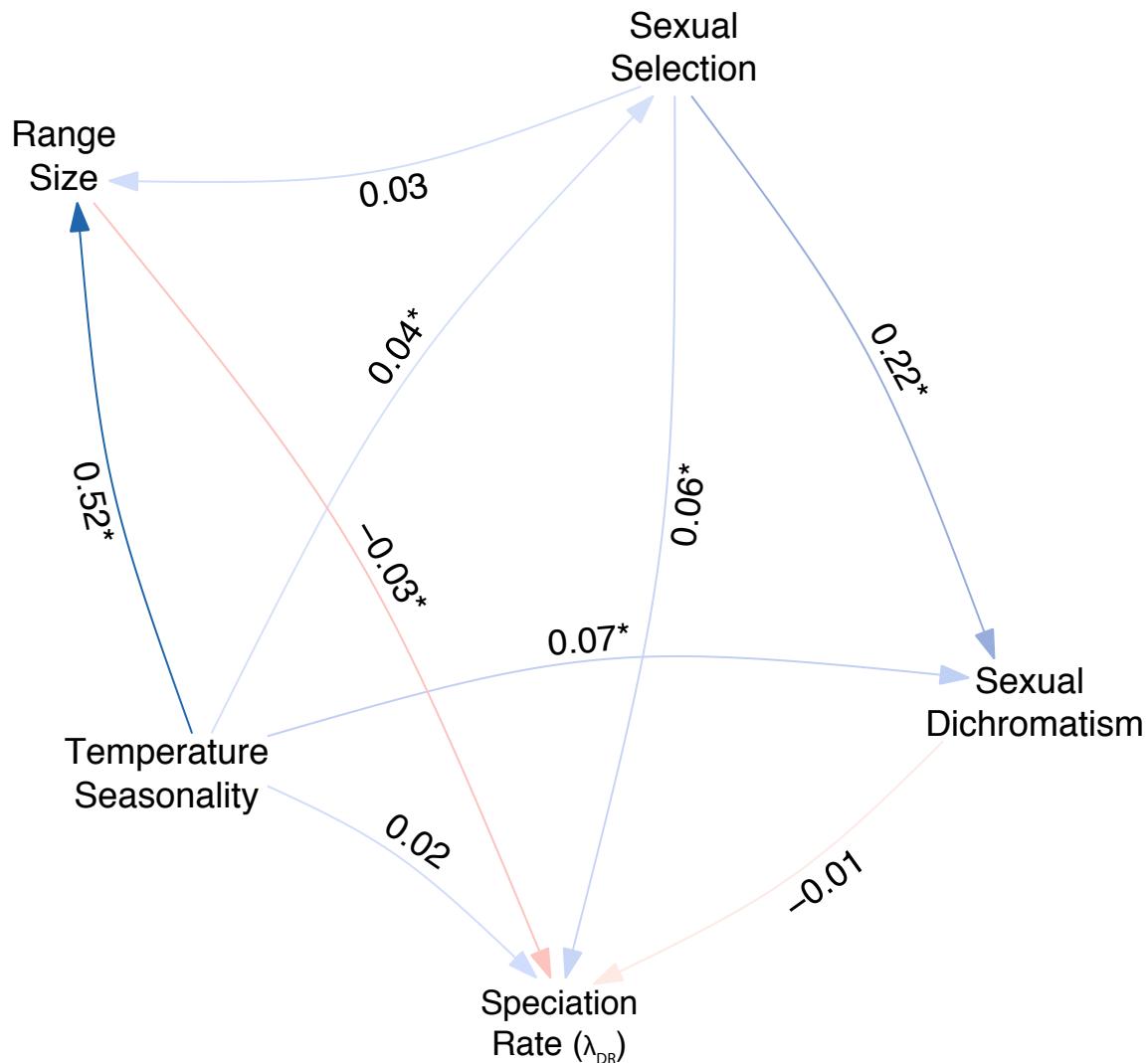


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with the direction of effect corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95 % confidence intervals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

310 DISCUSSION

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

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

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

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

383 One outcome of our analyses was the fact that different measures of speciation rates presented different results.
384 This is not completely unexpected, given that each of the rates is calculated in a different way (discussed in
385 detail in Title and Rabosky (2018)). For instance, λ_{DR} is weighted higher towards speciation events close to
386 the tips, and allows more rate heterogeneity compared to BAMM estimates (although increasing error rate).
387 The higher variation in λ_{DR} could explain why we detected a significant pattern using this metric and not
388 the other two. Moreover, it has been shown that the power of PGLS approaches is reduced compared to
389 other alternatives such as simulations (Harvey Michael et al. 2017), however given the complexity of our
390 model this was the most straight forward approach. This opens the possibility that the patterns detected
391 with λ_{DR} are also present in the other speciation metrics but there is not enough statistical power to detect
392 them (at least for λ_{BAMM}). We think it is unlikely that the significant correlation between λ_{DR} and sexual

393 selection is spurious given the limited power of the PGLS approach, the large heterogeneity in λ_{DR} values
394 and the consistency in the calculated estimates across the 1,000 trees.

395 In addition to speciation, sexual selection has frequently been invoked as a driver of extinction. Sexual
396 selection may increase extinction risk as it often leads individuals (usually males) to invest in exaggerated
397 mating signals as opposed to traits — such as parental care — that elevate offspring fitness (*reviewed in*
398 Kokko and Brooks 2003). Using the model-based approach of BAMM, we found no association between
399 extinction rate and sexual dichromatism, male-biased sexual selection or measures of environmental variability.
400 Extinction is notoriously difficult to estimate accurately from phylogenies, principally because many different
401 combinations of speciation and extinction rates can give rise to similar patterns of diversity (*see* Rabosky
402 2016). Phylogenetic methods such as BAMM allow for speciation and extinction rates to be estimated
403 using moderately-sized phylogenies, although the ability of BAMM to model evolutionary rate shifts and
404 extinction rates remains a subject of debate (*see*, Beaulieu and O'Meara 2015; Rabosky 2016; Moore et al.
405 2016; Rabosky et al. 2017). Additionally, while several tip-rate estimates exist for speciation rate (*e.g.*, λ_{DR}
406 and λ_{ND}), tip-rate estimates of extinction rate are difficult to obtain without complex Bayesian models and
407 are fraught with issues of sampling bias (Davis et al. 2013). Although extinction rates can be estimated from
408 alternative sources, such as the fossil record, documented recent extinctions and IUCN extinction threat
409 status, each approach has limitations. Across the passerine bird phylogeny, we found that BAMM often
410 produced homogeneous speciation and extinction rates for smaller clades showing few rate shifts, which might
411 reduce our power to detect small differences in extinction rates among closely-related taxa (Rabosky et al.
412 2017; Title and Rabosky 2018). Thus, this methodological constraint likely decreases our ability to accurately
413 measure the correlation between metrics of sexual selection and the probability of extinction.

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

425 REFERENCES

- 426 Agrawal, A. F. 2001. Sexual selection and the maintenance of sexual reproduction. *Nature* 411:692–695.
- 427 Armenta, J. K., P. O. Dunn, and L. A. Whittingham. 2008. Quantifying avian sexual dichromatism: A
428 comparison of methods. *Journal of Experimental Biology* 211:2423.
- 429 Barraclough, T. G., P. H. Harvey, and S. Nee. 1995. Sexual selection and taxonomic diversity in passerine
430 birds. *Proceedings of the Royal Society B-Biological Sciences* 259:211–215.
- 431 Bartoń, K. 2017. MuMIn: Multi-model inference.
- 432 Beaulieu, J. M., and B. C. O'Meara. 2015. Extinction can be estimated from moderately sized molecular
433 phylogenies. *Evolution* 69:1036–1043.
- 434 Belmaker, J., and W. Jetz. 2015. Relative roles of ecological and energetic constraints, diversification rates
435 and region history on global species richness gradients. *Ecology Letters* 18:563–571.
- 436 Berger, D., K. Grieshop, M. I. Lind, J. Goenaga, A. A. Maklakov, and G. Arnqvist. 2014. Intralocus sexual
437 conflict and environmental stress. *Evolution* 68:2184–2196.
- 438 Bijl, W. van der. 2018. *Phylopath*: Easy phylogenetic path analysis in R. *PeerJ* 6:e4718.
- 439 Birand, A., A. Vose, and S. Gavrilets. 2012. Patterns of species ranges, speciation, and extinction. *The
440 American Naturalist* 179:1–21.
- 441 BirdLife International and Handbook of the Birds of the World. 2017. Bird species distribution maps of the
442 world. <http://datazone.birdlife.org/species/requestdis>.
- 443 Bonduriansky, R. 2011. Sexual selection and conflict as engines of ecological diversification. *The American
444 Naturalist* 178:729–745.
- 445 Bonduriansky, R., and S. F. Chenoweth. 2009. Intralocus sexual conflict. *Trends in Ecology & Evolution*
446 24:280–8.
- 447 Boughman, J. W. 2002. How sensory drive can promote speciation. *Trends in Ecology & Evolution* 17:571–577.
- 448 Cally, J. G., D. Stuart-Fox, and L. Holman. 2019. Meta-analytic evidence that sexual selection improves
449 population fitness. *Nature communications* 10:2017. Nature Publishing Group.
- 450 Candolin, U., and J. Heuschele. 2008. Is sexual selection beneficial during adaptation to environmental
451 change? *Trends in Ecology & Evolution* 23:446–452.
- 452 Castiglione, S., A. Mondanaro, M. Melchionna, C. Serio, M. Di Febbraro, F. Carotenuto, and P. Raia. 2017.
453 Diversification rates and the evolution of species range size frequency distribution. *Frontiers in Ecology and
454 Evolution* 5:147. Frontiers.
- 455 Charge, R., C. Teplitsky, G. Sorci, and M. Low. 2014. Can sexual selection theory inform genetic management
456 of captive populations? A review. *Evolutionary Applications* 7:1120–1133.
- 457 Claramunt, S., E. P. Derryberry, J. V. Remsen, and R. T. Brumfield. 2012. High dispersal ability inhibits
458 speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*
459 279:1567.

- 460 Connallon, T., and M. D. Hall. 2016. Genetic correlations and sex-specific adaptation in changing environments. 70:2198.
- 462 Cooney, C. R., H. E. A. MacGregor, N. Seddon, and J. A. Tobias. 2018. Multi-modal signal evolution in birds: Re-examining a standard proxy for sexual selection. Proceedings of the Royal Society of London B: Biological Sciences 285.
- 465 Cooney, C. R., J. A. Tobias, J. T. Weir, C. A. Botero, and N. Seddon. 2017. Sexual selection, speciation and constraints on geographical range overlap in birds. Ecology Letters 20:863–871.
- 467 Dale, J., C. J. Dey, K. Delhey, B. Kempenaers, and M. Valcu. 2015. The effects of life history and sexual selection on male and female plumage colouration. Nature 527:367–370.
- 469 Darwin, C. 1871. The descent of man and selection in relation to sex. 1st ed. John Murray, London.
- 470 Davis, M. P., P. E. Midford, and W. Maddison. 2013. Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. BMC Evolutionary Biology 13:38.
- 472 Del Hoyo, J., A. Elliott, and D. Christie. 2011. Handbook of the birds of the world. Lynx Edicions 2003–2011.
- 473 Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.
- 475 Fromhage, L., and M. D. Jennions. 2016. Coevolution of parental investment and sexually selected traits drives sex-role divergence. Nature Communications 7:12517.
- 477 Hackett, S. J., R. T. Kimball, S. Reddy, R. C. K. Bowie, E. L. Braun, M. J. Braun, J. L. Chojnowski, W. A. Cox, K.-L. Han, J. Harshman, C. J. Huddleston, B. D. Marks, K. J. Miglia, W. S. Moore, F. H. Sheldon, D. W. Steadman, C. C. Witt, and T. Yuri. 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320:1763–1768.
- 481 Harris, G., and S. L. Pimm. 2008. Range size and extinction risk in forest birds. Conservation Biology 22:163–171.
- 483 Harvey, M. G., G. F. Seeholzer, B. T. Smith, D. L. Rabosky, A. M. Cuervo, and R. T. Brumfield. 2017. Positive association between population genetic differentiation and speciation rates in new world birds. Proceedings of the National Academy of Sciences 114:6328–6333.
- 486 Harvey Michael, G., L. Rabosky Daniel, and N. Cooper. 2017. Continuous traits and speciation rates: Alternatives to state-dependent diversification models. Methods in Ecology and Evolution 9:984–993.
- 488 Holman, L., and H. Kokko. 2013. The consequences of polyandry for population viability, extinction risk and conservation. Philosophical Transactions of the Royal Society B-Biological Sciences 368.
- 490 Hoyo, J. del, and N. J. Collar. 2016. HBW and birdlife international illustrated checklist of the birds of the world. Lynx Edicions; BirdLife International.
- 492 Huang, H. T., and D. L. Rabosky. 2014. Sexual selection and diversification: Reexamining the correlation between dichromatism and speciation rate in birds. The American Naturalist 184:E101–E114.
- 494 Huber, S. K., L. F. De Leon, A. P. Hendry, E. Bermingham, and J. Podos. 2007. Reproductive isolation of sympatric morphs in a population of darwin's finches. Proceedings of the Royal Society of London B: Biological Sciences 274:1709–1714.

- 497 Jablonski, D., and K. Roy. 2003. Geographical range and speciation in fossil and living molluscs. *Proceedings*
498 of the Royal Society of London. Series B: Biological Sciences 270:401–406. The Royal Society.
- 499 Janicke, T., I. K. Häderer, M. J. Lajeunesse, and N. Anthes. 2016. Darwinian sex roles confirmed across the
500 animal kingdom. *Science Advances* 2:e1500983.
- 501 Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in
502 space and time. *Nature* 491:444–448.
- 503 Kokko, H., and R. Brooks. 2003. Sexy to die for? Sexual selection and the risk of extinction. *Annales*
504 *Zoologici Fennici* 40:207–219.
- 505 Kokko, H., and M. D. Jennions. 2008. Parental investment, sexual selection and sex ratios. *Journal of*
506 *Evolutionary Biology* 21:919–948.
- 507 Kokko, H., and D. J. Rankin. 2006. Lonely hearts or sex in the city? Density-dependent effects in mating
508 systems. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361:319–334.
- 509 Kottler, M. J. 1980. Darwin, Wallace, and the origin of sexual dimorphism. *Proceedings of the American*
510 *Philosophical Society* 124:203–226.
- 511 Kraaijeveld, K., F. J. L. Kraaijeveld-Smit, and M. E. Maan. 2011. Sexual selection and speciation: The
512 comparative evidence revisited. *Biological Reviews* 86:367–377.
- 513 Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National*
514 *Academy of Sciences* 78:3721–3725.
- 515 Lande, R. 1982. Rapid origin of sexual isolation and character divergence in a cline. *Evolution* 36:213–223.
- 516 Long, T. A. F., A. F. Agrawal, and L. Rowe. 2012. The effect of sexual selection on offspring fitness depends
517 on the nature of genetic variation. *Current Biology* 22:204–208.
- 518 Lorch, P. D., S. Proulx, L. Rowe, and T. Day. 2003. Condition-dependent sexual selection can accelerate
519 adaptation. *Evolutionary Ecology Research* 5:867–881.
- 520 Maan, M. E., and O. Seehausen. 2011. Ecology, sexual selection and speciation. *Ecology Letters* 14:591–602.
- 521 Martinossi-Allibert, I., U. Savković, M. Đorđević, G. Arnqvist, B. Stojković, and D. Berger. 2017. The
522 consequences of sexual selection in well-adapted and maladapted populations of bean beetles. *Evolution*
523 72:518–530.
- 524 Medina, I., K. Delhey, A. Peters, K. E. Cain, M. L. Hall, R. A. Mulder, and N. E. Langmore. 2017. Habitat
525 structure is linked to the evolution of plumage colour in female, but not male, fairy-wrens. *BMC evolutionary*
526 *biology* 17:35.
- 527 Miles, M. C., and M. J. Fuxjager. 2018. Synergistic selection regimens drive the evolution of display
528 complexity in birds of paradise. *Journal of Animal Ecology* 87:1149–1159.
- 529 Moore, B. R., S. Hohna, M. R. May, B. Rannala, and J. P. Huelsenbeck. 2016. Critically evaluating the
530 theory and performance of bayesian analysis of macroevolutionary mixtures. *Proceedings of the National*
531 *Academy of Sciences* 113:9569–9574.

- 532 Morrow, E. H., T. E. Pitcher, and G. Arnqvist. 2003. No evidence that sexual selection is an 'engine of
533 speciation' in birds. *Ecology Letters* 6:228–234.
- 534 Otto-Bliesner, B. L., S. J. Marshall, J. T. Overpeck, G. H. Miller, A. Hu, and. 2006. Simulating arctic
535 climate warmth and icefield retreat in the last interglaciation. *Science* 311:1751–1753.
- 536 Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: Body size, life history,
537 sexual selection or ecology? *Proceedings of the Royal Society B-Biological Sciences* 266:933–939.
- 538 Pagel, M. 1999. Inferring the historical patterns of biological evolution. *Nature* 401:877.
- 539 Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of phylogenetics and evolution in R language.
540 *Bioinformatics* 20:289–290.
- 541 Pennell, T. M., and E. H. Morrow. 2013. Two sexes, one genome: The evolutionary dynamics of intralocus
542 sexual conflict. *Ecology and Evolution* 3:1819–1834.
- 543 Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2018. nlme: Linear and nonlinear mixed
544 effects models.
- 545 Pischedda, A., and A. K. Chippindale. 2006. Intralocus sexual conflict diminishes the benefits of sexual
546 selection. *PLOS Biology* 4:e356.
- 547 Price, J. J., and M. D. Eaton. 2014. Reconstructing the evolution of sexual dichromatism: Current color
548 diversity does not reflect past rates of male and female change. *Evolution* 68:2026–2037.
- 549 Pryke, S. R., S. Andersson, and M. J. Lawes. 2001. Sexual selection of multiple handicaps in the red-collared
550 widowbird: Female choice of tail length but not carotenoid display. *Evolution* 55:1452–1463.
- 551 Quintero, I., and W. Jetz. 2018. Global elevational diversity and diversification of birds. *Nature* 555:246.
- 552 Rabosky, D., M. Grundler, C. Anderson, P. Title, J. Shi, J. Brown, H. Huang, and J. Larson. 2014.
553 BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in
554 Ecology and Evolution* 5:701–707.
- 555 Rabosky, D. L. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on
556 phylogenetic trees. *PLOS ONE* 9:e89543.
- 557 Rabosky, D. L. 2016. Challenges in the estimation of extinction from molecular phylogenies: A response to
558 Beaulieu and O'Meara. *Evolution* 70:218–228.
- 559 Rabosky, D. L., J. Chang, P. O. Title, P. F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T. J.
560 Near, M. Coll, and others. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*
561 559:392.
- 562 Rabosky, D. L., J. S. Mitchell, and J. Chang. 2017. Is BAMM flawed? Theoretical and practical concerns in
563 the analysis of multi-rate diversification models. *Systematic biology* 66:477–498.
- 564 Radwan, J., L. Engqvist, and K. Reinhold. 2016. A paradox of genetic variance in epigamic traits: Beyond
565 "good genes" view of sexual selection. *Evolutionary Biology* 43:267–275.
- 566 Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press.

- 567 Safran, R. J., E. S. Scordato, L. B. Symes, R. L. Rodri'guez, and T. C. Mendelson. 2013. Contributions of
568 natural and sexual selection to the evolution of premating reproductive isolation: A research agenda. Trends
569 in Ecology & Evolution 28:643–650.
- 570 Seddon, N., C. A. Botero, J. A. Tobias, P. O. Dunn, H. E. A. MacGregor, D. R. Rubenstein, J. A. C. Uy, J.
571 T. Weir, L. A. Whittingham, and R. J. Safran. 2013. Sexual selection accelerates signal evolution during
572 speciation in birds. Proceedings of the Royal Society B: Biological Sciences 280.
- 573 Seddon, N., R. M. Merrill, and J. A. Tobias. 2008. Sexually selected traits predict patterns of species richness
574 in a diverse clade of suboscine birds. The American Naturalist 171:620–631.
- 575 Servedio, M. R., G. S. V. Doorn, M. Kopp, A. M. Frame, and P. Nosil. 2011. Magic traits in speciation:
576 “Magic” but not rare? Trends in Ecology & Evolution 26:389–397.
- 577 Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. The
578 Quarterly Review of Biology 64:419–461.
- 579 Siller, S. 2001. Sexual selection and the maintenance of sex. Nature 411:689.
- 580 Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution 38:622–630.
- 581 Title, P. O., and D. L. Rabosky. 2018. Diversification rates and phylogenies: What are we estimating, and
582 how good are the estimates? bioRxiv 369124.
- 583 Uy, J. A. C., and G. Borgia. 2000. Sexual selection drives rapid divergence in bowerbird display traits.
584 Evolution 54:273–278.
- 585 Wallace, A. R. 1889. Colours and ornaments characteristic of sex. *in* Darwinism, an exponent of the theory
586 of natural selection, with some of its applications. Macmillan; Company.
- 587 Weaver, R. J., E. S. Santos, A. M. Tucker, A. E. Wilson, and G. E. Hill. 2018. Carotenoid metabolism
588 strengthens the link between feather coloration and individual quality. Nature Communications 9:73.
- 589 Weir, J. T., and T. D. Price. 2011. Limits to speciation inferred from times to secondary sympatry and ages
590 of hybridizing species along a latitudinal gradient. The American Naturalist 177:462–469.
- 591 Whitlock, M. C. 2000. Fixation of new alleles and the extinction of small populations: Drift load, beneficial
592 alleles, and sexual selection. Evolution 54:1855–1861.
- 593 Whitlock, M. C., and A. F. Agrawal. 2009. Purging the genome with sexual selection: Reducing mutation
594 load through selection on males. Evolution 63:569–582.
- 595 Zhao, M., F. A. Heinsch, R. R. Nemani, and S. W. Running. 2005. Improvements of the modis terrestrial
596 gross and net primary production global data set. Remote Sensing of Environment 95:164–176.