

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

3 Justin G. Cally*§, Devi Stuart-Fox§, Luke Holman§ and Iliana Medina Guzmán§

**justin.g.cally@gmail.com*

4 Abstract

5 Sexual selection is thought to shape phylogenetic diversity by affecting speciation or extinction rates.
6 However, the net effect of sexual selection on diversification is hard to predict *a priori*, because many
7 of the hypothesised effects on speciation or extinction have opposing signs and uncertain magnitudes.
8 Here, we test whether the strength of sexual selection predicts variation in speciation and extinction
9 rates across passerine birds (up to 5,812 species, covering most genera). We tested for associations
10 between two measures of sexual selection (sexual dichromatism, plus an index that captures variance in
11 sexual size dimorphism, polygyny, and male parental care), several environmental variables, and multiple
12 measures of speciation and extinction rates. Our results show that male-biased sexual selection, but
13 not sexual dichromatism, predicts speciation rates (λ_{DR}) in passerines, and found no evidence that
14 this relationship varies with the environment. We also found a strong negative relationship between
15 range size and speciation rate. There was no correlation between sexual selection and extinction rate
16 XXXXXX. Our findings support the view that sexual selection is a potent evolutionary force that has
17 shaped diversification in songbirds.

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

§School of BioSciences, The University of Melbourne, Victoria, Australia.

19 INTRODUCTION

20 Sexual selection results from competition between same-sex individuals for mates, their gametes, or associated
21 resources, and in most species it predominantly operates on males (Kokko and Jennions 2008; Fromhage
22 and Jennions 2016; Janicke et al. 2016). There is long-standing interest in the relationship between sexual
23 selection and the processes of speciation, extinction, and phylogenetic diversification (e.g. Lande 1981, 1982;
24 West-Eberhard 1983; Seddon et al. 2008; Cooney et al. 2018). Recent empirical and methodological advances,
25 such as growing evidence that sexual selection can profoundly affect many traits (e.g. life history, body mass,
26 and immunocompetence; Cally et al. 2019), larger and more accurate phylogenies (Jetz et al. 2012), and
27 new phylogenetic methods (**REFERENCES**), present new opportunities to test whether and how sexual
28 selection drives diversification.

29 Several hypotheses predict a positive relationship across species between the strength of sexual selection
30 and the rate of speciation and/or extinction. For example, sexual selection is involved in reinforcement, a
31 speciation-promoting process in which members of different phylogenetic lineages evolve to avoid unproductive
32 inter-lineage mating/fertilisation (**REF**). Additionally, sexual selection often operates on traits that can
33 create reproductive isolation when they diverge between lineages, such as signals and preferences involved in
34 mate selection (Lande 1981, 1982; Safran et al. 2013), sperm-egg interactions (Swanson and Vacquier 1998),
35 or genital morphology (Sloan and Simmons 2019). Furthermore, sexual selection has been hypothesised to
36 increase diversification by maintaining trait combinations that would be selected out under pure natural
37 selection (Bonduriansky 2011; Radwan et al. 2016), and by helping to prevent extinction by purging
38 deleterious mutations (Whitlock and Agrawal 2009), fixing beneficial ones (Whitlock 2000), and accelerating
39 adaptation in environments (Lorch et al. 2003; Candolin and Heuschele 2008; Cally et al. 2019). Also, sexual
40 selection sometimes favours individuals with rare phenotypes (Holman et al. 2013), providing a source of
41 diversifying selection that might increase the rate at which isolated populations diverge genetically.

42 Conversely, there are multiple ways in which sexual selection might hinder speciation or make extinction more
43 likely. Firstly, sexual selection might promote extinction by favouring traits that improve mating success
44 but reduce population fitness. For example, species with expensive sexual signals may be less resilient to
45 environmental change (Kokko and Brooks 2003), and sexual selection often creates a ‘tragedy of the commons’
46 by selecting for traits that increase the reproductive success of individuals while reducing population-wide
47 productivity (e.g. infanticide, harassment, and reduced parental care by mate-seeking males; Rankin et al.
48 2011; Kokko and Jennions 2008; Holman and Kokko 2013; Fromhage and Jennions 2016). Sexual selection
49 might also promote extinction by causing maladaptation (‘gender load’) in female traits that are genetically
50 correlated with sexually-selected male traits (Pischedda and Chippindale 2006; Bonduriansky and Chenoweth
51 2009; Harano et al. 2010; Pennell and Morrow 2013; Berger et al. 2014). Secondly, sexual selection might
52 promote evolutionary stasis by ensuring that individuals with novel trait values have low mating success.

53 Importantly, the relationship between sexual selection and diversification might be contingent on the
54 environment. Theoretical work predicts that sexual selection should have a more positive effect on adaptation
55 and population fitness in variable environments relative to stable ones (e.g. Long et al. 2012; Connallon and
56 Hall 2016), though the empirical evidence for this theory is mixed and largely limited to insects (Cally et
57 al. 2019). The mechanism underpinning this prediction is that the environment and the selective history of
58 the population should influence the relative amounts of genetic variation at sexually concordant loci (*i.e.*

59 loci where the same allele is fittest for both sexes) and sexually antagonistic loci (where different alleles are
60 favoured in each sex). In stable environments, variation is thought to be preferentially depleted at sexually
61 concordant loci, leading to stronger gender load and reduced net benefits of sexual selection (e.g. Connallon
62 and Hall 2016), and potentially to a more negative relationship between sexual selection and diversification
63 rates across species. Conversely, sexual selection might be especially important at promoting local adaptation
64 when the environment displays variability at the relevant spatial and temporal scales (e.g. Boughman 2002;
65 Lorch et al. 2003; Kokko and Heubel 2008; Maan and Seehausen 2011)

66 Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification (e.g.
67 Barraclough et al. 1995; Morrow et al. 2003; Seddon et al. 2008, 2013; Huang and Rabosky 2014). Birds are
68 well-suited for this purpose due to their diverse and well-characterised mating systems and sexually-selected
69 traits, and because their phylogenetic relationships are comparatively well-known. A 2011 meta-analysis
70 covering 20 primary studies of birds and other taxa found a small but significant positive association between
71 sexual selection and speciation, with the average effect size in birds stronger than in mammals but weaker than
72 in insects or fish (Kraaijeveld et al. 2011). However, there was large variation in effect size estimates across
73 the 20 studies, likely reflecting differences in methodology, such as metrics used to characterise speciation and
74 sexual selection, in addition to true biological differences. More recently, Huang and Rabosky (2014) found no
75 association between sexual dichromatism and speciation ($n = 918$ species) in a study using spectrophotometric
76 measurements of museum specimens (Armenta et al. 2008) and tip-rate estimates from a molecular-only
77 phylogeny (Jetz et al. 2012). Similarly, Cooney et al. (2017) found no effect of sexual dichromatism on
78 diversification across 1,306 pairs of species, using dichromatism scores provided by human observers.

79 Here, we investigate the association between sexual selection and diversification in birds while building upon
80 previous approaches in multiple ways. We use two measures of the strength of sexual selection: sexual
81 dichromatism ($n = 5,812$ species; estimated from illustrations by Dale et al. 2015), as well as an index of
82 male-biased sexual selection ($n = 2,465$ species; derived via principal components analysis by Dale et al. 2015),
83 which captures (co)variation in sexual size dimorphism, social polygyny and paternal care. Most **OR ALL??**
84 earlier macroevolutionary studies of this topic only quantified sexual selection using dichromatism, which
85 is problematic since dichromatism does not always signal the presence of strong sexual selection and *vice*
86 *versa* (Dale et al. 2015). For example, male and female dunnocks (*Prunella modularis*) are similarly coloured
87 yet sexual selection appears to be strong (Davies and Houston 1986). Furthermore, a recent comparative
88 study found a negative relationship between dichromatism and another sexually-selected trait (song) across
89 species, suggesting that a multi-trait focus would improve estimates of sexual selection intensity (Cooney et al.
90 2018). Additionally, our analysis includes multiple ecological and environmental variables on diversification,
91 allowing us to adjust for potential confounds, to identify environmental factors driving diversification, and
92 to test whether environmental factors interact with sexual selection as theory predicts (Connallon and Hall
93 2016). We use multiple approaches for quantifying speciation and extinction rates at the tips of phylogenetic
94 trees, including BAMM (Bayesian Analysis of Macroevolutionary Mixtures; *see*, Beaulieu and O'Meara 2015;
95 Rabosky 2016; Moore et al. 2016; Rabosky et al. 2017), as well as older but reliable tip-rate statistics, such
96 as diversification rate (λ_{DR}) and node density (λ_{ND}). Finally, we incorporate phylogenetic uncertainty into
97 our analyses, improving over earlier work which assumed the statistically best-fitting phylogeny is correct.

98 RESULTS

99 Variability across phylogenetic trees and speciation rate measures

100 [Is it possible to move this later in the Results? It's possibly not ideal to start by highlighting
101 the dependence of our conclusions on the methods we choose, and not mentioning our main
102 non-null finding regarding the SS index. Having said that I can see a case for leaving it here
103 too. - Luke]

104 We first estimated speciation rates across the phylogeny, using the maximum clade credibility (MCC) tree, as
105 well as 100 or 1000 trees sampled from the posterior distribution of trees in Jetz et al. (2012). Estimates
106 of speciation rates varied between phylogenetic trees, especially for rates calculated by BAMM (λ_{BAMM})
107 and μ_{BAMM}), where the 95% highest posterior density (HPD) interval across 100 trees was >20-fold larger
108 than the **95% confidence interval [SHOULD THIS BE HPD TOO?]** calculated for the MCC tree.
109 Conversely, for our estimates of diversification rate (λ_{DR}) and node density (λ_{ND}), the 95% HPD interval
110 across 1,000 trees was near-identical to the 95% confidence interval calculated for the MCC tree (Table S9).
111 Given the computational requirements of BAMM, the great majority of earlier studies have based their
112 estimates on a single consensus tree, and so the inconsistency of the BAMM estimates between different
113 phylogenies with similar statistical support is notable. Mean measures of speciation rate across 100 trees
114 were positively correlated between measures (DR - BAMM: $r=0.75$, DR - ND: $r=0.65$, ND- BAMM: $r=0.51$;
115 Figure S15). Given that the calculation of BAMM rates can be affected by the settings of the run and the
116 use of different priors, we compared the estimate of our MCC tree with that of previous published analyses
117 on birds, and found a high correlation ($r=0.81$, Figure S8). Full details of the BAMM results are presented
118 as supplementary materials.

119 No evidence that the relationship between sexual selection and speciation
120 depends on environmental variability

121 [I think this part should go after the next 2 sections, as it's a more confusing being about
122 interactions, and we should preserve the order of ideas from the Abstract and Intro. - Luke]

123 We next fit Phylogenetic Generalized Least Squares (PGLS) models with **2-way [CORRECT?]** interaction
124 terms between each measure of sexual dichromatism/selection and the five measures of environmental variability
125 (seasonal temperature variation, log-range size, long-term temperature variation, spatial temperature variation,
126 and NPP) and compared them using AICc model selection. However, no interaction terms were present in
127 the top models (δ AICc > 4) for any measure of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) or sexual selection (RGB
128 values, spectrophotometry and male-biased sexual selection; δ AICc > 4 ; Table S5, Table S6, Table S10,
129 Table S13). Thus we found no evidence that the effect of sexual selection on speciation is dependent on our
130 measures of environmental variation. Furthermore, we found no evidence that these environmental factors
131 (seasonal temperature variation, long-term temperature variation, spatial temperature variation, and NPP)
132 predict speciation independently from sexual dichromatism/selection (Figure 1, Figure S11).

133

134 No evidence that sexual dichromatism affects speciation

135 We found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation.
136 Using three different measures of speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) as the response variable, the effect of
137 sexual dichromatism was not significant in any PGLS model based on tip-rate estimates and correlation
138 structures from the MCC tree. Specifically, sexual dichromatism showed no association with λ_{DR} ($\beta =$
139 $-1.279e-03$, $p = 0.147$; [Figure 1a](#), [Figure 2a](#)) or λ_{ND} ($\beta = -5.745e-05$, $p = 0.078$; [Figure 1a](#)). Furthermore,
140 speciation rates from BAMM (λ_{BAMM}) were also unaffected by sexual dichromatism ($\beta = -1.429e-05$, $p =$
141 0.872 ; [Figure 1a](#)). PGLS analyses using sexual dichromatism ($n = 581$) measured by spectrophotometry
142 (Armenta et al. 2008) yielded results concordant with the full dataset; *i.e.* no association between sexual
143 dichromatism and speciation ([Figure S11](#)). Our results from models based on the MCC tree are largely
144 corroborated by model estimates from PGLS analyses of the rates and correlation structures from 1,000 trees
145 (for λ_{DR} , λ_{ND}) and 100 trees for λ_{BAMM} . The HPD intervals show model estimates are distributed around
146 zero when using complete taxon sampling models and RGB measures of sexual dichromatism ([Figure 1a](#),
147 [Table S8](#)). For PGLS models using spectrophotometry-based measures of sexual dichromatism, the estimates
148 from the 100 trees in the λ_{DR} models are positively skewed (HPD Interval = $-1.780e-02$, $3.489e-02$) but
149 normally distributed around zero for λ_{ND} and λ_{BAMM} ([Table S12](#)).

150 Male-biased sexual selection increases speciation rate

151 We found a significant positive association between male-biased sexual selection ($n = 2,465$) and λ_{DR} for
152 the MCC tree ($\beta = 3.887e-02$, $p = 0.012$; [Figure 1b](#)). However, this association was not significant for the
153 other two measures of speciation rate (λ_{ND} : $\beta = 4.383e-04$, $p = 0.351$; λ_{BAMM} : $\beta = 9.423e-04$, $p = 0.764$;
154 [Figure 1b](#)). The distribution of estimates from PGLS models on 1,000 trees was similar to the estimate from
155 the MCC tree: among the 1,000 trees there was a positive association between sexual selection and λ_{DR}
156 (HPD Interval = $4.513e-03$, $5.718e-02$), and a smaller positive association between sexual selection and λ_{ND}
157 (HPD Interval = $-5.044e-04$, $1.585e-03$;) as well as the 100 models using λ_{BAMM} (HPD Interval = $-1.295e-02$,
158 $3.088e-02$). Complete HPD intervals for models using male-bias sexual selection PPCA as a predictor can be
159 found within [Table S15](#).

160 Species with smaller ranges have increased rates of speciation

161 Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation, we found a negative association between range size and
162 speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This negative
163 association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.579e-03$, $p = 0.001$; λ_{ND} :
164 $\beta = -1.462e-04$, $p = 0.034$; [Figure 1a](#), [Figure 2](#)). This association was also evident across the estimates from
165 models using the 1,000 trees (λ_{DR} : HPD Interval = $-8.871e-03$, $-6.610e-04$; λ_{ND} : HPD Interval = $-1.514e-04$,
166 $1.724e-05$; [Figure 1a](#)). Subset models with reduced sample size and different measures of sexual selection —
167 but the same measure of range size — showed equivocal evidence that range size is negatively associated
168 with speciation. Range size significantly predicted λ_{DR} ([Figure 1b](#)) using data subset for male-biased sexual
169 selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} . Models using data subset for spectrophotometry-based
170 dichromatism ($n = 581$) gave non-significant estimates for the effect of range size on all measures of speciation

¹⁷¹ (Figure S11, Table S11, Table S12). Because the range size dataset is the same across the three data subsets
¹⁷² we draw our conclusions from the models with the highest power using near-complete taxon sampling ($n =$
¹⁷³ 5,812).

¹⁷⁴ Phylogenetic path analysis

¹⁷⁵ Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
¹⁷⁶ (Figure 3; Figure S14). There was a modest effect of male-biased sexual selection on sexual dimorphism (β
¹⁷⁷ = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism ($\beta = 0.07$) and strongly
¹⁷⁸ affected range size ($\beta = 0.52$). This suggests an indirect effect of temperature seasonality on λ_{DR} ($\beta_{indirect} =$
¹⁷⁹ -0.02; Figure 3), given the negative association we identified between λ_{DR} and range size in PGLS models.

¹⁸⁰ Extinction rate

¹⁸¹ We found no evidence that extinction (μ_{BAMM}) was impacted by the extent of sexual dichromatism for
¹⁸² full-taxon sampling ($\beta = 2.385\text{e-}05$, $p = 0.93$; Figure 1a), nor spectrophotometry-based measures of sexual
¹⁸³ dichromatism (Figure S11, Table S11, Table S12) or male-biased sexual selection (Figure 1b, Table S14, Table
¹⁸⁴ S15).

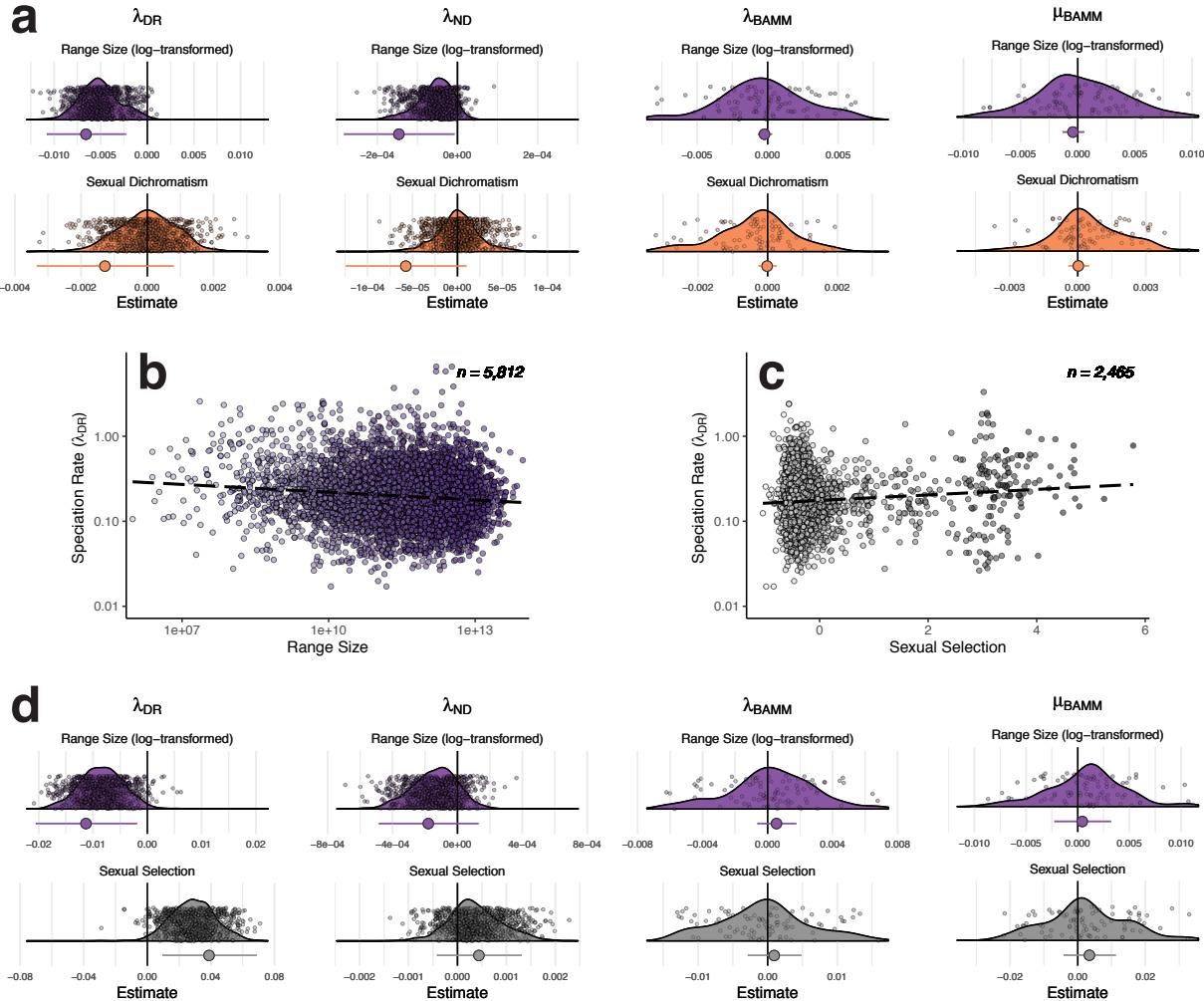


Figure 1: Model estimates (a) for the effect of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset (RGB values, $n = 5,812$). (b) depicts the scatter plot of speciation rate (λ_{DR}) and log-range size with the model estimate presented as a dashed line. (c) shows the scatter plot of speciation rate (λ_{DR}) and male-biased sexual selection ($n = 2,465$). Similar to (a), (d) presents model estimates for PGLS analyses using a restricted dataset with measures of male-biased sexual selection ($n = 2,465$) and shows the effect of log-range size and male-biased sexual selection on speciation and extinction rates. 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 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.

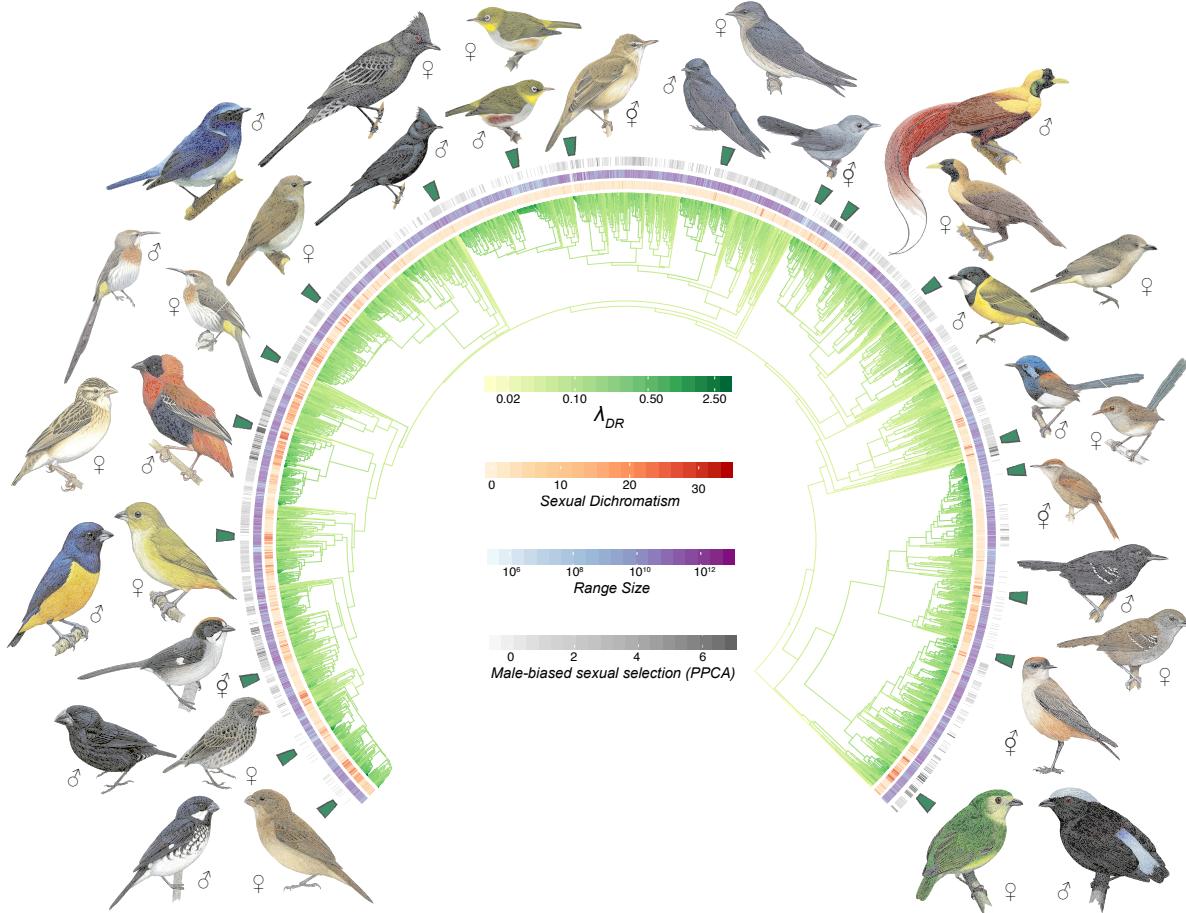


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism, range size available for 5,812 species and male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative association between λ_{DR} 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.

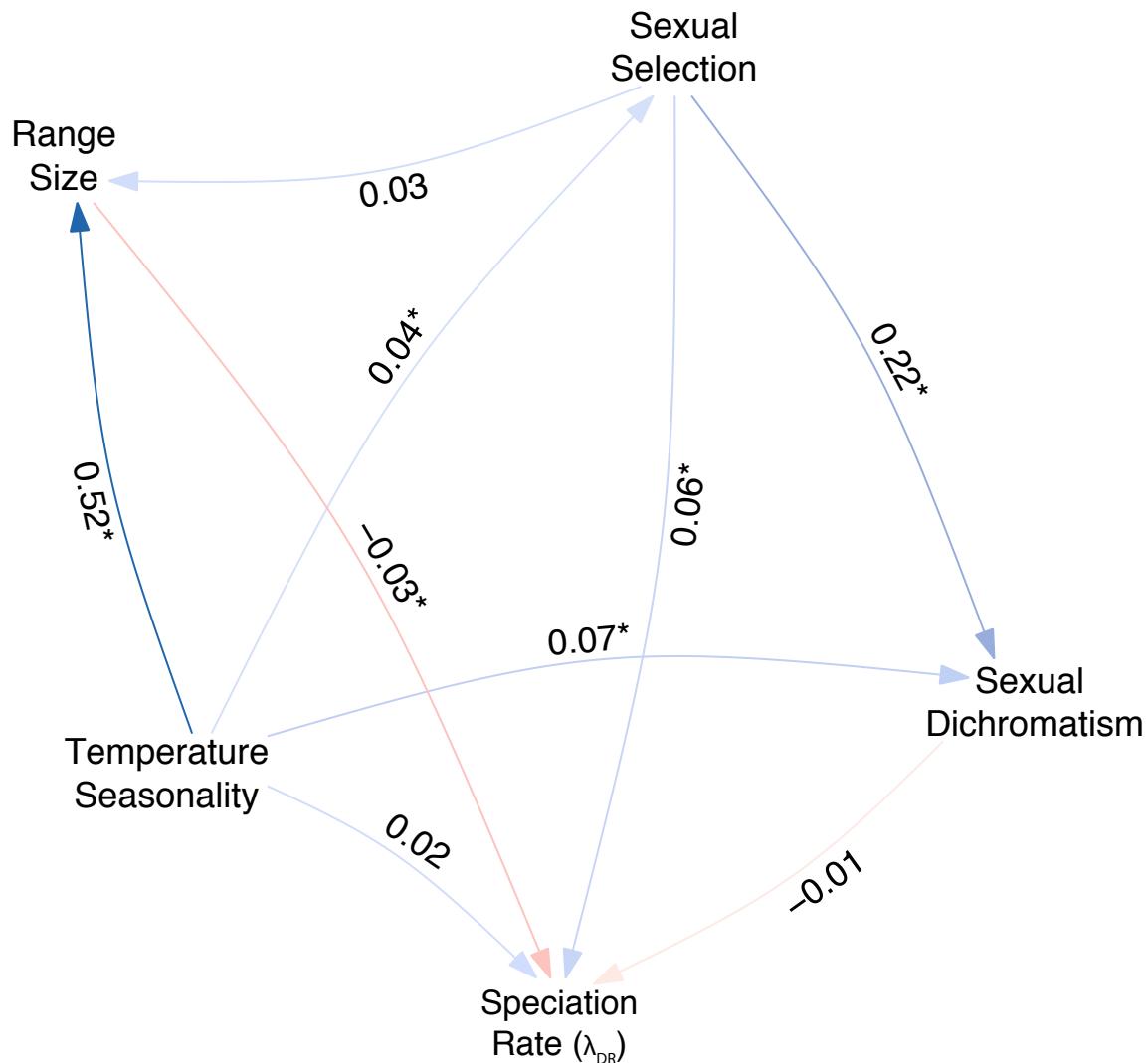


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with the direction of effect corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95% confidence intervals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

185 DISCUSSION

186 We found evidence that the composite index of male-biased sexual selection, but not measures of sexual
187 dichromatism, is correlated with the rate of speciation in passerine birds. The absence of a detectable
188 correlation between sexual dichromatism and speciation rate was consistent across different measures of
189 speciation (λ_{DR} , λ_{ND} and λ_{BAMM}) and both measures of dichromatism (spectral and RGB), and it cannot
190 be explained by a difference in statistical power since the sample size for the dichromatism analyses was much
191 larger. These findings reaffirm the conclusions of previous, smaller studies in which sexual dichromatism was
192 measured using spectrophotometry (Huang and Rabosky 2014) or human observers (Cooney et al. 2017).
193 The correlation between speciation rate and the index of male-biased sexual selection (which encapsulates
194 variation in sexual size dimorphism, social polygyny, and paternal care) was statistically significant for
195 λ_{DR} , but not for λ_{ND} and λ_{BAMM} , although the estimated direction and magnitude of the correlation was
196 broadly similar across all three measures. Interestingly, we also found a consistent negative relationship
197 between range size and speciation rate, at least when this rate was quantified using λ_{DR} and λ_{ND} . None
198 of the bioclimatic measures of environmental variability that we investigated (*i.e.*, temperature seasonality,
199 long-term temperature variation, and spatial temperature variation) significantly predicted speciation rate.

200 The difference in findings between the analyses of sexual dichromatism *versus* the index of sexual selection
201 is noteworthy, because the majority of earlier studies used dichromatism alone as their proxy for sexual
202 selection (*e.g.*, Barraclough et al. 1995; Owens et al. 1999; Morrow et al. 2003; Seddon et al. 2013; Huang
203 and Rabosky 2014). Given our findings, and the modest correlation between dichromatism and the sexual
204 selection index ($r = 0.34$; Dale et al. 2015), we hypothesise that sexual dichromatism may not be a robust
205 proxy for sexual selection. Although dichromatism clearly reflects sexual selection to some extent, it is
206 possibly that it is too indirect a measure to detect any association with speciation rate, even with a high
207 sample size. There are several reasons why the use of sexual dichromatism as a proxy for sexual selection is
208 problematic. Firstly, sexual dichromatism can evolve for reasons other than sexual selection, such as when
209 males and females occupy different ecological niches (Wallace 1889; Kottler 1980; Slatkin 1984; Shine 1989) or
210 experience different selective pressures in contexts other than competition for mates (Price and Eaton 2014).
211 For example, in superb fairy-wrens (*Malurus cyaneus*) female colouration has probably evolved in response to
212 spatial variation in predation pressure, increasing dichromatism (Medina et al. 2017). Ecological selection on
213 sexual dichromatism was implicated by our path analysis, which found that sexual dichromatism is positively
214 affected by temperature seasonality (a measure of environmental variation), albeit weakly. Secondly, colour is
215 only one of the traits subject to sexual selection (Miles and Fuxjager 2018; Cally et al. 2019). For instance,
216 sexual selection may promote investments in other mating signals (*e.g.* song) that trade-off against plumage
217 colour, leading to variable investment in different sexually selected signals across species (Cooney et al.
218 2018). Lastly, not all plumage colouration honestly reflects mate quality. A recent meta-analysis found that
219 converted carotenoids (but not carotenoids sourced from the diet) predict mate quality through improvements
220 in parasite resistance and reproductive success (Weaver et al. 2018). Thus, bright colours may signal direct
221 benefits or ‘good genes’ in some species but not others, and some of the colours used to calculate dichromatism
222 might be more functionally relevant than others.

223 In-line with some theoretical predictions and previous studies (Kraaijeveld et al. 2011) we found that male-
224 biased sexual selection increases speciation rate, at least when speciation is measured by λ_{DR} . Additionally,
225 we found that this association appears to be independent of net primary productivity and spatiotemporal

226 variation in the environment. The lack of an effect of these environmental variables on speciation rate
227 has several possible interpretations. Firstly, the effects of sexual selection on adaptation and speciation
228 may depend on the type of environmental variability under which the species is evolving. Specifically,
229 speciation rates might be impacted by genetic constraints on adaptation, that vary across environments.
230 Theory suggests that sexual antagonism (which is often exacerbated in species with strong sexual selection)
231 may be lower in habitats experiencing cyclical environmental variation (*e.g.* seasonality), relative to those
232 experiencing directional change in the environment (Connallon and Hall 2016). Another possibility is that the
233 environmental predictors we chose may not account for the key ecological sources of selection that interact
234 with sexual selection to drive speciation. For example, our study does not include direct measure of food
235 availability or the severity of predation and parasitism, which are both hypothesised to affect sexual selection
236 and speciation (*reviewed in* Maan and Seehausen 2011). Finally, it is possible that environmental variability
237 genuinely has little effect on speciation rates, at least in the taxa investigated here.

238 The most robust finding in our study is the finding that species with smaller ranges have elevated speciation
239 rates. This result is similar to a study of 329 amphibian genera, which found higher diversification rates
240 in taxa with smaller range size (Greenberg and Mooers 2017). Intuitively, large range size should promote
241 speciation by creating more opportunities for geographic barriers to form (Rosenzweig 1995; Castiglione
242 et al. 2017). However, the opposite pattern is also plausible because birds with limited dispersal or more
243 specialised niches can have more fragmented populations, which would promote vicariant divergence and
244 higher speciation rates (Jablonski and Roy 2003; Birand et al. 2012; Claramunt et al. 2012). **Please**
245 **check this sentence, I didn't understand the original but I tried to re-draft for clarity** It is also
246 possible that high speciation rates cause smaller range sizes, rather than the other way around, for example
247 because repeatedly-speciating lineages tend to fill niches in ways that hinder the geographical expansion of
248 new species (Rosenzweig 1995; Weir and Price 2011; Price and Eaton 2014). However, species undergoing
249 adaptive radiation in new habitats are unlikely to be limited by competition for resources from existing
250 taxa. Across islands, we expect to see a correlation between speciation and small range size because small
251 islands often reflect newly formed environments with empty niches. **As a jerk reviewer, I would say**
252 **“can’t you re-run it without the island radiations??”** Thus, our findings might be driven by island
253 radiations (*e.g.* “Darwin’s finches”, *Geospiza* spp.). One further explanation for the negative association
254 between range size and sexual dichromatism/sexual selection is the potential bias of taxonomic classification,
255 whereby over-splitting of species in clades with large ranges leads to increased recent phylogenetic branching
256 as well as smaller ranges.

257 In addition to speciation, sexual selection is hypothesised to affect extinction. Using the model-based
258 approach of BAMM, we found no association between the estiamted extinction rate and sexual dichromatism,
259 male-biased sexual selection, or our measures of environmental variability. However, these extinction results
260 should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from
261 phylogenies, principally because different combinations of speciation and extinction rates can give rise to
262 similar patterns of diversity (see Rabosky 2016). Phylogenetic methods such as BAMM allow for speciation
263 and extinction rates to be estimated using moderately-sized phylogenies, although the ability of BAMM to
264 model evolutionary rate shifts and extinction rates is debated (*see*, Beaulieu and O’Meara 2015; Rabosky
265 2016; Moore et al. 2016; Rabosky et al. 2017). Additionally, while several tip-rate estimates exist for
266 speciation rate (*e.g.*, λ_{DR} and λ_{ND}), tip-rate estimates of extinction rate are difficult to obtain without
267 complex Bayesian models which are sensitive to sampling bias (Davis et al. 2013). Although extinction rates

268 can be inferred from alternative sources, such as the fossil record (Martins et al. 2018), direct observation
269 extinction, or IUCN red list status (Greenberg and Mooers 2017), each approach has its limitations. Across
270 the passerine bird phylogeny, we found that BAMM often produced homogeneous speciation and extinction
271 rates for smaller clades showing few rate shifts, which might reduce our power to detect small differences
272 in extinction rates among closely-related taxa (Rabosky et al. 2017; Title and Rabosky 2018). Thus, this
273 methodological constraint likely decreases our ability to accurately measure the correlation between metrics
274 of sexual selection and the probability of extinction.

275 One outcome of our analyses was that different measures of speciation rates presented different results.
276 This is not completely surprising, because each of the rates is calculated differently (see Title and Rabosky
277 (2018)). For instance, λ_{DR} is weighted more towards speciation events close to the tips and allows more rate
278 heterogeneity compared to BAMM estimates. This leads to greater variation in λ_{DR} relative to the BAMM
279 estimates, potentially explaining the difference in results. The BAMM estimates were also more sensitive to
280 phylogenetic uncertainty.

281 To summarise, we have shown that male-biased sexual selection, but not sexual dichromatism, predicts
282 speciation in passernines, and that this relationship is not markedly affected by environmental variability.
283 These findings imply that sexual dechromatism is not a reliable proxy for sexual selection, and that alternative
284 measures of sexual selection are more directly related to diversification. Our results also add indirect support
285 to the hypothesis that sexual selection promotes adaptation, which has implications for conservation (Holman
286 and Kokko 2013) and captive breeding programs for threatened species (Charge et al. 2014). Furthermore, our
287 finding that high speciation rate is associated with smaller range size highlights the threat to the persistence
288 of rapidly-speciating lineages in a world with increased habitat loss and anthropogenic stress. This concern
289 arises as the best predictor of extinction risk is range size (Harris and Pimm 2008) and the association found
290 here implies that many newly-speciated clades have small range sizes and could thus be at greater risk of
291 extinction.

292 MATERIALS AND METHODS

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

298 Compiling data for sexual selection and environmental stress

299 Sexual dichromatism

300 We used a previously published measure of sexual dichromatism for 5,983 species of passerines (Dale et al.
301 2015). Briefly, Dale et al. (2015) obtained sex-specific RGB (red, green and blue) values across six body
302 patches (nape, crown, forehead, throat, upper breast, and lower breast) from *Handbook of the Birds of the*
303 *World* (Del Hoyo et al. 2011). The relative contribution of male and female RGB colour values were averaged
304 across body patches and provide ‘male-like’ and ‘female-like’ plumage scores. Here we use the absolute
305 difference between male and female plumage scores as an estimate of sexual dichromatism. Additionally, we
306 used another measure of dichromatism corresponding to colour distance in avian colour space derived from
307 spectral data (Armenta et al. 2008). These measurements include variation in the ultraviolet and bird-visible
308 range and — unlike the RGB measures — are sourced from museum samples (as opposed to colour drawings).
309 However, this spectrophotometry data is not as extensive as the RGB measures; with only 581 passerine
310 species available for this analysis. While there is a correlation between these two measures, there is residual
311 variation ($r = 0.79$; [Figure S10](#)).

312 Male-biased sexual selection

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

321 Environmental variables

322 We obtained estimates of species range size using expert range maps (BirdLife International and Handbook
323 of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the *Birdlife* database
324 (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-second ($\sim 1 \text{ km}^2$) 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). We include estimates of climate variability during recent evolutionary history as they may be a better indicators of environmental effects on speciation than present-day environmental variability. 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).

340 Generating biologically relevant predictors for environmental stress

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. Similar 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](#).

360 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

363 hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without
 364 genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using
 365 tip-rate measures (1000 trees) and BAMM (100 trees)(Rabosky 2014). These trees used a ‘Hackett backbone’
 366 (Hackett et al. 2008) and were constructed using a pure birth (Yule) model. We calculated three different
 367 tip-rate metrics of speciation and one of extinction across all trees.

368 Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes
 369 and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating
 370 the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES),
 371 also known as diversification rate (DR) (e.g., Jetz et al. 2012; Quintero and Jetz 2018; Rabosky et al. 2018),
 372 is derived from the sum of edge lengths branching from a node, with each edge towards the root having
 373 the length down-weighted. Studies have suggested that DR and ND (henceforth referred to as λ_{DR} and
 374 λ_{ND}) are more reflective estimates of speciation than diversification; this is because λ_{DR} and λ_{ND} cannot
 375 account for whole-clade extinctions and thus under-estimate extinction rate, which makes the composite
 376 measure of diversification more dependent on speciation (Belmaker and Jetz 2015; Title and Rabosky 2018).
 377 Therefore, λ_{DR} is a measure of speciation rate more heavily weighted to recent speciation events and λ_{ND} is a
 378 measure of speciation across the root-to-tip path. These tip-rate measures are alternatives to state-dependent
 379 diversification models such as Quantitative State Speciation-Extinction (QuaSSE); but, based on previous
 380 simulation studies, λ_{DR} and λ_{ND} are robust and intuitive measures that provide high power and low false
 381 discovery rate with large phylogenies when incorporated into Phylogenetic Generalized Least Squares (PGLS)
 382 models (Harvey Michael et al. 2017).

383 Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic
 384 trees (Rabosky 2014). This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo)
 385 to generate probability distributions of evolutionary rate-shift configurations with variable speciation and
 386 extinction rates. Importantly, these models provide tip-rate estimates of speciation and extinction rate. The
 387 parameters of the 100 BAMM runs are detailed in full in the [ESM](#); briefly, we used a time-variable model with
 388 100 expected number of shifts and prior rates set from the initial speciation and extinction values using the
 389 **BAMMtools** R package (Rabosky et al. 2014). Each BAMM model (one MCC tree and 100 random draws of
 390 the posterior) was run for 100 million generations, and given the computationally intensive nature of BAMM,
 391 runs were conducted across multiple CPUs. Each run of BAMM reached convergence with effective sample
 392 size (ESS) of MCMC (Markov Chain Monte Carlo) samples surpassing 200 (an arbitrary value, above which
 393 posterior distributions can often be accurately inferred) for the key model parameters of log-likelihood and
 394 number of rate shifts ([Table S3](#), [Table S4](#)). Further details of BAMM parameters and output are available in
 395 the [ESM](#), with tip-rate means and variances provided. Additionally, given the variability in BAMM estimates,
 396 we also provide analysis of BAMM shift configurations and tip-rate estimates from our run on the MCC
 397 tree and within a BAMM run on the MCC tree from a genetic-only phylogeny across all birds (Harvey et al.
 398 2017). All analyses were conducted on log-rates.

399 Phylogenetic comparative analysis

400 To test the association between speciation/extinction and sexual selection, environmental variability and
 401 their interaction, we used phylogenetic least squares (PGLS) models in the **nlme** package (Pinheiro et al.
 402 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.

⁴³⁴ **ACKNOWLEDGEMENTS**

⁴³⁵ We would like to acknowledge Adnan Moussalli for his assistance in conducting BAMM runs across 100
⁴³⁶ phylogenetic trees. **Any others?**

437 REFERENCES

- 438 Armenta, J. K., P. O. Dunn, and L. A. Whittingham. 2008. Quantifying avian sexual dichromatism: A
439 comparison of methods. *Journal of Experimental Biology* 211:2423.
- 440 Barraclough, T. G., P. H. Harvey, and S. Nee. 1995. Sexual selection and taxonomic diversity in passerine
441 birds. *Proceedings of the Royal Society B-Biological Sciences* 259:211–215.
- 442 Bartoń, K. 2017. MuMIn: Multi-model inference.
- 443 Beaulieu, J. M., and B. C. O'Meara. 2015. Extinction can be estimated from moderately sized molecular
444 phylogenies. *Evolution* 69:1036–1043.
- 445 Belmaker, J., and W. Jetz. 2015. Relative roles of ecological and energetic constraints, diversification rates
446 and region history on global species richness gradients. *Ecology Letters* 18:563–571.
- 447 Berger, D., K. Grieshop, M. I. Lind, J. Goenaga, A. A. Maklakov, and G. Arnqvist. 2014. Intralocus sexual
448 conflict and environmental stress. *Evolution* 68:2184–2196.
- 449 Bijl, W. van der. 2018. *Phylopath*: Easy phylogenetic path analysis in R. *PeerJ* 6:e4718.
- 450 Birand, A., A. Vose, and S. Gavrillets. 2012. Patterns of species ranges, speciation, and extinction. *American
451 Naturalist* 179:1–21.
- 452 BirdLife International and Handbook of the Birds of the World. 2017. Bird species distribution maps of the
453 world. <http://datazone.birdlife.org/species/requestdis>.
- 454 Bonduriansky, R. 2011. Sexual selection and conflict as engines of ecological diversification. *American
455 Naturalist* 178:729–745.
- 456 Bonduriansky, R., and S. F. Chenoweth. 2009. Intralocus sexual conflict. *Trends in Ecology & Evolution*
457 24:280–8.
- 458 Boughman, J. W. 2002. How sensory drive can promote speciation. *Trends in Ecology & Evolution* 17:571–577.
- 459 Cally, J. G., D. Stuart-Fox, and L. Holman. 2019. Meta-analytic evidence that sexual selection improves
460 population fitness. *Nature communications* 10:2017. Nature Publishing Group.
- 461 Candolin, U., and J. Heuschele. 2008. Is sexual selection beneficial during adaptation to environmental
462 change? *Trends in Ecology & Evolution* 23:446–452.
- 463 Castiglione, S., A. Mondanaro, M. Melchionna, C. Serio, M. Di Febbraro, F. Carotenuto, and P. Raia. 2017.
464 Diversification rates and the evolution of species range size frequency distribution. *Frontiers in Ecology and
465 Evolution* 5:147. Frontiers.
- 466 Charge, R., C. Teplitsky, G. Sorci, and M. Low. 2014. Can sexual selection theory inform genetic management
467 of captive populations? A review. *Evolutionary Applications* 7:1120–1133.
- 468 Claramunt, S., E. P. Derryberry, J. V. Remsen, and R. T. Brumfield. 2012. High dispersal ability inhibits
469 speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*
470 279:1567.

- 471 Connallon, T., and M. D. Hall. 2016. Genetic correlations and sex-specific adaptation in changing environments. 70:2198.
- 472 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.
- 473 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.
- 474 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.
- 475 Davies, N., and A. Houston. 1986. Reproductive success of dunnocks, *Prunella modularis*, in a variable mating system. II. Conflicts of interest among breeding adults. Journal of Animal Ecology 55:139–154.
- 476 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.
- 477 Del Hoyo, J., A. Elliott, and D. Christie. 2011. Handbook of the birds of the world. Lynx Edicions 2003-2011.
- 478 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.
- 479 Fromhage, L., and M. D. Jennions. 2016. Coevolution of parental investment and sexually selected traits drives sex-role divergence. Nature Communications 7:12517.
- 480 Greenberg, D. A., and A. Ø. Mooers. 2017. Linking speciation to extinction: Diversification raises contemporary extinction risk in amphibians. Evolution Letters 1:40–48.
- 481 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.
- 482 Harano, T., K. Okada, S. Nakayama, T. Miyatake, and D. J. Hosken. 2010. Intralocus sexual conflict unresolved by sex-limited trait expression. Current Biology 20:2036–2039.
- 483 Harris, G., and S. L. Pimm. 2008. Range size and extinction risk in forest birds. Conservation Biology 22:163–171.
- 484 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.
- 485 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.
- 486 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.
- 487 Holman, L., J. S. Van Zweden, T. A. Linksvayer, and P. d'Ettorre. 2013. Crozier's paradox revisited: Maintenance of genetic recognition systems by disassortative mating. BMC Evolutionary Biology 13:211.

- 508 Hoyo, J. del, and N. J. Collar. 2016. HBW and birdlife international illustrated checklist of the birds of the
509 world. Lynx Edicions; BirdLife International.
- 510 Huang, H. T., and D. L. Rabosky. 2014. Sexual selection and diversification: Reexamining the correlation
511 between dichromatism and speciation rate in birds. *American Naturalist* 184:E101–E114.
- 512 Jablonski, D., and K. Roy. 2003. Geographical range and speciation in fossil and living molluscs. *Proceedings*
513 *of the Royal Society of London. Series B: Biological Sciences* 270:401–406. The Royal Society.
- 514 Janicke, T., I. K. Häderer, M. J. Lajeunesse, and N. Anthes. 2016. Darwinian sex roles confirmed across the
515 animal kingdom. *Science Advances* 2:e1500983.
- 516 Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in
517 space and time. *Nature* 491:444–448.
- 518 Kokko, H., and R. Brooks. 2003. Sexy to die for? Sexual selection and the risk of extinction. *Annales*
519 *Zoologici Fennici* 40:207–219.
- 520 Kokko, H., and K. Heubel. 2008. Condition-dependence, genotype-by-environment interactions and the lek
521 paradox. *Genetica* 134:55–62.
- 522 Kokko, H., and M. D. Jennions. 2008. Parental investment, sexual selection and sex ratios. *Journal of*
523 *Evolutionary Biology* 21:919–948.
- 524 Kottler, M. J. 1980. Darwin, Wallace, and the origin of sexual dimorphism. *Proceedings of the American*
525 *Philosophical Society* 124:203–226.
- 526 Kraaijeveld, K., F. J. L. Kraaijeveld-Smit, and M. E. Maan. 2011. Sexual selection and speciation: The
527 comparative evidence revisited. *Biological Reviews* 86:367–377.
- 528 Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National*
529 *Academy of Sciences* 78:3721–3725.
- 530 Lande, R. 1982. Rapid origin of sexual isolation and character divergence in a cline. *Evolution* 36:213–223.
- 531 Long, T. A. F., A. F. Agrawal, and L. Rowe. 2012. The effect of sexual selection on offspring fitness depends
532 on the nature of genetic variation. *Current Biology* 22:204–208.
- 533 Lorch, P. D., S. Proulx, L. Rowe, and T. Day. 2003. Condition-dependent sexual selection can accelerate
534 adaptation. *Evolutionary Ecology Research* 5:867–881.
- 535 Maan, M. E., and O. Seehausen. 2011. Ecology, sexual selection and speciation. *Ecology Letters* 14:591–602.
- 536 Martins, M. J. F., T. M. Puckett, R. Lockwood, J. P. Swaddle, and G. Hunt. 2018. High male sexual
537 investment as a driver of extinction in fossil ostracods. *Nature* 556:366.
- 538 Medina, I., K. Delhey, A. Peters, K. E. Cain, M. L. Hall, R. A. Mulder, and N. E. Langmore. 2017. Habitat
539 structure is linked to the evolution of plumage colour in female, but not male, fairy-wrens. *BMC evolutionary*
540 *biology* 17:35.
- 541 Miles, M. C., and M. J. Fuxjager. 2018. Synergistic selection regimens drive the evolution of display
542 complexity in birds of paradise. *Journal of Animal Ecology* 87:1149–1159.

- 543 Moore, B. R., S. Hohna, M. R. May, B. Rannala, and J. P. Huelsenbeck. 2016. Critically evaluating the
544 theory and performance of bayesian analysis of macroevolutionary mixtures. Proceedings of the National
545 Academy of Sciences 113:9569–9574.
- 546 Morrow, E. H., T. E. Pitcher, and G. Arnqvist. 2003. No evidence that sexual selection is an 'engine of
547 speciation' in birds. Ecology Letters 6:228–234.
- 548 Otto-Btiesner, B. L., S. J. Marshall, J. T. Overpeck, G. H. Miller, A. Hu, and. 2006. Simulating arctic
549 climate warmth and icefield retreat in the last interglaciation. Science 311:1751–1753.
- 550 Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: Body size, life history,
551 sexual selection or ecology? Proceedings of the Royal Society B-Biological Sciences 266:933–939.
- 552 Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature 401:877.
- 553 Paradis, E., J. Claude, and K. Strimmer. 2004. APE: Analyses of phylogenetics and evolution in R language.
554 Bioinformatics 20:289–290.
- 555 Pennell, T. M., and E. H. Morrow. 2013. Two sexes, one genome: The evolutionary dynamics of intralocus
556 sexual conflict. Ecology and Evolution 3:1819–1834.
- 557 Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2018. nlme: Linear and nonlinear mixed
558 effects models.
- 559 Pischedda, A., and A. K. Chippindale. 2006. Intralocus sexual conflict diminishes the benefits of sexual
560 selection. PLOS Biology 4:e356.
- 561 Price, J. J., and M. D. Eaton. 2014. Reconstructing the evolution of sexual dichromatism: Current color
562 diversity does not reflect past rates of male and female change. Evolution 68:2026–2037.
- 563 Quintero, I., and W. Jetz. 2018. Global elevational diversity and diversification of birds. Nature 555:246.
- 564 Rabosky, D., M. Grundler, C. Anderson, P. Title, J. Shi, J. Brown, H. Huang, and J. Larson. 2014.
565 BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. Methods in
566 Ecology and Evolution 5:701–707.
- 567 Rabosky, D. L. 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on
568 phylogenetic trees. PLOS ONE 9:e89543.
- 569 Rabosky, D. L. 2016. Challenges in the estimation of extinction from molecular phylogenies: A response to
570 Beaulieu and O'Meara. Evolution 70:218–228.
- 571 Rabosky, D. L., J. Chang, P. O. Title, P. F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T. J.
572 Near, M. Coll, and others. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. Nature
573 559:392.
- 574 Rabosky, D. L., J. S. Mitchell, and J. Chang. 2017. Is BAMM flawed? Theoretical and practical concerns in
575 the analysis of multi-rate diversification models. Systematic biology 66:477–498.
- 576 Radwan, J., L. Engqvist, and K. Reinhold. 2016. A paradox of genetic variance in epigamic traits: Beyond
577 "good genes" view of sexual selection. Evolutionary Biology 43:267–275.

- 578 Rankin, D. J., U. Dieckmann, and H. Kokko. 2011. Sexual conflict and the tragedy of the commons. *American
579 Naturalist* 177:780–791.
- 580 Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press.
- 581 Safran, R. J., E. S. Scordato, L. B. Symes, R. L. Rodri'guez, and T. C. Mendelson. 2013. Contributions of
582 natural and sexual selection to the evolution of premating reproductive isolation: A research agenda. *Trends
583 in Ecology & Evolution* 28:643–650.
- 584 Seddon, N., C. A. Botero, J. A. Tobias, P. O. Dunn, H. E. A. MacGregor, D. R. Rubenstein, J. A. C. Uy, J.
585 T. Weir, L. A. Whittingham, and R. J. Safran. 2013. Sexual selection accelerates signal evolution during
586 speciation in birds. *Proceedings of the Royal Society B: Biological Sciences* 280.
- 587 Seddon, N., R. M. Merrill, and J. A. Tobias. 2008. Sexually selected traits predict patterns of species richness
588 in a diverse clade of suboscine birds. *American Naturalist* 171:620–631.
- 589 Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *The
590 Quarterly Review of Biology* 64:419–461.
- 591 Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38:622–630.
- 592 Sloan, N. S., and L. W. Simmons. 2019. The evolution of female genitalia. *Journal of Evolutionary Biology*
593 in press.
- 594 Swanson, W. J., and V. D. Vacquier. 1998. Concerted evolution in an egg receptor for a rapidly evolving
595 abalone sperm protein. *Science* 281:710–712.
- 596 Title, P. O., and D. L. Rabosky. 2018. Diversification rates and phylogenies: What are we estimating, and
597 how good are the estimates? *bioRxiv* 369124.
- 598 Wallace, A. R. 1889. Colours and ornaments characteristic of sex. *in* Darwinism, an exponent of the theory
599 of natural selection, with some of its applications. Macmillan; Company.
- 600 Weaver, R. J., E. S. Santos, A. M. Tucker, A. E. Wilson, and G. E. Hill. 2018. Carotenoid metabolism
601 strengthens the link between feather coloration and individual quality. *Nature Communications* 9:73.
- 602 Weir, J. T., and T. D. Price. 2011. Limits to speciation inferred from times to secondary sympatry and ages
603 of hybridizing species along a latitudinal gradient. *American Naturalist* 177:462–469.
- 604 West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology*
605 58:155–183.
- 606 Whitlock, M. C. 2000. Fixation of new alleles and the extinction of small populations: Drift load, beneficial
607 alleles, and sexual selection. *Evolution* 54:1855–1861.
- 608 Whitlock, M. C., and A. F. Agrawal. 2009. Purging the genome with sexual selection: Reducing mutation
609 load through selection on males. *Evolution* 63:569–582.
- 610 Zhao, M., F. A. Heinsch, R. R. Nemani, and S. W. Running. 2005. Improvements of the modis terrestrial
611 gross and net primary production global data set. *Remote Sensing of Environment* 95:164–176.