

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

3

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 of
7 the hypothesised effects on speciation or extinction have opposing signs and uncertain magnitudes. Here,
8 we test whether the strength of sexual selection predicts variation in speciation and extinction rates across
9 passerine birds (up to 5,812 species, covering most genera). We use two measures of sexual selection
10 (sexual dichromatism and a multivariate measure of male-biased sexual selection) and adjust for range
11 size and environmental variability. Male-biased sexual selection, but not sexual dichromatism, predicted
12 speciation rates (λ_{DR}) in passserines. This relationship was independent of range size or environmental
13 variability, though species with smaller ranges had higher speciation rates. There was no association
14 between sexual selection and extinction rate (μ_{BAMM}). Our findings suggest that sexual dichromatism is
15 a poor proxy for sexual selection at least a broad-scale and support the view that sexual selection has
16 shaped diversification in songbirds.

17 Sexual selection is a ubiquitous evolutionary process whose effect on diversification is much debated^{1–5}. Sexual
 18 selection can promote speciation because it operates on traits that can create reproductive isolation when they
 19 diverge between lineages, such as signals and preferences involved in mate selection^{1,2,6}, sperm-egg interactions⁷,
 20 or genital morphology⁸. Sexual selection could also promote speciation or prevent extinction by purging
 21 deleterious mutations⁹, fixing beneficial ones¹⁰, and accelerating adaptation in different environments^{11–13}.
 22 Conversely, sexual selection might hinder speciation or make extinction more likely by favouring traits that
 23 improve mating success but reduce population fitness^{14–17}. For example, species with costly sexual signals
 24 may be less resilient to environmental change¹⁸. Extinction risk may also be exacerbated by sexual selection
 25 causing maladaptation ('gender load') in female traits that are genetically correlated with sexually-selected
 26 male traits^{19–23}. Although numerous studies have examined the relationship between sexual selection and
 27 speciation or extinction rates^{4,24–28}, the availability of more complete phenotypic, ecological and phylogenetic
 28 data²⁹, together with significant advances in phylogenetic methods^{30,31}, present new opportunities to test
 29 whether and how sexual selection drives diversification.

30 The relationship between sexual selection and diversification may depend on the environment. Theoretical
 31 work predicts that sexual selection should have a more positive effect on adaptation and population fitness
 32 in variable environments relative to stable ones^{32,33}. In stable environments, consistent selection depletes
 33 genetic variation at sexually concordant loci (i.e. loci where the same allele is fittest for both sexes). In these
 34 environments, genetic variation remains disproportionately at sexually antagonistic loci, leading to stronger
 35 gender load and reduced net benefits of sexual selection³³. By contrast, in spatially or temporally variable
 36 environments, sexual selection can enhance local adaptation. For example, in Darwin's finches (*Geospiza*
 37 *fortis*) divergent beak morphology is an adaptation to local food availability that has been maintained through
 38 assortative mating³⁴. Despite the potential interaction between sexual selection and environmental variability
 39 in diversification, phylogenetic tests are currently lacking.

40 Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification^{4,24,25,27,28}
 41 because their biology and phylogenetic relationships are comparatively well-known. A 2011 meta-analysis
 42 covering 20 primary studies of birds and other taxa found a small but significant positive association between
 43 sexual selection and speciation, with the average effect size in birds stronger than in mammals but weaker
 44 than in insects or fish²⁶. However, there was large variation in effect size estimates across the 20 studies, likely
 45 reflecting differences in methodology, such as metrics used to characterise speciation and sexual selection,
 46 in addition to true biological differences. More recently, Huang & Rabosky²⁸ found no association between
 47 sexual dichromatism and speciation ($n = 918$ species) in a study using spectrophotometric measurements of
 48 museum specimens³⁵ and tip-rate estimates from a molecular-only phylogeny²⁹. Similarly, Cooney et al.³⁶
 49 found no effect of sexual dichromatism on diversification across 1,306 pairs of species, using dichromatism
 50 scores provided by human observers. More recently, social polygyny (a proxy for sexual selection) was found
 51 to have a positive association with speciation rate across 954 species of birds³⁷.

52 Here, we investigate the association between sexual selection and diversification in birds while building upon
 53 previous approaches in multiple ways. We use two measures of the strength of sexual selection: sexual
 54 dichromatism³⁸, as well as an index of male-biased sexual selection³⁸, which captures (co)variation in sexual
 55 size dimorphism, social polygyny and paternal care. We use these two measures because sexual dichromatism
 56 does not always signal the presence of strong sexual selection and *vice versa*³⁸. For example, male and
 57 female dunnocks (*Prunella modularis*) are similarly coloured yet sexual selection appears to be strong³⁹.
 58 Furthermore, a recent comparative study found a negative relationship between dichromatism and another

59 sexually-selected trait (song) across species, suggesting that a multi-trait focus would improve estimates of
60 sexual selection intensity⁵. Additionally, our analysis includes multiple ecological and environmental variables,
61 allowing us to adjust for potential confounds, to identify environmental factors driving diversification, and
62 to test whether environmental factors interact with sexual selection as theory predicts³³. We use multiple
63 approaches for quantifying speciation and extinction rates at the tips of phylogenetic trees, including BAMM
64 (Bayesian Analysis of Macroevolutionary Mixtures)^{40–43}, as well as older but reliable tip-rate statistics, namely
65 diversification rate (λ_{DR}) and node density (λ_{ND})²⁹. Our results show that (i) a composite measure of sexual
66 selection, but not sexual dichromatism, significantly predicts speciation rates, (ii) species with smaller ranges
67 have higher speciation rates and (iii) there is no evidence that environmental variables or their interaction
68 with sexual selection have an impact on diversification rates. Therefore, we provide evidence at a very
69 large scale that sexual selection can have positive effects on diversification in the largest radiation of birds.
70 Furthermore, we suggest that the use of sexual dichromatism as the sole proxy for sexual selection should be
71 reconsidered, since it can misguide conclusions about the role of sexual selection in different scenarios.

72 RESULTS

73 Male-biased sexual selection, but not sexual dichromatism, affects speciation

74 We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines ($n = 5,812$
75 species; 58% of all birds). To do this, we tested the association between speciation/extinction and sexual
76 selection, environmental variability and their interaction using phylogenetic least squares (PGLS) models
77 with λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} as the response variable. These are three different tip-rate metrics of
78 speciation (λ_{DR} , λ_{ND} , λ_{BAMM}) and one of extinction (μ_{BAMM} , see Methods for details). Predictors included
79 one measure of sexual selection (one of two measures of sexual dichromatism or the index of male-biased
80 sexual selection), four measures of environmental variation, range size and 2-way interactions between the
81 measure of sexual selection and each of the environmental measures including range size, with subsequent
82 model simplification using AIC model selection.

83 We found a significant positive association between the index of male-biased sexual selection ($n = 2,465$) and
84 λ_{DR} maximum credibility (MCC) tree ($\beta = 3.89 \times 10^{-2}$, $p = 0.01$; Figure 1b). However, this association
85 was not significant for the other two measures of speciation rate (λ_{ND} : $\beta = 4.38 \times 10^{-4}$, $p = 0.35$; λ_{BAMM} :
86 $\beta = 9.42 \times 10^{-4}$, $p = 0.76$; Figure 1b). When we took into account phylogenetic uncertainty by running
87 the models using 1,000 trees, the distribution of estimates from PGLS models was similar to the estimate
88 from the MCC tree: among the 1,000 trees there was a positive association between sexual selection and λ_{DR}
89 (highest posterior density (HPD) Interval = 4.51×10^{-3} , 5.72×10^{-2}), and the distribution skewed towards a
90 positive association between sexual selection and λ_{ND} (HPD Interval = -5.04×10^{-4} , 1.58×10^{-3} ;) as well
91 as the 100 models using λ_{BAMM} (HPD Interval = -1.30×10^{-2} , 3.09×10^{-2} ; Table S15).

92 In contrast to male-biased sexual selection, we found no evidence that species with increased sexual dichro-
93 matism have higher or lower rates of speciation. Sexual dichromatism showed no association with λ_{DR} (β
94 = -1.28×10^{-3} , $p = 0.15$; Figure 1a, Figure 2), λ_{ND} ($\beta = -5.75 \times 10^{-5}$, $p = 0.08$; Figure 1a) or λ_{BAMM}
95 ($\beta = -1.43 \times 10^{-5}$, $p = 0.87$; Figure 1a). PGLS analyses using sexual dichromatism ($n = 581$) measured
96 by spectrophotometry³⁵ yielded results concordant with the full dataset; i.e. no association between sexual

97 dichromatism and speciation (Figure S11). Our results from models based on the MCC tree are largely
 98 corroborated by model estimates from PGLS analyses of the rates and correlation structures from 1,000 trees
 99 (for λ_{DR} , λ_{ND}) and 100 trees for λ_{BAMM} . The HPD intervals show model estimates are distributed around
 100 zero when using complete taxon sampling models and RGB measures of sexual dichromatism (λ_{DR} : HPD
 101 Interval = -1.63×10^{-3} , 1.66×10^{-3} , λ_{ND} : HPD Interval = -4.26×10^{-5} , 5.50×10^{-5} , Figure 1a, Table S8).
 102 For PGLS models using spectrophotometry-based measures of sexual dichromatism, the estimates from the
 103 100 trees in the λ_{DR} models are positively skewed (HPD Interval = -1.78×10^{-2} , 3.49×10^{-2}) but normally
 104 distributed around zero for λ_{ND} and λ_{BAMM} (Table S12).

105 No interaction terms were present in the top models ($\Delta AICc > 4$) for any measure of speciation (λ_{DR} ,
 106 λ_{ND} , λ_{BAMM}) or sexual selection (RGB values, spectrophotometry and the index of male-biased sexual
 107 selection; $\Delta AICc > 4$; Table S5, Table S6, Table S10, Table S13). Thus we found no evidence that the
 108 effect of sexual selection on speciation is dependent on our measures of environmental variation or range
 109 size. Furthermore, we found no evidence that these environmental factors — seasonal temperature variation,
 110 long-term temperature variation, spatial temperature variation, and Net Primary Productivity (NPP) —
 111 predict speciation independently from sexual dichromatism/selection (Figure 1, Figure S11).

112 Species with smaller ranges have increased rates of speciation

113 Based on λ_{DR} and λ_{ND} tip-rate metrics of speciation, we found a negative association between range size
 114 and speciation; that is, species with smaller ranges show marginally higher values for λ_{DR} and λ_{ND} . This
 115 negative association was small but significant for models using the MCC tree (λ_{DR} : $\beta = -6.58 \times 10^{-3}$, p
 116 = 0; λ_{ND} : $\beta = -1.46 \times 10^{-4}$, $p = 0.03$; Figure 1a, Figure 2). This association was also evident across the
 117 estimates from models using the 1,000 trees (λ_{DR} : HPD Interval = -8.87×10^{-3} , -6.61×10^{-4} ; λ_{ND} : HPD
 118 Interval = -1.51×10^{-4} , 1.72×10^{-5} ; Figure 1a). Subset models with reduced sample size and different
 119 measures of sexual selection — but the same measure of range size — showed equivocal evidence that range
 120 size is negatively associated with speciation. Range size significantly predicted λ_{DR} (Figure 1b) using data
 121 subset for species with an index of male-biased sexual selection ($n = 2,465$) but not λ_{ND} or λ_{BAMM} . Models
 122 using data subset for spectrophotometry-based dichromatism ($n = 581$) gave non-significant estimates for the
 123 effect of range size on all measures of speciation (Figure S11, Table S11, Table S12). Because the range size
 124 dataset is the same across the three data subsets we draw our conclusions from the models with the highest
 125 power using near-complete taxon sampling ($n = 5,812$).

126 Phylogenetic path analysis

127 Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS
 128 (Figure 3; Figure S14). There was a modest effect of male-biased sexual selection on sexual dimorphism (β
 129 = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism ($\beta = 0.07$) and strongly
 130 affected range size ($\beta = 0.52$). This suggests an indirect effect of temperature seasonality on λ_{DR} ($\beta_{indirect} =$
 131 -0.02; Figure 3), given the negative association we identified between λ_{DR} and range size in PGLS models.

132 Extinction rate

133 We found no evidence that extinction (μ_{BAMM}) was impacted by the extent of sexual dichromatism for
134 full-taxon sampling ($\beta = 2.38 \times 10^{-5}$, $p = 0.93$; Figure 1a), nor spectrophotometry-based measures of sexual
135 dichromatism (Figure S11, Table S11, Table S12) or male-biased sexual selection (Figure 1b, Table S14, Table
136 S15).

137 Variability across phylogenetic trees and speciation rate measures

138 Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially in
139 the BAMM rates (λ_{BAMM} and μ_{BAMM}), where the 95 % HPD interval across PGLS model estimates from
140 100 trees was often > 20 times larger than the 95 % confidence interval for estimates from a single PGLS
141 model using the MCC tree. This contrasts with variation across trees for the other rate estimates (λ_{DR} and
142 λ_{ND}), where the 95 % HPD interval of model estimates for pgl models using 1,000 trees was near-equivalent
143 to the 95 % confidence interval calculated for PGLS model estimates of the MCC tree (Table S9). Given
144 the computational requirements of BAMM, the great majority of earlier studies have based their estimates
145 on a single consensus tree, and so the inconsistency of the BAMM estimates between different phylogenies
146 with similar statistical support is notable. Mean measures of speciation rate across 100 trees were positively
147 correlated between measures ($\lambda_{DR} - \lambda_{BAMM}$: $r=0.75$, $\lambda_{DR} - \lambda_{ND}$: $r=0.65$, $\lambda_{ND} - \lambda_{BAMM}$: $r=0.51$; Figure
148 S15). Given that the calculation of BAMM rates can be affected by the settings of the run and the use of
149 different priors, we compared the estimate of our MCC tree with that of previous published analyses on
150 birds, and found a high correlation ($r=0.81$, Figure S8). Full details of the BAMM results are presented as
151 supplementary materials.

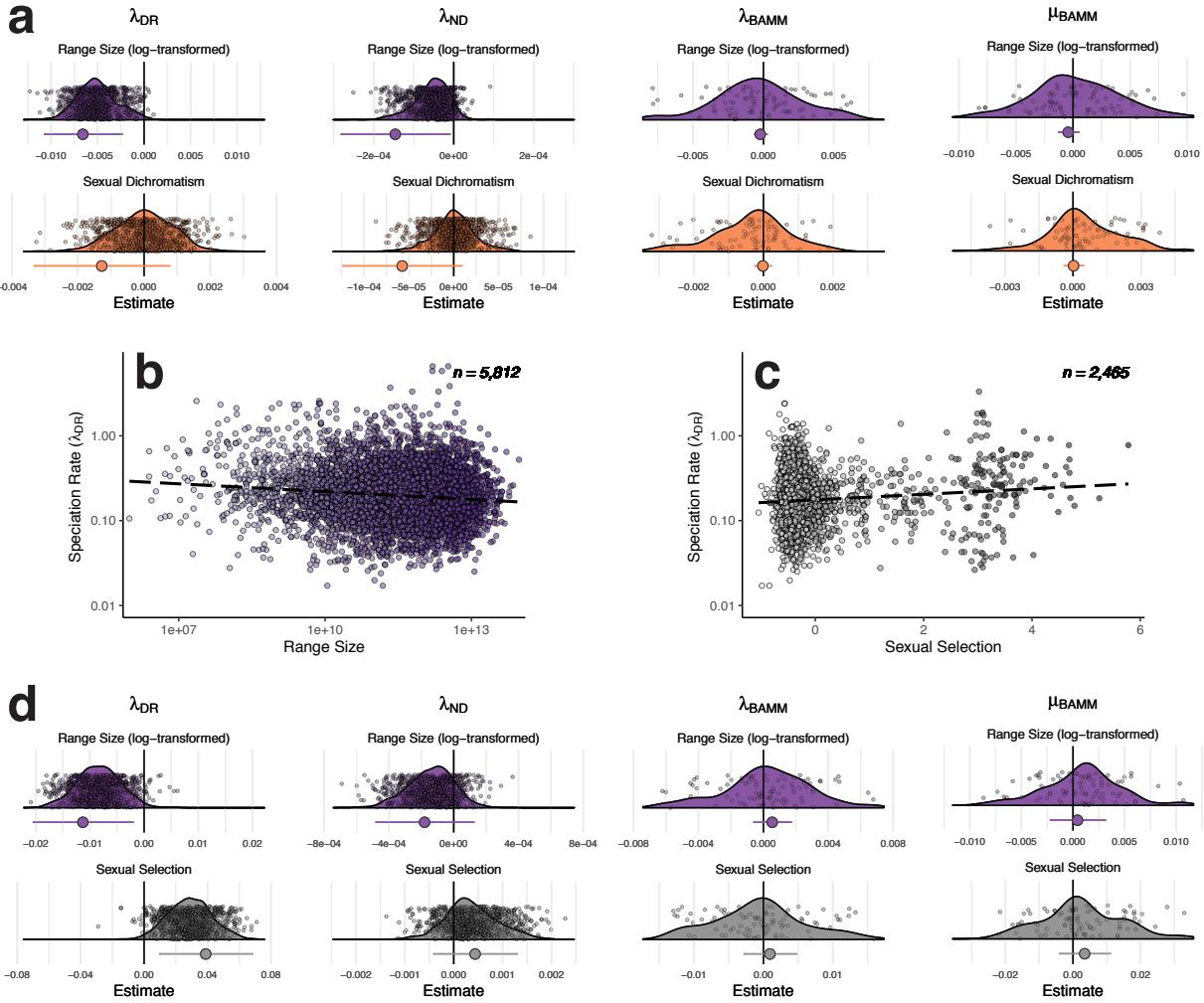


Figure 1: Model estimates (a) for the effect of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset (RGB values, $n = 5,812$). (b) depicts the scatter plot of speciation rate (λ_{DR}) and log-range size with the model estimate 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 an index 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 randomly sampled trees (for λ_{DR} and λ_{ND}) or 100 randomly sampled 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 randomly sampled trees for BAMM models in order to be able to visualise the MCC 95% CIs.

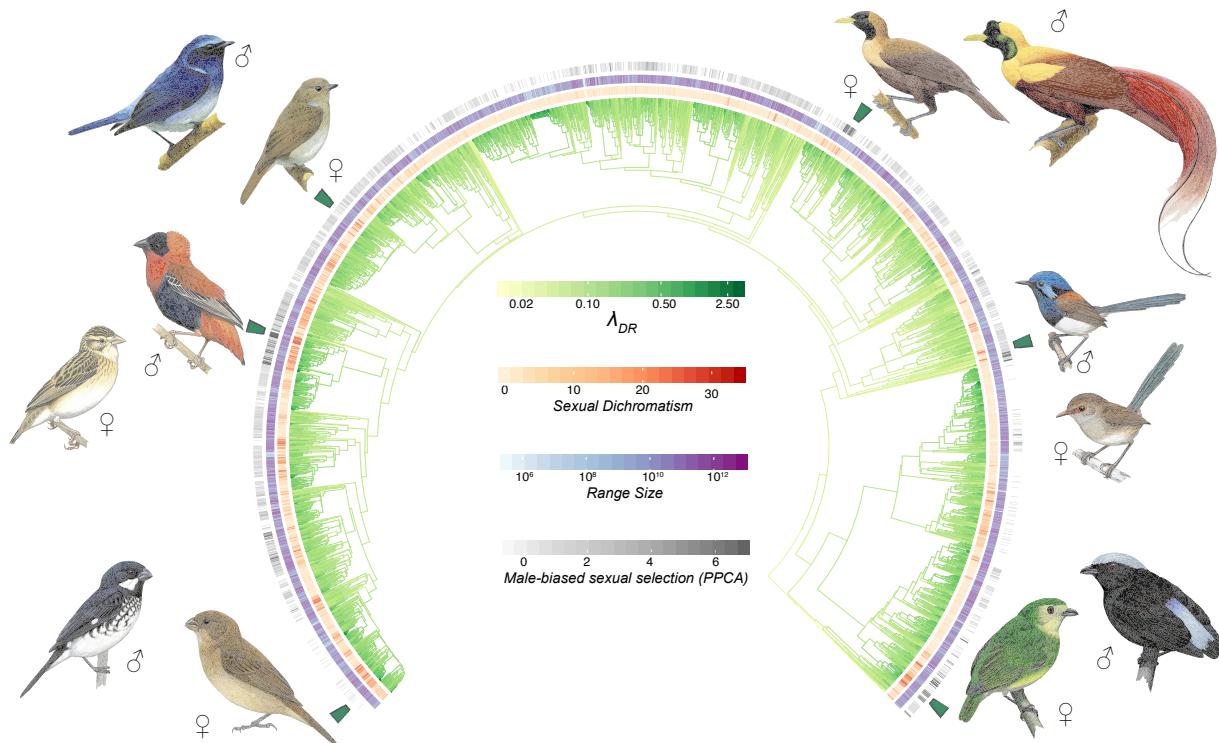


Figure 2: Speciation rate (λ_{DR}) across all passerine birds ($n = 5,965$) with estimates of sexual dichromatism, range size available for 5,812 species and an index of male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative association 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 six species are: *Sporophila bouvronides*, *Euplectes franciscanus*, *Phainopepla nitens*, *Paradisaea rubra*, *Malurus pulcherrimus*, *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. Illustrations reproduced by permission of Lynx Editions.

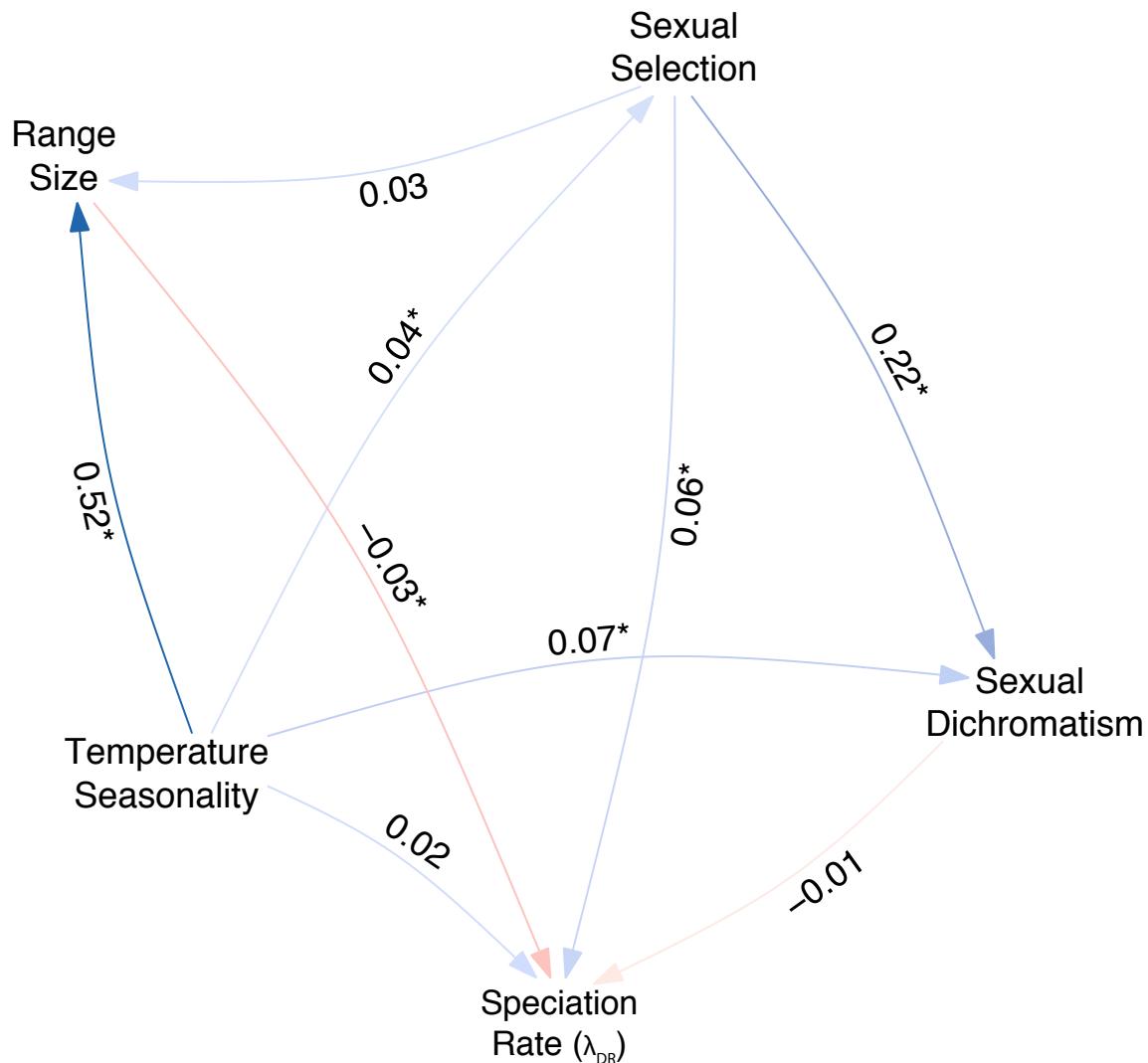


Figure 3: Path analysis of evolutionary and ecological variables. Arrows represent direct effects with the direction of effect corresponding to colours (blue = positive, red = negative). The numeric values are standardised regression slopes and the asterisks indicates that the 95% confidence intervals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

152 DISCUSSION

153 We found evidence that the composite index of male-biased sexual selection, but not measures of sexual
154 dichromatism, is correlated with the rate of speciation in passerine birds. The absence of a detectable
155 correlation between sexual dichromatism and speciation rate was consistent across different measures of
156 speciation (λ_{DR} , λ_{ND} and λ_{BAMM}) and both measures of dichromatism (spectral and RGB), and it cannot
157 be explained by a difference in statistical power since the sample size for the dichromatism analyses was
158 larger. These findings reaffirm the conclusions of previous, smaller studies in which sexual dichromatism
159 was measured using spectrophotometry²⁸ or human observers³⁶. The correlation between speciation rate
160 and the index of male-biased sexual selection (which encapsulates variation in sexual size dimorphism, social
161 polygyny, and paternal care) was statistically significant for λ_{DR} , but not for λ_{ND} and λ_{BAMM} . Interestingly,
162 we also found a consistent negative relationship between range size and speciation rate, at least when this
163 rate was quantified using λ_{DR} and λ_{ND} . None of the bioclimatic measures of environmental variability that
164 we investigated (i.e., temperature seasonality, long-term temperature variation, and spatial temperature
165 variation) significantly predicted speciation rate.

166 The difference in findings between the analyses of sexual dichromatism *versus* the index of sexual selection
167 is noteworthy, because the majority of earlier studies used dichromatism alone as their proxy for sexual
168 selection^{24,25,27,28,44}. Given our findings, and the modest correlation between dichromatism and the sexual
169 selection index³⁸, we suggest that sexual dichromatism may not be a robust proxy for sexual selection.
170 Although dichromatism almost certainly provides some insight into the operation of sexual selection, it may
171 be too indirect a measure to detect any association with speciation rate, even with large sample size. There
172 are several reasons why the use of sexual dichromatism as a proxy for sexual selection is problematic. Firstly,
173 sexual dichromatism can evolve for reasons other than sexual selection, such as when males and females occupy
174 different ecological niches^{45–48} or experience different selective pressures in contexts other than competition
175 for mates⁴⁹. For example, in superb fairy-wrens (*Malurus cyaneus*) female colouration has probably evolved
176 in response to spatial variation in predation pressure, increasing dichromatism⁵⁰. Ecological selection on
177 sexual dichromatism was implicated by our path analysis, which found that sexual dichromatism is positively
178 affected by temperature seasonality (a measure of environmental variation), albeit weakly. Secondly, colour is
179 only one of the traits subject to sexual selection^{13,51}. For instance, sexual selection may promote investments
180 in other mating signals (e.g. song) that trade-off against plumage colour, leading to variable investment in
181 different sexually selected signals across species⁵. Lastly, not all plumage colouration honestly reflects mate
182 quality. A recent meta-analysis found that converted carotenoids (but not carotenoids sourced from the diet)
183 predict mate quality through improvements in parasite resistance and reproductive success⁵². Given the
184 importance of honest signaling in sexual selection and the variability in colour production mechanisms across
185 birds, sexual dichromatism in many species may be an unreliable measure of mate quality for female birds
186 and sexual selection for researchers.

187 In line with some theoretical predictions and previous studies²⁶ we found that male-biased sexual selection
188 increases speciation rate, at least when speciation is measured by λ_{DR} . Additionally, we found that this
189 association appears to be independent of net primary productivity and spatiotemporal variation in the
190 environment. The lack of an effect of these environmental variables on speciation rate has several possible
191 interpretations. Firstly, the effects of sexual selection on adaptation and speciation may depend on the type of
192 environmental variability under which the species is evolving. Specifically, speciation rates might be impacted

193 by genetic constraints on adaptation, that vary across environments. Theory suggests that sexual antagonism
194 (which is often exacerbated in species with strong sexual selection) may be lower in habitats experiencing
195 cyclical environmental variation (e.g. seasonality), relative to those experiencing directional change in the
196 environment³³. Another possibility is that the environmental predictors we chose may not account for the
197 key ecological sources of selection that interact with sexual selection to drive speciation. For example, our
198 study does not include direct measure of food availability or the severity of predation and parasitism, which
199 are both hypothesised to affect sexual selection and speciation⁵³. Finally, it is possible that environmental
200 variability genuinely has little effect on speciation rates, at least in the taxa investigated here.

201 The most robust finding in our study is the finding that species with smaller ranges have elevated speciation
202 rates. This result is similar to a study of 329 amphibian genera, which found higher diversification rates
203 in taxa with smaller range size⁵⁴. Intuitively, large range size should promote speciation by creating more
204 opportunities for geographic barriers to form^{55,56}. However, the opposite pattern is also plausible because
205 birds with limited dispersal or more specialised niches can have more fragmented populations, which would
206 promote vicariant divergence and higher speciation rates^{57–59}. It is also possible that high speciation rates
207 cause smaller range sizes, rather than the other way around, for example because repeatedly-speciating
208 lineages tend to fill niches in ways that hinder the geographical expansion of new species^{49,55,60}. However,
209 species undergoing adaptive radiation in new habitats are unlikely to be limited by competition for resources
210 from existing taxa. One further explanation for the negative association between range size and sexual
211 dichromatism/sexual selection is the potential bias of taxonomic classification, whereby over-splitting of
212 species in clades with large ranges leads to increased recent phylogenetic branching as well as smaller ranges.

213 In addition to speciation, sexual selection is hypothesised to affect extinction. Using the model-based
214 approach of BAMM, we found no association between the estimated extinction rate and sexual dichromatism,
215 male-biased sexual selection, or our measures of environmental variability. However, these extinction results
216 should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from
217 phylogenies, principally because different combinations of speciation and extinction rates can give rise to
218 similar patterns of diversity⁴¹. Phylogenetic methods such as BAMM allow for speciation and extinction rates
219 to be estimated using moderately-sized phylogenies, although the ability of BAMM to model evolutionary rate
220 shifts and extinction rates is debated^{40–43}. Additionally, while several tip-rate estimates exist for speciation
221 rate (e.g., λ_{DR} and λ_{ND}), tip-rate estimates of extinction rate are difficult to obtain without complex Bayesian
222 models which are sensitive to sampling bias⁶¹. Although extinction rates can be inferred from alternative
223 sources, such as the fossil record⁶², direct observation extinction, or IUCN red list status⁵⁴, each approach
224 has its limitations. Across the passerine bird phylogeny, we found that BAMM often produced homogeneous
225 speciation and extinction rates for smaller clades showing few rate shifts, which might reduce our power
226 to detect small differences in extinction rates among closely-related taxa^{43,63}. Thus, this methodological
227 constraint likely decreases our ability to accurately measure the correlation between metrics of sexual selection
228 and the probability of extinction.

229 One outcome of our analyses was that different measures of speciation rates presented different results. This is
230 not completely surprising, because each of the rates is calculated differently⁶³. For instance, λ_{DR} is weighted
231 more towards speciation events close to the tips and allows more rate heterogeneity compared to BAMM
232 estimates. This leads to greater variation in λ_{DR} relative to the BAMM estimates, potentially explaining the
233 difference in results. The BAMM estimates were also more sensitive to phylogenetic uncertainty.

234 To summarise, we have shown that male-biased sexual selection, but not sexual dichromatism, predicts

235 speciation in passerines, that the magnitude of this effect is modest, and that this relationship is not markedly
236 affected by environmental variability. These findings imply that sexual dichromatism is not a reliable proxy for
237 sexual selection, and that alternative measures of sexual selection are more directly related to diversification.
238 Our results also add indirect support to the hypothesis that sexual selection promotes adaptation, which
239 has implications for conservation¹⁶ and captive breeding programs for threatened species⁶⁴. Furthermore, our
240 finding that high speciation rate is associated with smaller range size highlights the threat to the persistence
241 of rapidly-speciating lineages in a world with increased habitat loss and anthropogenic stress. This concern
242 arises as the best predictor of extinction risk is range size⁶⁵ and the association found here implies that many
243 newly-speciated clades have small range sizes and could thus be at greater risk of extinction.

244 MATERIALS AND METHODS

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

250 Compiling data for sexual selection and environmental stress

251 Sexual dichromatism

252 We used a previously-published measure of sexual dichromatism for 5,983 species of passerines³⁸. Briefly, Dale
253 et al.³⁸ obtained sex-specific RGB (red-green-blue) values across six body patches (nape, crown, forehead,
254 throat, upper breast, and lower breast) from *Handbook of the Birds of the World*⁶⁶. The relative contribution
255 of male and female RGB colour values were averaged across body patches and provide ‘male-like’ and
256 ‘female-like’ plumage scores. Here we use the absolute difference between male and female plumage scores as
257 an estimate of sexual dichromatism. Technically, this measures differences in the ‘degree of male-ness’ between
258 males and females, rather than sex differences in colour *per se* (i.e. dichromatism in the strict sense). For
259 example, the metric would fail to capture dichromatism when both the male and female possess a single, but
260 differently coloured ‘male-like’ patch. However, the metric is highly correlated with dichromatism measured
261 from spectral data (see below).

262 Additionally, we used another measure of dichromatism corresponding to colour distance in avian colour
263 space derived from spectral data³⁵. These measurements include variation in the ultraviolet and bird-visible
264 range and — unlike the RGB measures — are sourced from museum specimens as opposed to illustrations.
265 The spectrophotometry data covers only 581 passerine species (10-fold fewer than the RGB data), although
266 there was a substantial correlation between the two dichromatism measures ($r = 0.79$; Figure S10).

267 Male-biased sexual selection

268 Because sexual dichromatism is presumably imperfectly correlated with variation in the strength of sexual
269 selection across taxa, we sourced an additional measure of sexual selection³⁸, referred to here as the ‘index
270 of male-biased sexual selection’. This index is the first principal component from a phylogenetic principal
271 component analysis (PPCA) of three characteristics positively associated with sexual selection (sexual size
272 dimorphism, social polygyny and [lack of] paternal care). This measure of male-biased sexual selection
273 is available for only 2,465 species, and shows a moderate correlation with the RGB measure of sexual
274 dichromatism ($r = 0.34$; Figure S12).

275 Environmental variables

276 We obtained estimates of species range size using expert range maps⁶⁷. Because of taxonomic changes
277 to 1,230 species in the Birdlife database⁶⁸ we manually matched these taxa with the names used in the
278 sexual dichromatism dataset³⁸. From these distributions, we obtained estimates of climatic conditions that
279 each species is exposed to. That is, we took 1,000 random point samples in each range and extracted 19
280 present-day bioclimatic variables (representing a variety of biologically relevant annual trends in temperature
281 and precipitation) with 30-second (~1 km²) spatial resolution⁶⁹. From these values, we obtained means and standard
282 deviations for each species. Using the same spatial sampling, we extracted means and standard
283 deviations of bioclimatic variables from the paleoclimate during the last interglacial (LIG; 120,000 - 140,000
284 years ago)⁷⁰. To estimate variability in the energy available to species, we obtained the mean and standard
285 deviation of net primary productivity (NPP) values between 2000 - 2015 across each species distribution.
286 Estimates of NPP had 30-second resolution and were obtained through MODIS (Moderate Resolution Imaging
287 Spectroradiometer) primary production products stage 3 (MOD17A3)⁷¹. Using these data, which we provide
288 as a potentially useful data resource (see ESM), we generated five predictors of speciation associated with
289 different patterns in environmental variability (see below).

290 Generating biologically relevant predictors for environmental stress

291 Given that stressful environments are expected to interact with sexual selection and have a positive effect on
292 adaptation¹³, we used the extracted environmental variables from each species range size to create predictors
293 of environmental variation/stress. Firstly we used (i) the average NPP in each species’ range and (v) the
294 log-transformed range size as potentially informative predictors of speciation rates. We also used three
295 environmental predictors derived from bioclimatic data. These predictors relate to seasonal climate variation,
296 spatial climate variation and long-term climate variation. To obtain seasonal climate variation we used (iii)
297 mean values of temperature seasonality (BIO4) for each range. (iv) To estimate levels of spatial environmental
298 variation a species may endure we used the first principle component (PC1) from a PCA on standard
299 deviations from all bioclimatic variables, excluding temperature and precipitation seasonality (BIO4 and
300 BIO15). PC1 was heavily loaded towards bioclimatic variables relating to temperature, thus PC1 reflects
301 the variation in temperature across a species’ range (Table S1). Species range is a potentially informative
302 predictor of speciation and extinction, so we controlled for the correlation between environmental spatial
303 variation and range size — where larger ranges have larger variation in PC1 — by using the residuals of a
304 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.org²⁹. 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 (1,000 trees) and BAMM (100 trees)³⁰. These trees used a ‘Hackett backbone’⁷² 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)^{29,73,74}, 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; this is because λ_{DR} and λ_{ND} cannot account for whole-clade extinctions and thus under-estimate extinction rate, which makes the composite measure of diversification more dependent on speciation^{63,75}. Therefore, λ_{DR} is a measure of speciation rate more heavily weighted to recent speciation events while λ_{ND} measures 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) models³¹.

Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic trees³⁰. 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 package⁷⁶. 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

345 on the MCC tree from a genetic-only phylogeny across all birds⁷⁷. All analyses were conducted on log-rates.

346 Phylogenetic comparative analysis

347 To test the association between speciation/extinction and sexual selection, environmental variability and their
348 interaction, we used phylogenetic least squares (PGLS) models in the `nlme` package⁷⁸. Firstly, we conducted
349 model selection to compare models in which λ_{DR} , λ_{ND} , λ_{BAMM} or μ_{BAMM} were the response variable: these
350 tip-rate estimates all came from the same MCC tree (derived from 2,500 draws of the posterior distribution²⁹).
351 For models of λ_{BAMM} and μ_{BAMM} we used the inverse of the variance associated with each tip rate estimate
352 as weights, to account for the variable precision of the estimates provided by BAMM. The most complicated
353 model in each set under comparison contained one of the measures of sexual selection (sexual dichromatism
354 or the index of male-biased sexual selection), all of the environmental measures (i.e. log-transformed range
355 size, seasonal temperature variation, spatial temperature variation, long-term temperature variation, and
356 NPP), and all of the 2-way interactions between sexual selection and each of the environmental measures.
357 The simpler models contained all of the same main effects, but had fewer 2-way interaction terms (potentially
358 none). Model selection was done in MuMIn using the `dredge` function⁷⁹. Using the terms from the top-ranked
359 model (ranked by AICc), we ran the equivalent model for each of the 1,000 phylogenetic trees used to derive
360 λ_{DR} , λ_{ND} and each of the 100 trees used to derive λ_{BAMM} and μ_{BAMM} . In each model we used the unique
361 response variables and phylogenetic tree correlation structure. Specifically, for models using tip-rate metrics
362 (λ_{DR} , λ_{ND}) we estimated the phylogenetic signal — Pagel's λ ⁸⁰ — using the `corPagel` function in the `ape`
363 package⁸¹ independently for each of the 1,000 trees/models. Alternatively, for models using speciation and
364 extinction estimates derived using BAMM (λ_{BAMM} and μ_{BAMM}) we found λ was consistently estimated at 1
365 and hence assumed Brownian motion (using the `corBrownian` function) to estimate the correlation structure.
366 This method enabled us to present model estimates for an MCC tree alongside 1,000/100 trees from the
367 posterior distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three
368 datasets corresponding to each measure of sexual selection: dichromatism derived from RGB values of images
369 ($n = 5,812$); dichromatism from spectrophotometry ($n = 581$) and the index of male-biased sexual selection
370 ($n = 2,465$).

371 Finally, using the subset of species with an index of male-biased sexual selection, we conducted a phylogenetic
372 path analysis using the `phylopath` R package⁸². The phylogenetic path analysis was used to assess causal paths
373 between variables not able to be modelled within the univariate response of PGLS. That is, a phylogenetic
374 path analysis allowed us to model relationships between the predictor variables used in our PGLS analysis as
375 we anticipate environmental variability, sexual dichromatism/selection, and range size to have effects on each
376 other and not just on speciation rate. To minimise path complexity we used temperature seasonality (BIO4)
377 as the single measure for environmental variability, λ_{DR} as the single measure of speciation and the tip-rates
378 from the MCC tree. Further details of the path analysis, including our rationale for each path's directions,
379 can be found within the ESM along with all other analyses and the relevant R code to reproduce results.

380 REFERENCES

- 381 1. Lande, R. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences* **78**, 3721–3725 (1981).
- 382 2. Lande, R. Rapid origin of sexual isolation and character divergence in a cline. *Evolution* **36**, 213–223 (1982).
- 383 3. West-Eberhard, M. J. Sexual selection, social competition, and speciation. *Quarterly Review of Biology* **58**, 155–183 (1983).
- 384 4. Seddon, N., Merrill, R. M. & Tobias, J. A. Sexually selected traits predict patterns of species richness in a diverse clade of suboscine birds. *American Naturalist* **171**, 620–631 (2008).
- 385 5. Cooney, C. R., MacGregor, H. E. A., Seddon, N. & Tobias, J. A. 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**, (2018).
- 386 6. Safran, R. J., Scordato, E. S., Symes, L. B., Rodri'guez, R. L. & Mendelson, T. C. Contributions of natural and sexual selection to the evolution of premating reproductive isolation: A research agenda. *Trends in Ecology & Evolution* **28**, 643–650 (2013).
- 387 7. Swanson, W. J. & Vacquier, V. D. Concerted evolution in an egg receptor for a rapidly evolving abalone sperm protein. *Science* **281**, 710–712 (1998).
- 388 8. Sloan, N. S. & Simmons, L. W. The evolution of female genitalia. *Journal of Evolutionary Biology* **in press**, (2019).
- 389 9. Whitlock, M. C. & Agrawal, A. F. Purging the genome with sexual selection: Reducing mutation load through selection on males. *Evolution* **63**, 569–582 (2009).
- 390 10. Whitlock, M. C. Fixation of new alleles and the extinction of small populations: Drift load, beneficial alleles, and sexual selection. *Evolution* **54**, 1855–1861 (2000).
- 391 11. Lorch, P. D., Proulx, S., Rowe, L. & Day, T. Condition-dependent sexual selection can accelerate adaptation. *Evolutionary Ecology Research* **5**, 867–881 (2003).
- 392 12. Candolin, U. & Heuschele, J. Is sexual selection beneficial during adaptation to environmental change? *Trends in Ecology & Evolution* **23**, 446–452 (2008).
- 393 13. Cally, J. G., Stuart-Fox, D. & Holman, L. Meta-analytic evidence that sexual selection improves population fitness. *Nature communications* **10**, 2017 (2019).
- 394 14. Rankin, D. J., Dieckmann, U. & Kokko, H. Sexual conflict and the tragedy of the commons. *American Naturalist* **177**, 780–791 (2011).
- 395 15. Kokko, H. & Jennions, M. D. Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology* **21**, 919–948 (2008).
- 396 16. Holman, L. & Kokko, H. The consequences of polyandry for population viability, extinction risk and conservation. *Philosophical Transactions of the Royal Society B-Biological Sciences* **368**, (2013).

- 415 17. Fromhage, L. & Jennions, M. D. Coevolution of parental investment and sexually selected traits drives
416 sex-role divergence. *Nature Communications* **7**, 12517 (2016).
- 417 18. Kokko, H. & Brooks, R. Sexy to die for? Sexual selection and the risk of extinction. *Annales Zoologici
418 Fennici* **40**, 207–219 (2003).
- 419 19. Pischedda, A. & Chippindale, A. K. Intralocus sexual conflict diminishes the benefits of sexual selection.
420 *PLOS Biology* **4**, e356 (2006).
- 421 20. Harano, T., Okada, K., Nakayama, S., Miyatake, T. & Hosken, D. J. Intralocus sexual conflict unresolved
422 by sex-limited trait expression. *Current Biology* **20**, 2036–2039 (2010).
- 423 21. Berger, D. *et al.* Intralocus sexual conflict and environmental stress. *Evolution* **68**, 2184–2196 (2014).
- 424 22. Bonduriansky, R. & Chenoweth, S. F. Intralocus sexual conflict. *Trends in Ecology & Evolution* **24**,
425 280–8 (2009).
- 426 23. Pennell, T. M. & Morrow, E. H. Two sexes, one genome: The evolutionary dynamics of intralocus sexual
427 conflict. *Ecology and Evolution* **3**, 1819–1834 (2013).
- 428 24. Barraclough, T. G., Harvey, P. H. & Nee, S. Sexual selection and taxonomic diversity in passerine birds.
429 *Proceedings of the Royal Society B-Biological Sciences* **259**, 211–215 (1995).
- 430 25. Morrow, E. H., Pitcher, T. E. & Arnqvist, G. No evidence that sexual selection is an 'engine of speciation'
431 in birds. *Ecology Letters* **6**, 228–234 (2003).
- 432 26. Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Maan, M. E. Sexual selection and speciation: The
433 comparative evidence revisited. *Biological Reviews* **86**, 367–377 (2011).
- 434 27. Seddon, N. *et al.* Sexual selection accelerates signal evolution during speciation in birds. *Proceedings of
435 the Royal Society B: Biological Sciences* **280**, (2013).
- 436 28. Huang, H. T. & Rabosky, D. L. Sexual selection and diversification: Reexamining the correlation between
437 dichromatism and speciation rate in birds. *American Naturalist* **184**, E101–E114 (2014).
- 438 29. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in
439 space and time. *Nature* **491**, 444–448 (2012).
- 440 30. Rabosky, D. L. Automatic detection of key innovations, rate shifts, and diversity-dependence on
441 phylogenetic trees. *PLOS ONE* **9**, e89543 (2014).
- 442 31. Harvey Michael, G., Rabosky Daniel, L. & Cooper, N. Continuous traits and speciation rates: Alternatives
443 to state-dependent diversification models. *Methods in Ecology and Evolution* **9**, 984–993 (2017).
- 444 32. Long, T. A. F., Agrawal, A. F. & Rowe, L. The effect of sexual selection on offspring fitness depends on
445 the nature of genetic variation. *Current Biology* **22**, 204–208 (2012).
- 446 33. Connallon, T. & Hall, M. D. Genetic correlations and sex-specific adaptation in changing environments.
447 *Science* **70**, 2198 (2016).
- 448 34. Huber, S. K., De Leon, L. F., Hendry, A. P., Bermingham, E. & Podos, J. Reproductive isolation
449 of sympatric morphs in a population of darwin's finches. *Proceedings of the Royal Society of London B:
450 Biological Sciences* **274**, 1709–1714 (2007).

- 451 35. Armenta, J. K., Dunn, P. O. & Whittingham, L. A. Quantifying avian sexual dichromatism: A comparison
452 of methods. *Journal of Experimental Biology* **211**, 2423 (2008).
- 453 36. Cooney, C. R., Tobias, J. A., Weir, J. T., Botero, C. A. & Seddon, N. Sexual selection, speciation and
454 constraints on geographical range overlap in birds. *Ecology Letters* **20**, 863–871 (2017).
- 455 37. Iglesias-Carrasco, M., Jennions, M. D., Ho, S. Y. W. & Duchêne, D. A. Sexual selection, body mass and
456 molecular evolution interact to predict diversification in birds. *Proceedings of the Royal Society B: Biological
457 Sciences* **286**, 20190172 (2019).
- 458 38. Dale, J., Dey, C. J., Delhey, K., Kempenaers, B. & Valcu, M. The effects of life history and sexual
459 selection on male and female plumage colouration. *Nature* **527**, 367–370 (2015).
- 460 39. Davies, N. & Houston, A. Reproductive success of dunnocks, *Prunella modularis*, in a variable mating
461 system. II. Conflicts of interest among breeding adults. *Journal of Animal Ecology* **55**, 139–154 (1986).
- 462 40. Beaulieu, J. M. & O'Meara, B. C. Extinction can be estimated from moderately sized molecular
463 phylogenies. *Evolution* **69**, 1036–1043 (2015).
- 464 41. Rabosky, D. L. Challenges in the estimation of extinction from molecular phylogenies: A response to
465 Beaulieu and O'Meara. *Evolution* **70**, 218–228 (2016).
- 466 42. Moore, B. R., Hohna, S., May, M. R., Rannala, B. & Huelsenbeck, J. P. Critically evaluating the theory
467 and performance of bayesian analysis of macroevolutionary mixtures. *Proceedings of the National Academy
468 of Sciences* **113**, 9569–9574 (2016).
- 469 43. Rabosky, D. L., Mitchell, J. S. & Chang, J. Is BAMM flawed? Theoretical and practical concerns in the
470 analysis of multi-rate diversification models. *Systematic biology* **66**, 477–498 (2017).
- 471 44. Owens, I. P. F., Bennett, P. M. & Harvey, P. H. Species richness among birds: Body size, life history,
472 sexual selection or ecology? *Proceedings of the Royal Society B-Biological Sciences* **266**, 933–939 (1999).
- 473 45. Wallace, A. R. Colours and ornaments characteristic of sex. in *Darwinism, an exponent of the theory of
474 natural selection, with some of its applications* (Macmillan; Company, 1889).
- 475 46. Kottler, M. J. Darwin, Wallace, and the origin of sexual dimorphism. *Proceedings of the American
476 Philosophical Society* **124**, 203–226 (1980).
- 477 47. Slatkin, M. Ecological causes of sexual dimorphism. *Evolution* **38**, 622–630 (1984).
- 478 48. Shine, R. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *The
479 Quarterly Review of Biology* **64**, 419–461 (1989).
- 480 49. Price, J. J. & Eaton, M. D. Reconstructing the evolution of sexual dichromatism: Current color diversity
481 does not reflect past rates of male and female change. *Evolution* **68**, 2026–2037 (2014).
- 482 50. Medina, I. *et al.* Habitat structure is linked to the evolution of plumage colour in female, but not male,
483 fairy-wrens. *BMC evolutionary biology* **17**, 35 (2017).
- 484 51. Miles, M. C. & Fuxjager, M. J. Synergistic selection regimens drive the evolution of display complexity in
485 birds of paradise. *Journal of Animal Ecology* **87**, 1149–1159 (2018).

- 486 52. Weaver, R. J., Santos, E. S., Tucker, A. M., Wilson, A. E. & Hill, G. E. Carotenoid metabolism strengthens
487 the link between feather coloration and individual quality. *Nature Communications* **9**, 73 (2018).
- 488 53. Maan, M. E. & Seehausen, O. Ecology, sexual selection and speciation. *Ecology Letters* **14**, 591–602
489 (2011).
- 490 54. Greenberg, D. A. & Mooers, A. Ø. Linking speciation to extinction: Diversification raises contemporary
491 extinction risk in amphibians. *Evolution Letters* **1**, 40–48 (2017).
- 492 55. Rosenzweig, M. L. *Species diversity in space and time*. (Cambridge University Press, 1995).
- 493 56. Castiglione, S. *et al.* Diversification rates and the evolution of species range size frequency distribution.
494 *Frontiers in Ecology and Evolution* **5**, 147 (2017).
- 495 57. Birand, A., Vose, A. & Gavrilovs, S. Patterns of species ranges, speciation, and extinction. *American
496 Naturalist* **179**, 1–21 (2012).
- 497 58. Claramunt, S., Derryberry, E. P., Remsen, J. V. & Brumfield, R. T. High dispersal ability inhibits
498 speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences*
499 **279**, 1567 (2012).
- 500 59. Jablonski, D. & Roy, K. Geographical range and speciation in fossil and living molluscs. *Proceedings of
501 the Royal Society of London. Series B: Biological Sciences* **270**, 401–406 (2003).
- 502 60. Weir, J. T. & Price, T. D. Limits to speciation inferred from times to secondary sympatry and ages of
503 hybridizing species along a latitudinal gradient. *American Naturalist* **177**, 462–469 (2011).
- 504 61. Davis, M. P., Midford, P. E. & Maddison, W. Exploring power and parameter estimation of the BiSSE
505 method for analyzing species diversification. *BMC Evolutionary Biology* **13**, 38 (2013).
- 506 62. Martins, M. J. F., Puckett, T. M., Lockwood, R., Swaddle, J. P. & Hunt, G. High male sexual investment
507 as a driver of extinction in fossil ostracods. *Nature* **556**, 366 (2018).
- 508 63. Title, P. O. & Rabosky, D. L. Diversification rates and phylogenies: What are we estimating, and how
509 good are the estimates? *bioRxiv* 369124 (2018).
- 510 64. Charge, R., Teplitsky, C., Sorci, G. & Low, M. Can sexual selection theory inform genetic management of
511 captive populations? A review. *Evolutionary Applications* **7**, 1120–1133 (2014).
- 512 65. Harris, G. & Pimm, S. L. Range size and extinction risk in forest birds. *Conservation Biology* **22**, 163–171
513 (2008).
- 514 66. Del Hoyo, J., Elliott, A. & Christie, D. *Handbook of the birds of the world*. **8-16**, (Lynx Edicions
515 2003-2011, 2011).
- 516 67. BirdLife International and Handbook of the Birds of the World. *Bird species distribution maps of the
517 world*. (<http://datazone.birdlife.org/species/requestdis>, 2017).
- 518 68. Hoyo, J. del & Collar, N. J. *HBW and birdlife international illustrated checklist of the birds of the world*.
519 **1**, (Lynx Edicions; BirdLife International, 2016).
- 520 69. Fick, S. E. & Hijmans, R. J. WorldClim 2: New 1-km spatial resolution climate surfaces for global land
521 areas. *International Journal of Climatology* **37**, 4302–4315 (2017).

- 522 70. Otto-Bliesner, B. L. *et al.* Simulating arctic climate warmth and icefield retreat in the last interglaciation.
523 *Science* **311**, 1751–1753 (2006).
- 524 71. Zhao, M., Heinsch, F. A., Nemani, R. R. & Running, S. W. Improvements of the modis terrestrial gross
525 and net primary production global data set. *Remote Sensing of Environment* **95**, 164–176 (2005).
- 526 72. Hackett, S. J. *et al.* A phylogenomic study of birds reveals their evolutionary history. *Science* **320**,
527 1763–1768 (2008).
- 528 73. Quintero, I. & Jetz, W. Global elevational diversity and diversification of birds. *Nature* **555**, 246 (2018).
- 529 74. Rabosky, D. L. *et al.* An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392
530 (2018).
- 531 75. Belmaker, J. & Jetz, W. Relative roles of ecological and energetic constraints, diversification rates and
532 region history on global species richness gradients. *Ecology Letters* **18**, 563–571 (2015).
- 533 76. Rabosky, D. *et al.* BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic
534 trees. *Methods in Ecology and Evolution* **5**, 701–707 (2014).
- 535 77. Harvey, M. G. *et al.* Positive association between population genetic differentiation and speciation rates
536 in new world birds. *Proceedings of the National Academy of Sciences* **114**, 6328–6333 (2017).
- 537 78. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. *nlme: Linear and nonlinear mixed effects*
538 *models*. (2018).
- 539 79. Bartoń, K. *MuMin: Multi-model inference*. (2017).
- 540 80. Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401**, 877 (1999).
- 541 81. Paradis, E., Claude, J. & Strimmer, K. APE: Analyses of phylogenetics and evolution in R language.
542 *Bioinformatics* **20**, 289–290 (2004).
- 543 82. Bijl, W. van der. *Phylopath*: Easy phylogenetic path analysis in R. *PeerJ* **6**, e4718 (2018).