

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

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## Abstract

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

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

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## INTRODUCTION

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

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

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

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

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

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

## MATERIALS AND METHODS

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

### Compiling data for sexual selection and environmental stress

#### Sexual dichromatism

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

#### Male-biased sexual selection

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

#### Environmental variables

We obtained estimates of species range size using expert range maps (BirdLife International and Handbook of the Birds of the World 2017). Because of taxonomic changes to 1,230 species in the *Birdlife* database (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). Furthermore, to estimate variability in the energy available to species, we obtained the mean and standard deviation of net primary productivity (NPP) values between 2000 - 2015 across each species distribution. Estimates of NPP had 30-second resolution and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production products stage 3 (MOD17A3; Zhao et al. 2005). Using these data, which we provide as a potentially useful data resource (see ESM), we generated five predictors of speciation associated with different patterns in environmental variability (see below).

### Generating biologically relevant predictors for environmental variation

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

### Estimating extinction and speciation

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

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

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

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

## Phylogenetic comparative analysis

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we used phylogenetic least squares (PGLS) models in the **nlme** package (Pinheiro et al. 2018). We began by estimating the phylogenetic signal — Pagel's  $\lambda$  (Pagel 1999) — using the **corPagel** function in the **ape** package (Paradis et al. 2004) on the MCC tree. The estimate of  $\lambda$  was then fixed for model selection, which was conducted on the same MCC tree derived from 2,500 draws of the posterior distribution (Jetz et al. 2012). Model selection used either  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  or  $\mu_{BAMM}$  tip-rate estimates from the MCC tree as the response variable. For  $\lambda_{BAMM}$  and  $\mu_{BAMM}$  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 100 phylogenetic trees used to derive  $\lambda_{DR}$ ,  $\lambda_{ND}$ ,  $\lambda_{BAMM}$  and  $\mu_{BAMM}$ , using the unique response variables and phylogenetic tree correlation structure in each model. This method enabled us to present model estimates for an MCC tree alongside 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,  $\lambda_{DR}$  as the single measure of speciation and the tip-rates from the MCC tree. Further details of the path analysis, including reasons for path directions, can be found within the ESM along with all other analyses and the relevant R code to reproduce results.

## RESULTS

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

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

## No evidence that sexual dichromatism affects speciation

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

## Male-biased sexual selection increases speciation

We found a significant positive association between male-biased sexual selection ( $n = 2,465$ ) and  $\lambda_{DR}$  ( $\beta = 3.887e-02$ ,  $p = 0.012$ ; Figure 1b). However, this association was not significant for the other two measures of speciation rate ( $\lambda_{ND}$ :  $\beta = 4.383e-04$ ,  $p = 0.351$ ;  $\lambda_{BAMM}$ :  $\beta = 9.423e-04$ ,  $p = 0.764$ ; Figure 1b). The distribution of estimates from PGLS models on 100 random trees was similar to the estimate from the MCC tree: among the 100 trees there was a positive association between sexual selection and  $\lambda_{DR}$  (HPD Interval =  $9.111e-03$ ,  $6.085e-02$ ), and a smaller positive association between sexual selection and  $\lambda_{ND}$  (HPD Interval =  $-3.111e-04$ ,  $1.536e-03$ ; ) as well as  $\lambda_{BAMM}$  (HPD Interval =  $-1.295e-02$ ,  $3.088e-02$ ). Complete HPD intervals for models using male-bias sexual selection PPCA as a predictor can be found within Table S15.

## Species with smaller ranges have increased rates of speciation

Based on  $\lambda_{DR}$  and  $\lambda_{ND}$  tip-rate metrics of speciation, we found a negative association between range size and speciation; that is, species with smaller ranges show marginally higher values for  $\lambda_{DR}$  and  $\lambda_{ND}$ . This negative association was small but significant for models using the MCC tree ( $\lambda_{DR}$ :  $\beta = -6.579e-03$ ,  $p = 0.001$ ;  $\lambda_{ND}$ :  $\beta = -1.462e-04$ ,  $p = 0.034$ ; Figure 1a, Figure 2). This association was also evident across the estimates from models using the 100 trees ( $\lambda_{DR}$ : HPD Interval =  $-8.438e-03$ ,  $-1.823e-03$ ;  $\lambda_{ND}$ : HPD Interval =  $-1.898e-04$ ,  $9.115e-06$ ; Figure 1a). Subset models with reduced sample size and different measures of sexual selection — but the same measure of range size — showed variable evidence that range size is negatively associated with speciation. Range size significantly predicted  $\lambda_{DR}$  (Figure 1b) using data subset for male-biased sexual selection ( $n = 2,465$ ) but not  $\lambda_{ND}$  or  $\lambda_{BAMM}$ . Models using data subset for spectrophotometry-based dichromatism ( $n = 581$ ) gave non-significant estimates for the effect of range size on all measures of speciation (Figure S11, Table S11, Table S12). Because the range size dataset is the same across the three data subsets

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

## Phylogenetic path analysis

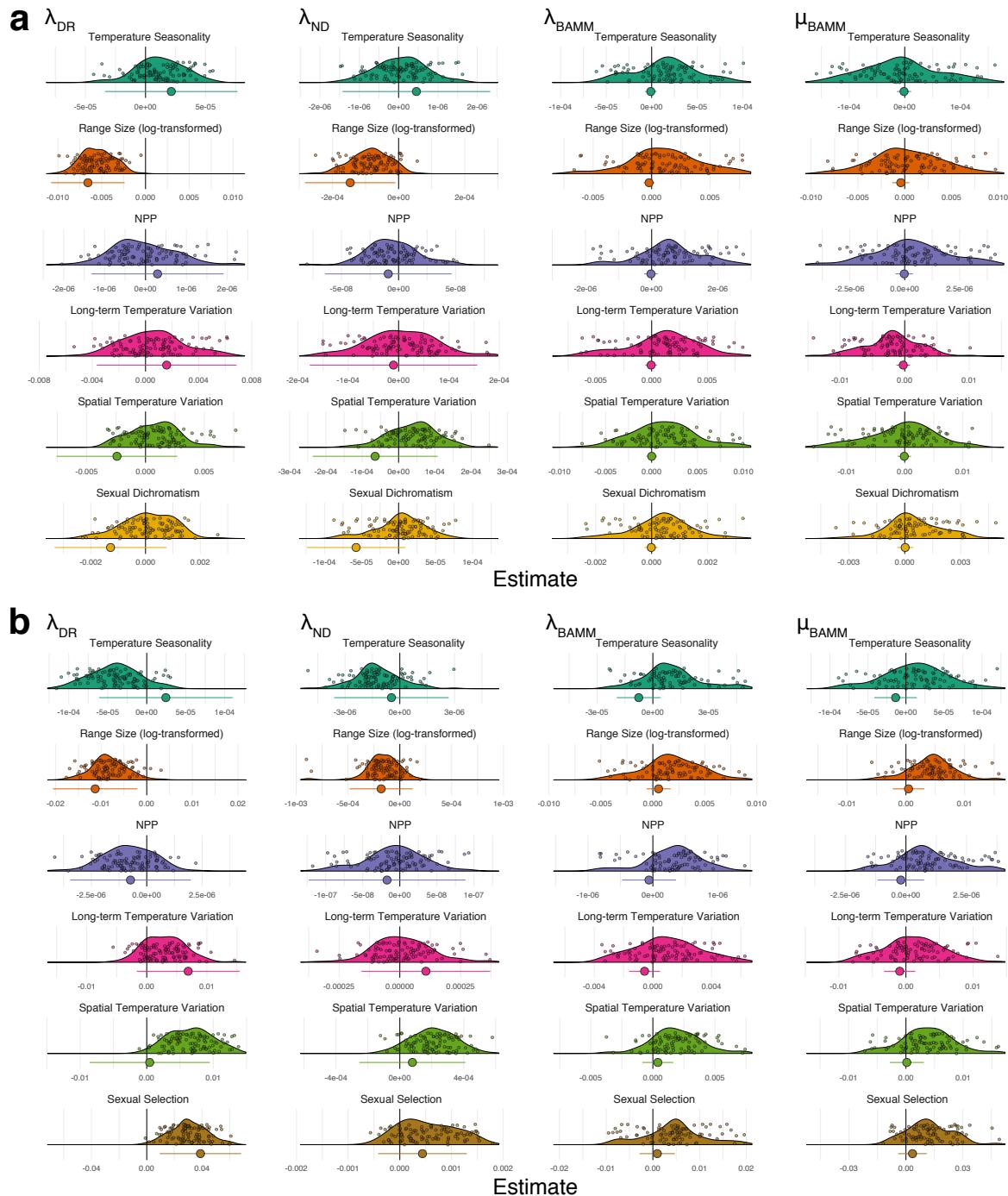
Using a phylogenetic path analysis, we found multiple significant paths between variables used in the PGLS (Figure 3; Figure S14). Notably, environmental variability (temperature seasonality) directly affected sexual dichromatism ( $\beta = 0.07$ ) and the path from male-biased sexual selection to sexual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

## Extinction rate

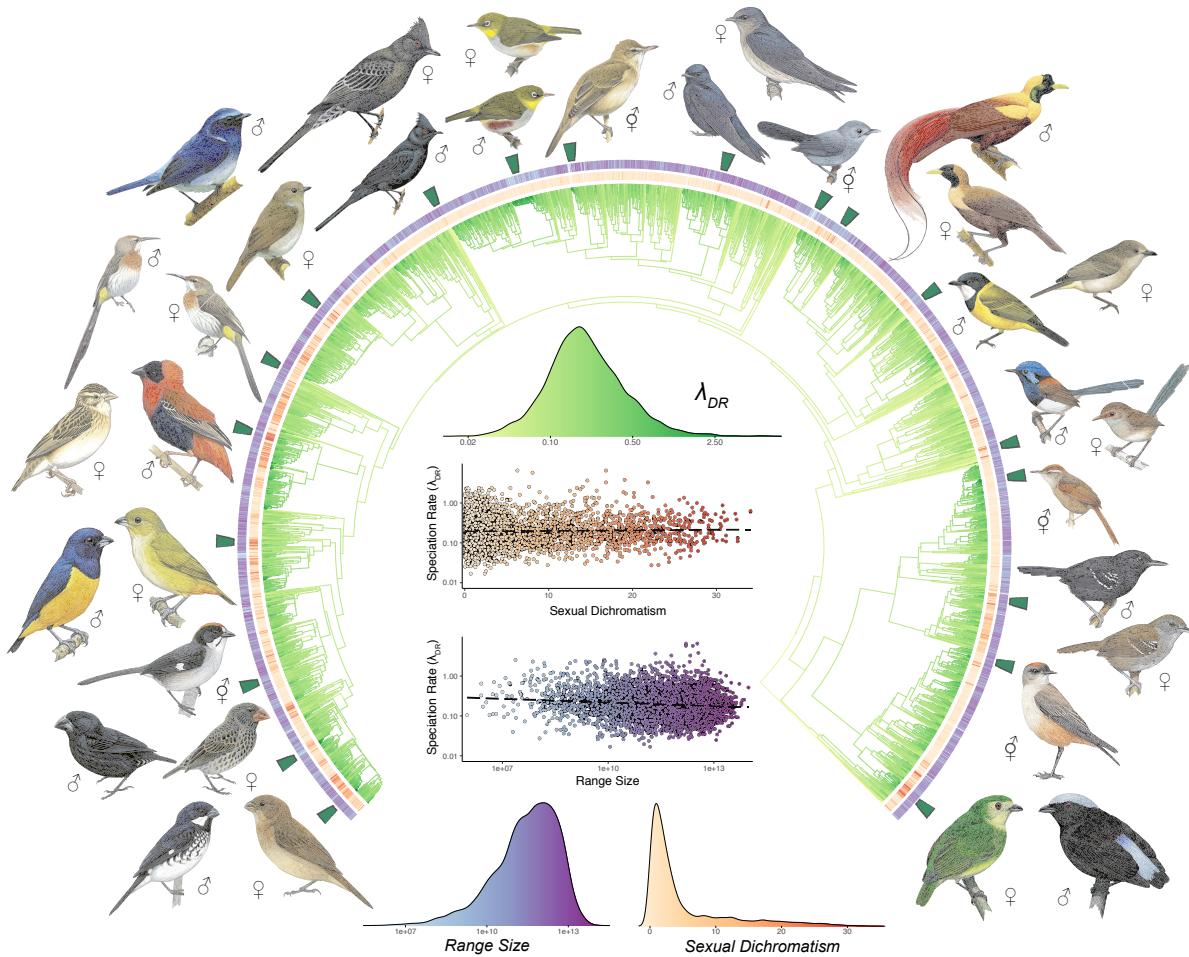
We found no evidence that extinction ( $\mu_{BAMM}$ ) was impacted by the extent of sexual dichromatism for full-taxon sampling ( $\beta = 2.385\text{e-}05$ ,  $p = 0.93$ ; Figure 1a), nor spectrophotometry-based measures of sexual dichromatism (Figure S11, Table S11, Table S12) or male-biased sexual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

## Variability across trees and methods

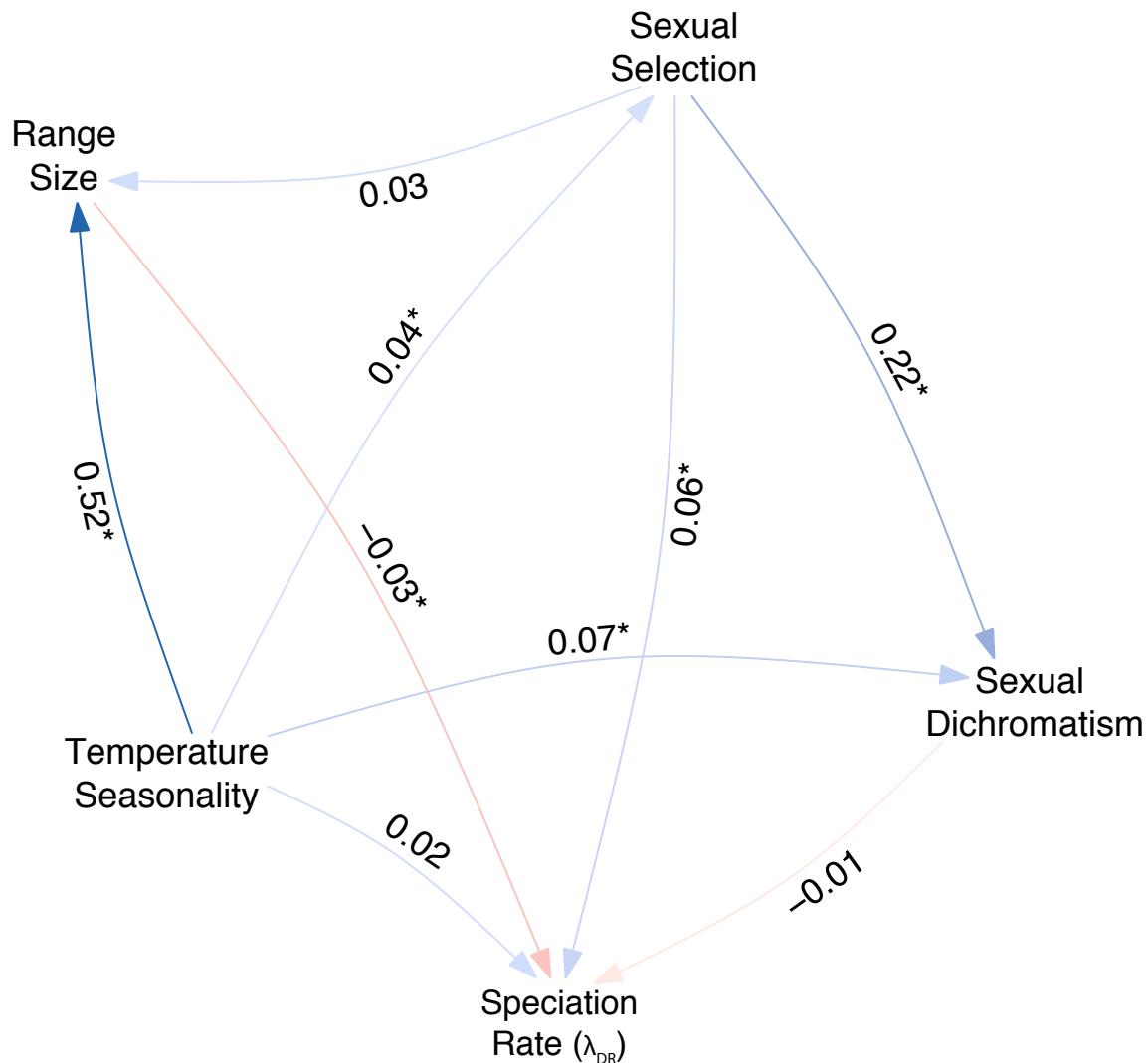
We tested our hypothesis that sexual selection is associated with speciation using several methods and across 100 trees drawn from the post-burn-in posterior (Jetz et al. 2012). We used a range of methods to overcome uncertainty in the power and precision of various tip-rate estimates as well as the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



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



**Figure 2:** Speciation rate ( $\lambda_{DR}$ ) across all passerine birds ( $n = 5,965$ ) with estimates of sexual dichromatism and range size available for 5,812 of them. Across these species there was a small but significant negative association between  $\lambda_{DR}$  and log-range size but no significant association between  $\lambda_{DR}$  and sexual dichromatism based on RGB.  $\lambda_{DR}$  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  $\lambda_{DR}$  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 ( $n = 2,465$ ).

## DISCUSSION

We found evidence that the composite measure of male-biased sexual selection, but not the measure of sexual dichromatism, explains variation in the rate of speciation in passerine birds. The absence of a detectable correlation between sexual dichromatism and speciation rate was consistent across different measures of speciation ( $\lambda_{DR}$ ,  $\lambda_{ND}$  and  $\lambda_{BAMM}$ ) and both measures of dichromatism (spectral and RGB). These findings substantiate previous studies performed at smaller scales in birds, where sexual dichromatism measures were obtained using spectrophotometry (Huang and Rabosky 2014) and human observers (Cooney et al. 2017). The correlation between speciation rate and the index of male-biased sexual selection (which reflects sexual size dimorphism, social polygyny, and [lack of] paternal care) was statistically significant for  $\lambda_{DR}$ , but not for  $\lambda_{ND}$  and  $\lambda_{BAMM}$ , although the estimated sign and magnitude of the correlation was broadly similar across all speciation measures. Interestingly, we found a negative relationship between range size and speciation rates, at least when this rate was quantified by  $\lambda_{DR}$  and  $\lambda_{ND}$ . This suggests that species with smaller range sizes have increased speciation rate. None of the bioclimatic measures of environmental variability that we investigated (*i.e.*, temperature seasonality, long-term temperature variation, and spatial temperature variation) predicted speciation rate.

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

In-line with some theoretical predictions and previous studies (Kraaijeveld et al. 2011) we found that

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

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

In addition to speciation, sexual selection has frequently been invoked as a driver of extinction. Sexual selection may increase extinction risk as it often leads individuals (usually males) to invest in exaggerated mating signals as opposed to traits — such as parental care — that elevate offspring fitness (*reviewed in* Kokko and Brooks 2003). Using the model-based approach of BAMM, we found no association between extinction rate and sexual dichromatism, male-biased sexual selection or measures of environmental variability. Extinction is notoriously difficult to estimate accurately from phylogenies, principally because many different combinations of speciation and extinction rates can give rise to similar patterns of diversity (*see* Rabosky 2016). Phylogenetic methods such as BAMM allow for speciation and extinction rates to be measured using moderately-sized phylogenies, although the ability of BAMM to model evolutionary rate shifts and extinction rates remains a subject of debate (*see*, Beaulieu and O’Meara 2015; Rabosky 2016; Moore et al. 2016; Rabosky et al. 2017). Additionally, while several tip-rate estimates exist for speciation rate (*e.g.*,  $\lambda_{DR}$  and

$\lambda_{ND}$ ), tip-rate estimates of extinction rate are difficult to obtain without complex Bayesian models and are fraught with issues of sampling bias (Davis et al. 2013). Although extinction rates can be estimated from alternative sources, such as the fossil record, documented recent extinctions and IUCN extinction threat status, each approach has limitations. Across the passerine bird phylogeny, we found that BAMM often produced homogeneous speciation and extinction rates for smaller clades showing few rate shifts, which might reduce our power to detect small differences in extinction rates among closely-related taxa (Rabosky et al. 2017; Title and Rabosky 2018). Thus, this methodological constraint likely decreases our ability to accurately measure the correlation between metrics of sexual selection and the probability of extinction.

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

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## CRITICAL ANALYSIS

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

— ALFRED RUSSEL WALLACE

### Strengths and limitations

One of the biggest unravelings of this project was the decoupling of male-biased sexual selection from sexual dichromatism in predicting speciation, remarkably this same controversy engrossed Wallace and Darwin 130 years ago (Kottler 1980). The widespread use of sexual dichromatism as a proxy for sexual selection often goes unchallenged as our instinctive Darwinian minds reminisce of peacocks and birds of paradise. Although sexual dichromatism measurements from illustrations were always going to be an imperfect estimate of sexual selection, across 5,831 species I anticipated a signal would permeate through the noise. Alas — this was not so — and male-biased sexual selection and sexual dichromatism had different effects on speciation. With this in mind, the practical use of sexual dichromatism in macroevolutionary research is severely weakened. This finding is pertinent, as efficient proxy measurements are invaluable for comparative analyses. Proxies of sexual selection increase the accessibility, available sample size and transferability of research, making a study more conducive to research synthesis. But, as Wallace remarks, the matter is inevitably more complex, despite the irresistibility of the Darwinian argument<sup>1</sup> (Kottler 1980; Caro 2017). On the bright side, the multivariate measure of male-biased sexual selection (sexual dimorphism, social polygyny and [lack of] paternal care) is a dataset that would benefit from being embiggened across birds. Future research may also benefit from expanding this multivariate measure to account for ornamentation, often overlooked by sexual dimorphism and dichromatism measures (Gomes et al. 2016).

Like sexual selection, estimates of speciation and extinction are a point of controversy, with macroevolutionary research often plagued by methodological uncertainty. Originally, I had planned to continue my meta-analysis by investigating extinction rate across a large taxonomic group. There were signs that extinction rate could be measured from phylogenies with confidence (*see* Pyron and Burbrink 2016). However, these hopes soon dissipated, and with them the seeming *raison d'être* of the study. Extinction rate is arguably the best measure of population fitness as it tracks survival over multiple generations. And while a high profile study has measured extinction rate in experimental evolution (Lumley et al. 2015), it has been rarely measured alongside sexual selection over evolutionarily meaningful timescales (*but see* Martins et al. 2018). We included measurements of extinction rate in this study, but the findings were played-down. The movement away from extinction and towards speciation is because of the controversy surrounding extinction rate measures as well as phylogenetic uncertainty. Measuring extinction rates from the Jetz et al. (2012) bird phylogeny is

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

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

The most severe limitation for environmental variation was the coarseness of the measures. In total, for 5,831 species, we extracted 338,203,831 point measures of environmental variability<sup>2</sup>. But these measures may not be as valuable as their volume implies since they do not account for variation in biotic components such as nutritional resources or predation. However, our methods are still improvements on using the range mid-point to obtain a measure of climate or using a single bioclimatic variable. While reducing the multivariate data into several biologically meaningful predictors is a conceptually challenging exercise, researchers should not feel limited by the amount of raw data that they can access<sup>3</sup>. In fact, previous to our study on birds the same methodology was applied to ~100 species of bovids with speciation, extinction and environmental variability estimates obtained. This study was prematurely halted as there was homogeneity in speciation and extinction rates across the smaller bovid phylogeny. However, this workflow was easily transferred over to passerine birds, with similar methods used for extracting environmental predictors. The use of extensive bioclimatic predictors and spatial data in macroevolutionary research is imperative as we scale-up studies. At very least, if bioclimatic variables do not encapsulate key ecological parameters (*e.g.*, resources, predation, habitat structure) these predictors may account for some of the noise in the dataset and may help isolate the effect of the key moderator variables of interest.

## Future directions

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

<sup>2</sup>5,831 species × 1,000 samples per range × 59 environmental variability measures including bioclimatic predictors now, in the last inter-glacial and the last glacial maximum as well as NPP.

<sup>3</sup>This statement applies to species with documented range sizes, which varies across clades but is comprehensive for birds, mammals, amphibians and many marine groups. The IUCN has a large and accessible database for research use.

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

Estimating extinction risk from the fossil record is difficult because many clades (*e.g.* birds) lack the stratigraphic sampling across time to statistically calculate extinction rates. But there are exceptions. Using fossil ostracods (a group of marine invertebrates), Martins et al. (2018) found that species with high levels of sexual dimorphism were quickly swept to extinction. From stratigraphic occurrence data, a capture–mark–recapture model was used to determine the extinction rate of 93 species. This finding challenges the results from experimental evolution studies that suggest sexual selection mitigates extinction (Jarzebowska and Radwan 2010; Plesnar-Bielak et al. 2012; Lumley et al. 2015). The use of fossil data overcomes limitations of other comparative analyses, which by contrast, show mixed evidence in the relationship between sexual selection and extinction in birds (Mitra et al. 1996; Doherty et al. 2003; Morrow and Pitcher 2003) and mammals (Morrow and Fricke 2004; Bro-Jorgensen 2014). In these cases, studies have often relied on extinction threat status from the IUCN Red List and are likely biased to species under greater anthropogenic threat, culturally valued or well researched. In future, it would be valuable to see whether other groups of marine invertebrates have the fossil data and recognisable sexual dimorphism to conduct such a study. In the interim, I would be eager to see how BAMM performs on a robust ostracod phylogeny and whether the same positive association between extinction rate and sexual dimorphism could be detected from the phylogeny. This will be a true test of the applicability of BAMM and a key step in the effort to reliably measure extinction rates across a wider variety of species.

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