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

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Sexual selection can shape phylogenetic diversity by affecting 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. Here, we investigate the relationship between sexual selection and diversification in passerine birds. Multiple studies use sexual dichromatism as a proxy for sexual selection, however, this relationship can be weak in many clades. Thus, we use two measures of sexual selection — sexual dichromatism and a multivariate measure of male-biased sexual selection — to test the link between sexual selection and diversification. We also test whether the effect of sexual selection on diversification is contingent on ecological variables. Our results show that male-biased sexual selection, but not sexual dichromatism, can explain speciation rates () in passerines. We also find that birds with smaller ranges have higher speciation rates, but there is no interaction between environmental variables and sexual selection. Our findings show that sexual dichromatism is a poor proxy for sexual selection at least a a broad-scale, and support the view that sexual selection is an evolutionary force shaping patterns of diversity amongst songbirds.

# Introduction

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). Experiments suggest that sexual selection can influence the evolution of a surprisingly diverse set of traits (Cally et al. 2019), and may therefore strongly influence extant patterns of species diversity. For instance, in antbirds (Thamnophilidae), genera with complex songs and striking dichromatism are more species-rich (Seddon et al. 2008). Divergent mating signals in one sex (usually males) co-evolves 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 variation over space and time) may lead to increased speciation rates.

Birds are a speciose and well-characterised group of organisms with remarkable and variable sexually-selected traits such as song and colourful plumage, thus 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, multiple macroevolutionary studies estimate the strength of sexual selection using proxies such as sexual dimorphism or dichromatism, but sexual selection in birds can involve many other traits, such as song, or the use of ornaments like long tail feathers, bowers, crests and displays (*e.g.*, Uy and Borgia 2000; Pryke et al. 2001). In fact, it was recently highlighted that song divergence is inversely correlated to sexual dichromatism in passerines, suggesting that there is a trade-off between signalling modalities (Cooney et al. 2018). Our study compares the role of sexual dichromatism and other sexual selection proxies in the generation of species. Additionally, we test the relative contribution of environmental variables to the generation of diversity, and how environment and sexual selection could interact to drive speciation processes (Long et al. 2012; Connallon and Hall 2016).

To test the link between different measures of sexual selection and diversification processes we use a large (*n* = 5,812) dataset of sexual dichromatism (estimated from illustrated drawings; Dale et al. 2015), as well as a reduced 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 majority of bird genera. Additionally, we use multiple metrics 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 reliable tip-rate statistics, such as diversification rate () and node density ().

# 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 .

## 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 another 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 museum 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 (; ).

### 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 possitively 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 (; ).

### 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 (~1 km2) 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 ), we generated five predictors of speciation associated with different patterns in environmental variability (see below).

### Generating biologically relevant predictors for environmental variation

Given that stressful environments are expected to interact with sexual selection and have a positive effect on adaptation (Cally et al. 2019), we used the extracted environmental variables from each species range size to develop biologically meaningful predictors of environmental variation/stress. Firstly we used (*i*) the average NPP in each species’ range and (*v*) the log-transformed range size as potentially informative predictors of speciation rates. We also used three environmental predictors dervived from bioclimatic data. These predictors relate to seasonal climate variation, spatial climate variation and long-term climate variation. To obtain seasonal climate variation we used (*iii*) mean values of temperature seasonality (BIO4) for each range. (*iV*) To estimate levels of spatial environmental variation a species may endure we used the first principle component (PC1) from a PCA on standard deviations from all bioclimatic variables, excluding temperature and precipitation seasonality (BIO 4 and BIO15). PC1 was heavily loaded towards bioclimatic variables relating to temperature, thus PC1 reflects the variation in temperature across a species’ range (). Species range is a potentially informative predictor of speciation and extinction, so we controlled for the correlation between environmental spatial variation and range size — where larger ranges have larger variation in PC1 — by using the residuals of a fitted general additive model (GAM; ) 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 (). The five predictors of environmental variability are not strongly correlated (). Details and R code to generate these predictors can be found within the .

## Estimating extinction and speciation

Phylogenetic information was obtained from www.birdtree.org (Jetz et al. 2012). We used a maximum clade credibility (MCC) tree from 2,500 samples of the posterior distribution (*n* = 5,965) as the main phylogenetic hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using tip-rate measures (1000 trees) and BAMM (100 trees)(Rabosky 2014). These trees used a ‘Hackett backbone’ (Hackett et al. 2008) and were constructed using a pure birth (Yule) model. We calculated three different tip-rate metrics of speciation and one of extinction across all trees.

Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES), also known as diversification rate (DR) (*e.g.*, Jetz et al. 2012; Quintero and Jetz 2018; Rabosky et al. 2018), is derived from the sum of edge lengths branching from a node, with each edge towards the root having the length down-weighted. Studies have suggested that DR and ND (henceforth referred to as and ) are more reflective estimates of speciation than diversification (Belmaker and Jetz 2015; Title and Rabosky 2018). Therefore, is a measure of speciation rate more heavily weighted to recent speciation events and 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, and 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 ; briefly, we used a time-variable model with 100 expected number of shifts and prior rates set from the initial speciation and extinction values using the BAMMtools R package (Rabosky et al. 2014). Each BAMM model (one MCC tree and 100 random draws of the posterior) was run for 100 million generations, and given the computationally intensive nature of BAMM, runs were conducted across multiple CPUs. Each run of BAMM reached convergence with effective sample size (ESS) of MCMC (Markov Chain Monte Carlo) samples surpassing 200 (an arbitrary value, above which posterior distributions can often be accurately inferred) for the key model parameters of log-likelihood and number of rate shifts (, ). Further details of BAMM parameters and output are available in the , with tip-rate means and variances provided. Additionally, given the variability in BAMM estimates, we also provide analysis of BAMM shift configurations and tip-rate estimates from our run on the MCC tree and within a BAMM run on the MCC tree from a genetic-only phylogeny across all birds (Harvey et al. 2017). All analyses were conducted on log-rates.

## Phylogenetic comparative analysis

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we used phylogenetic least squares (PGLS) models in the nlme package (Pinheiro et al. 2018). Firstly we conducted model selection using , , or tip-rate estimates from the same MCC tree, which was derived from 2,500 draws of the posterior distribution (Jetz et al. 2012). For and we were also able to use model weights sourced from the inverse of the variance of tip-rates for a given species from the posterior distribution (*n* = 1,000). Model weights thus reflect the degree of precision to which each species’ tip-rate is measured in BAMM. Using model selection we only compared interaction terms between a measure of sexual selection (sexual dichromatism or male-biased sexual selection) and environmental measures. That is, we fixed the individual predictors of dichromatism/male-biased sexual selection measures, log-transformed range size, seasonal temperature variation, spatial temperature variation, long-term temperature variation, and NPP while comparing 32 models with different combinations of interactions (including none). Model selection was done in MuMIn using the dredge function (Bartoń 2017). Using the terms from the top-ranking model (lowest AICc), we ran the equivalent model for each of the 1,000 phylogenetic trees used to derive , and each of the 100 used to derive and . In each model we used the unique response variables and phylogenetic tree correlation structure. Specifically, for models using tip-rate metrics (, ) we estimated the phylogenetic signal — Pagel’s (Pagel 1999) — using the corPagel function in the ape package (Paradis et al. 2004) independently for each of the 1,000 trees/models. Alternitively, for models using speciation and extinction estimates derived using BAMM ( and ) we found was consistently estimated at 1 and hence assumed Brownian motion (using the corBrownian function) to estimate the correlation structure. This method enabled us to present model estimates for an MCC tree alongside 1,000/100 trees from the posterior distribution of trees to account for phylogenetic uncertainty. This approach was repeated on three datasets corresponding to each measure of sexual selection: dichromatism derived from RGB values of images (*n* = 5,812); dichromatism from spectrophotometry (*n* = 581) and the multivariate measure of male-biased sexual selection (*n* = 2,465).

Finally, using data subset for species with measurements of male-biased sexual selection, we conducted a phylogenetic path analysis using the phylopath R package (Bijl 2018). The phylogenetic path analysis was used to assess causal paths *between* variables not able to be modelled within the univariate response of PGLS. That is, a phylogenetic path analysis allowed us to model relationships between the predictor variables used in our PGLS analysis as we anticipate environmental variability, sexual dichromatism/selection, and range size to have effects on each other and not just on speciation rate. To minimise path complexity we used temperature seasonality (BIO4) as the single measure for environmental variability, 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 along with all other analyses and the relevant R code to reproduce results.

# Results

## Variability across phylogenetic hypotheses and measures of speciation and sexual selection

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

There was a strong correlation between spectral measures of colour dichromatism and RGB values (; Figure S10) and a weaker correlation between sexual dichromatism and the sexual selection index (, Figure S12).

## 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 ( AICc > 4) for any measure of speciation (, , ) or sexual selection (RGB values, spectrophotometry and male-biased sexual selection; AICc > 4; , , , ). 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 (, ).

## 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 (, , ), 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 ( = -1.279e-03, p = 0.147; a, a) or ( = -5.745e-05, p = 0.078; a). Furthermore, speciation rates from BAMM () were also unaffected by sexual dichromatism ( = -1.429e-05, p = 0.872; a). 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 (). 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 1,000 random trees (for , ) and 100 random trees for . 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 (a, ). For PGLS models using spectrophotometry-based measures of sexual dichromatism, the estimates from the 100 trees in the models are positively skewed (HPD Interval = -1.780e-02, 3.489e-02) but normally distributed around zero for and ().

## Male-biased sexual selection increases speciation

We found a significant positive association between male-biased sexual selection (*n* = 2,465) and ( = 3.887e-02, p = 0.012; b). However, this association was not significant for the other two measures of speciation rate (: = 4.383e-04, p = 0.351; : = 9.423e-04, p = 0.764; b). The distribution of estimates from PGLS models on 1,000 random trees was similar to the estimate from the MCC tree: among the 1,000 tress there was a positive association between sexual selection and (HPD Interval = 4.513e-03, 5.718e-02), and a smaller positive association between sexual selection and (HPD Interval = -5.044e-04, 1.585e-03; ) as well as the 100 models using (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 .

## Species with smaller ranges have increased rates of speciation

Based on and 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 and . This negative association was small but significant for models using the MCC tree (: = -6.579e-03, p = 0.001; : = -1.462e-04, p = 0.034; a, ). This association was also evident across the estimates from models using the 1,000 trees (: HPD Interval = -8.871e-03, -6.610e-04; : HPD Interval = -1.514e-04, 1.724e-05; a). 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 (b) using data subset for male-biased sexual selection (*n* = 2,465) but not or . 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 (, , ). 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 (; ). Notably, environmental variability (temperature seasonality) directly affected sexual dichromatism ( = 0.07) and the path from male-biased sexual selection to sexual dichromatism was relatively weak, ( = 0.22). Additionally, the large direct effect of temperature seasonality on range size ( = 0.52) suggests an indirect effect of temperature seasonality on ( = -0.02; ), given the negative association we identified between and range size in PGLS models.

## Extinction rate

We found no evidence that extinction () was impacted by the extent of sexual dichromatism for full-taxon sampling ( = 2.385e-05, p = 0.93; a), nor spectrophotometry-based measures of sexual dichromatism (, , ) or male-biased sexual selection (b, , ).

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

Figure 2: Speciation rate () across all passerine birds (n = 5,965) with estimates of sexual dichromatism, range size available for 5,812 species and male-biased sexual selection available for 2,465 species. Across these species there was a small but significant negative association between and log-range size as well as a significant positive association between and male-biased sexual selection but no significant association between and sexual dichromatism based on RGB measures. 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 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 (, and ) 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) and no association was found. 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 , but not for and , although the estimated direction and magnitude of the correlation was broadly similar across all speciation measures. Interestingly, we found a consistent negative relationship between range size and speciation rates, at least when this rate was quantified by and . This suggests that species with smaller range sizes have increased speciation rates. 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 at least at this broad scale, 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 probably evolved in response to spatial variation in predation pressure, increasing dichromatism (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 and 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). Another possibility is that 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). Finally, 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; Castiglione et al. 2017). However, the opposite pattern has also been suggested and birds with limited dispersal or more specialised niches can have more fragmented populations, which would promote vicariant divergence and higher speciation rates (Jablonski and Roy 2003; Birand et al. 2012; Claramunt et al. 2012). Alternatively, reduced range size may be correlated but not causally related to 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 could 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.

One outcome of our analyses was the fact that different measures of speciation rates presented different results. This is not completely unexpected, given that each of the rates is calculated in a different way (discussed in detail in Title and Rabosky (2018)). For instance, is weighted higher towards speciation events close to the tips, and allows more rate heterogeneity compared to BAMM estimates (although increasing error rate). The higher variation in could explain why we detected a significant pattern using this metric and not the other two. Moreover, it has been shown that the power of PGLS approaches is reduced compared to other alternatives such as simulations (Harvey Michael et al. 2017), however given the complexity of our model this was the most straight forward approach. This opens the possibility that the patterns detected with are also present in the other speciation metrics but there is not enough statistical power to detect them (at least for ). We think it is unlikely that the significant correlation between and sexual selection is spurious given the limited power of the PGLS approach, the large heterogeneity in values and the consistency in the calculated estimates across the 1,000 trees.

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 estimated 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.*, and ), 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. These findings support the idea that sexual dechromatism is not a reliable proxy for sexual selection, and that alternative measures of sexual selection are more directly related to diversification. 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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