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Sexual selection is thought to shape phylogenetic diversity by affecting speciation or extinction rates. However, the net effect of sexual selection on diversification is hard to predict *a priori*, because many of the hypothesised effects on speciation or extinction have opposing signs and uncertain magnitudes. Here, we test whether the strength of sexual selection predicts variation in speciation and extinction rates across passerine birds (up to 5,812 species, covering most genera). We tested for associations between two measures of sexual selection (sexual dichromatism and a multivariate measure of male-biased sexual selection), several environmental variables, and multiple measures of speciation and extinction rates. Our results show that male-biased sexual selection, but not sexual dichromatism, predicts speciation rates () in passerines, and found no evidence that this relationship varies with the environment. We also found a strong negative relationship between range size and speciation rate. There was no correlation between sexual selection and extinction rate (). Our findings show that sexual dichromatism is a poor proxy for sexual selection at least a broad-scale and support the view that sexual selection is a potent evolutionary force that has shaped diversification analysis, Plumage dichromatism, Range size, Extinction rate. in songbirds.

Speciation rate, Comparative

# Introduction

Sexual selection results from competition between same-sex individuals for mates, their gametes, or associated resources, and in most species it predominently operates on males1–3. There is long-standing interest in the relationship between sexual selection and the processes of speciation, extinction, and phylogenetic diversification4–8. Recent empirical and methodological advances, such as growing evidence that sexual selection can profoundly affect many traits9, larger and more accurate phylogenies10, and new phylogenetic methods11,12, present new opportunities to test whether and how sexual selection drives diversification.

Several hypotheses predict a positive relationship across species between the strength of sexual selection and the rate of speciation and/or extinction. For example, sexual selection is involved in reinforcement, a speciation-promoting process in which members of different phylogenetic lineages evolve to avoid unproductive inter-lineage mating/fertilisation13. Additionally, sexual selection often operates on traits that can create reproductive isolation when they diverge between lineages, such as signals and preferences involved in mate selection4,5,14, sperm-egg interactions15, or genital morphology16. Furthermore, sexual selection has been hypothesised to increase diversification by maintaining trait combinations that would be selected out under pure natural selection17,18, and by helping to prevent extinction by purging deleterious mutations19, fixing beneficial ones20, and accelerating adapation in environments9,21,22.

Conversely, sexual selection might hinder speciation or make extinction more likely by favouring traits that improve mating success but reduce population fitness. For example, species with expensive sexual signals may be less resilient to environmental change23, and sexual selection often creates a ‘tragedy of the commons’ by selecting for traits that increase the reproductive success of individuals while reducing population-wide productivity1,2,24,25. Sexual selection might also promote extinction by causing maladaptation (‘gender load’) in female traits that are genetically correlated with sexually-selected male traits26–30.

Importantly, the relationship between sexual selection and diversification might be contingent on the environment. Theoretical work predicts that sexual selection should have a more positive effect on adaptation and population fitness in variable environments relative to stable ones31,32, though the empirical evidence for this theory is mixed and largely limited to insects9. The mechanism underpinning this prediction is that the environment and the selective history of the population should influence the relative amounts of genetic variation at sexually concordant loci (i.e. loci where the same allele is fittest for both sexes) and sexually antagonistic loci (where different alleles are favoured in each sex). In stable environments, variation is thought to be preferentially depleted at sexually concordant loci, leading to stronger gender load and reduced net benefits of sexual selection32, and potentially to a more negative relationship between sexual selection and diversification rates across species. Conversely, sexual selection might be especially important at promoting local adaptation when the environment displays variability at the relevant spatial and temporal scales21,33–35

Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification7,36–39. Birds are well-suited for this purpose due to their diverse and well-characterised mating systems and sexually-selected traits, and because their phylogenetic relationships are comparatively well-known. A 2011 meta-analysis covering 20 primary 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 or fish40. However, there was large variation in effect size estimates across the 20 studies, likely reflecting differences in methodology, such as metrics used to characterise speciation and sexual selection, in addition to true biological differences. More recently, 39 found no association between sexual dichromatism and speciation (*n* = 918 species) in a study using spectrophotometric measurements of museum specimens41 and tip-rate estimates from a molecular-only phylogeny10. Similarly, 42 found no effect of sexual dichromatism on diversification across 1,306 pairs of species, using dichromatism scores provided by human observers.

Here, we investigate the association between sexual selection and diversification in birds while building upon previous approaches in multiple ways. We use two measures of the strength of sexual selection: sexual dichromatism43, as well as an index of male-biased sexual selection43, which captures (co)variation in sexual size dimorphism, social polygyny and paternal care. These two measures are used because sexual dichromatism does not always signal the presence of strong sexual selection and *vice versa*43. For example, male and female dunnocks (*Prunella modularis*) are similarly coloured yet sexual selection appears to be strong44. Furthermore, a recent comparative study found a negative relationship between dichromatism and another sexually-selected trait (song) across species, suggesting that a multi-trait focus would improve estimates of sexual selection intensity8. Additionally, our analysis includes multiple ecological and environmental variables on diversification, allowing us to adjust for potential confounds, to identify environmental factors driving diversification, and to test whether environmental factors interact with sexual selection as theory predicts32. We use multiple approaches for quantifying speciation and extinction rates at the tips of phylogenetic trees, including BAMM45–48, as well as older but reliable tip-rate statistics, such as diversification rate () and node density ().

# Results

## Variability across phylogenetic trees and speciation rate measures

**[Is it possible to move this later in the Results? It’s possibly not ideal to start by highlighting the dependence of our conclusions on the methods we choose, and not mentioning our main non-null finding regarding the SS index. Having said that I can see a case for leaving it here too. - Luke] [We initially had this at the end but moved it up to the start. What do you think Devi? - Justin]**

Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially in the BAMM rates ( and ), where the 95 % highest posterior density (HPD) interval across phylogenetic least squares (PGLS) model estimates from 100 trees was often > 20 times larger than the 95 % confidence interval for estimates from a single PGLS model using the MCC (maximum clade credibility) tree. This contrasts with variation across trees for the other rate estimates ( and ), where the 95 % HPD interval of model estimates for pgls models using 1,000 trees was near-equivelant to the 95 % confidence interval calculated for pgls model estimates of the MCC tree (). Given the computational requirements of BAMM, the great majority of earlier studies have based their estimates on a single consensus tree, and so the inconsistency of the BAMM estimates between different phylogenies with similar statistical support is notable. Mean measures of speciation rate 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, ). Full details of the BAMM results are presented as supplementary materials.

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

**[I think this part should go after the next 2 sections, as it’s a more confusing being about interactions, and we should preserve the order of ideas from the Abstract and Intro. - Luke] [Statistically, I think it is best to rule out the interactions first but Yes I see your point - Justin]**

We next fit PGLS models with 2-way 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 the full model for posterior model selection. However, no interaction terms were 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 different measures of speciation (, , ) as the response variable, 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 spectrophotometry41 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 trees (for , ) and 100 trees for . The HPD intervals show model estimates are distributed around zero when using complete taxon sampling models and RGB measures of sexual dichromatism (: HPD Interval = -1.635e-03, 1.658e-03, : HPD Interval = -4.256e-05, 5.499e-05,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 rate

We found a significant positive association between male-biased sexual selection (*n* = 2,465) and for the MCC tree ( = 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 trees was similar to the estimate from the MCC tree: among the 1,000 trees there was a positive association between sexual selection and (HPD Interval = 4.513e-03, 5.718e-02), and the distribution skewed towards a 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 equivocal 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 (; ). There was a modest effect of male-biased sexual selection on sexual dimorphism ( = 0.22). Additionally, temperature seasonality weakly affected sexual dimorphism ( = 0.07) and strongly affected range size ( = 0.52). This 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, , ).

Model estimates (**a**) for the effect of log-range size and sexual dichromatism on speciation and extinction rates using PGLS analyses with the sexual dichromatism dataset (RGB values, n = 5,812). (**b**) depicts the scatter plot of speciation rate () 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 (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 randomly sampled trees (for and ) or 100 randomly sampled 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 randomly sampled trees for BAMM models in order to be able to visualise the MCC 95% CIs.

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 six species are: Sporophila bouvronides, Euplectes franciscanus, Phainopepla nitens, Paradisaea rubra, Malurus pulcherrimus, 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.

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 index of male-biased sexual selection, but not measures of sexual dichromatism, is correlated with 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), and it cannot be explained by a difference in statistical power since the sample size for the dichromatism analyses was much larger. These findings reaffirm the conclusions of previous, smaller studies in which sexual dichromatism was measured using spectrophotometry39 or human observers42. The correlation between speciation rate and the index of male-biased sexual selection (which encapsulates variation in sexual size dimorphism, social polygyny, and paternal care) was statistically significant for , but not for and , although the estimated direction and magnitude of the correlation was broadly similar across all three measures. Interestingly, we also found a consistent negative relationship between range size and speciation rate, at least when this rate was quantified using and . None of the bioclimatic measures of environmental variability that we investigated (i.e., temperature seasonality, long-term temperature variation, and spatial temperature variation) significantly predicted speciation rate.

The difference in findings between the analyses of sexual dichromatism *versus* the index of sexual selection is noteworthy, because the majority of earlier studies used dichromatism alone as their proxy for sexual selection36–39,49. Given our findings, and the modest correlation between dichromatism and the sexual selection index43, we hypothesise that sexual dichromatism may not be a robust proxy for sexual selection. Although dichromatism clearly reflects sexual selection to some extent, it is possibly that it is too indirect a measure to detectany association with speciation rate, even with a high sample size. 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 niches50–53 or experience different selective pressures in contexts other than competition for mates54. For example, in superb fairy-wrens (*Malurus cyaneus*) female colouration has probably evolved in response to spatial variation in predation pressure, increasing dichromatism55. 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 weakly. Secondly, colour is only one of the traits subject to sexual selection9,56. For instance, sexual selection may promote investments in other mating signals (e.g. song) that trade-off against plumage colour, leading to variable investment in different sexually selected signals across species8. 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 success57. 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 studies40 we found that male-biased sexual selection increases speciation rate, at least when speciation is measured by . 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 has several possible interpretations. Firstly, the effects of sexual selection on adaptation and speciation may depend on the type of environmental variability under which the species is evolving. Specifically, speciation rates might be impacted by genetic constraints on adaptation, that vary across environments. Theory suggests that sexual antagonism (which is often exacerbated in species with strong sexual selection) may be lower in habitats experiencing cyclical environmental variation (e.g. seasonality), relative to those experiencing directional change in the environment32. Another possibility is that the environmental predictors we chose may not account for the key ecological sources of selection that interact with sexual selection to drive speciation. For example, our study does not include direct measure of food availability or the severity of predation and parasitism, which are both hypothesised to affect sexual selection and speciation34. Finally, it is possible that environmental variability genuinely has little effect on speciation rates, at least in the taxa investigated here.

The most robust finding in our study is the finding that species with smaller ranges have elevated speciation rates. This result is similar to a study of 329 amphibian genera, which found higher diversification rates in taxa with smaller range size58. Intuitively, large range size should promote speciation by creating more opportunities for geographic barriers to form59,60. However, the opposite pattern is also plausible because birds with limited dispersal or more specialised niches can have more fragmented populations, which would promote vicariant divergence and higher speciation rates61–63. It is also possible that high speciation rates cause smaller range sizes, rather than the other way around, for example because repeatedly-speciating lineages tend to fill niches in ways that hinder the geographical expansion of new species54,59,64. However, species undergoing adaptive radiation in new habitats are unlikely to be limited by competition for resources from existing taxa. 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.

In addition to speciation, sexual selection is hypothesised to affect extinction. Using the model-based approach of BAMM, we found no association between the estiamted extinction rate and sexual dichromatism, male-biased sexual selection, or our measures of environmental variability. However, these extinction results should not be regarded as definitive because extinction is notoriously difficult to estimate accurately from phylogenies, principally because different combinations of speciation and extinction rates can give rise to similar patterns of diversity46. 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 is debated45–48. 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 which are sensitive to sampling bias65. Although extinction rates can be inferred from alternative sources, such as the fossil record66, direct observation extinction, or IUCN red list status58, each approach has its 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 taxa48,67. Thus, this methodological constraint likely decreases our ability to accurately measure the correlation between metrics of sexual selection and the probability of extinction.

One outcome of our analyses was that different measures of speciation rates presented different results. This is not completely surprising, because each of the rates is calculated differently (see 67). For instance, is weighted more towards speciation events close to the tips and allows more rate heterogeneity compared to BAMM estimates. This leads to greater variation in relative to the BAMM estimates, potentially explaining the difference in results. The BAMM estimates were also more sensitive to phylogenetic uncertainty.

To summarise, we have shown that male-biased sexual selection, but not sexual dichromatism, predicts speciation in passerines, and that this relationship is not markedly affected by environmental variability. These findings imply that sexual dechromatism is not a reliable proxy for sexual selection, and that alternative measures of sexual selection are more directly related to diversification. Our results also add indirect suppport to the hypothesis that sexual selection promotes adaptation, which has implications for conservation25 and captive breeding programs for threatened species68. 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 size69 and the association found here implies that many newly-speciated clades have small range sizes and could thus be at greater risk of extinction.

# 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 passerines43. Briefly, 43 obtained sex-specific RGB (red-green-blue) values across six body patches (nape, crown, forehead, throat, upper breast, and lower breast) from *Handbook of the Birds of the World*70. 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 data41. These measurements include variation in the ultraviolet and bird-visible range and — unlike the RGB measures — are sourced from museum specimens as opposed to illustrations. The spectrophotometry data covers only 581 passerine species (10-fold fewer than the RGB data), although there was a substantial correlation between the two dichromatism measures (; ).

### Male-biased sexual selection

Because sexual dichromatism is presumably imperfectly correlated with variation in the strength of sexual selection across taxa, we sourced an additional measure of sexual selection, also from 43, referred to here as the ‘index of male-biased sexual selection’. This index is the first principal component from a phylogenetic principal 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 shows a moderate correlation with the RGB measure of sexual dichromatism (; ).

### Environmental variables

We obtained estimates of species range size using expert range maps71. Because of taxonomic changes to 1,230 species in the Birdlife database72 we manually matched these taxa with the names used in the sexual dichromatism dataset43. 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 resolution73. 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 interglacial74. We include estimates of climate variability during recent evolutionary history as they may be a better indicators of environmental effects on speciation than present-day environmental variability. Furthermore, to estimate variability in the energy available to species, we obtained the mean and standard deviation of net primary productivity (NPP) values between 2000 - 2015 across each species distribution. Estimates of NPP had 30-second resolution and were obtained through MODIS (Moderate Resolution Imaging Spectroradiometer) primary production products stage 375. 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 stress

Given that stressful environments are expected to interact with sexual selection and have a positive effect on adaptation9, we used the extracted environmental variables from each species range size to create predictors of environmental variation/stress. Firstly we used (*i*) the average NPP in each species’ range and (*v*) the log-transformed range size as potentially informative predictors of speciation rates. We also used three environmental predictors derived from bioclimatic data. These predictors relate to seasonal climate variation, spatial climate variation and long-term climate variation. To obtain seasonal climate variation we used (*iii*) mean values of temperature seasonality (BIO4) for each range. (*iv*) To estimate levels of spatial environmental variation a species may endure we used the first principle component (PC1) from a PCA on standard deviations from all bioclimatic variables, excluding temperature and precipitation seasonality (BIO 4 and BIO15). PC1 was heavily loaded towards bioclimatic variables relating to temperature, thus PC1 reflects the variation in temperature across a species’ range (). 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.org10. 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)11. These trees used a ‘Hackett backbone’76 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)10,77,78, 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; this is because and cannot account for whole-clade extinctions and thus under-estimate extinction rate, which makes the composite measure of diversification more dependent on speciation67,79. Therefore, is a measure of speciation rate more heavily weighted to recent speciation events while measures speciation across the root-to-tip path. These tip-rate measures are alternatives to state-dependent diversification models such as Quantitative State Speciation-Extinction (QuaSSE); but, based on previous simulation studies, 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) models12.

Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic trees11. 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 package80. 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 birds81. 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 package82. Firstly, we conducted model selection to compare models in which , , or were the response variable: these tip-rate estimates all came from the same MCC tree (derived from 2,500 draws of the posterior distribution in 10). For models of and we used the inverse of the variance associated with each tip rate estimate as weights, to account for the variable precision of the estimates provided by BAMM. The most complicated model in each set under comparison contained one of the measures of sexual selection (sexual dichromatism or the index of male-biased sexual selection), all of the environmental measures (i.e. log-transformed range size, seasonal temperature variation, spatial temperature variation, long-term temperature variation, and NPP), and all of the 2-way interactions between sexual selection and each of the environmental measures. The simpler models contained all of the same main effects, but had fewer 2-way interaction terms (potentially none). Model selection was done in MuMIn using the dredge function83. Using the terms from the top-ranked model (ranked by AICc), we ran the equivalent model for each of the 1,000 phylogenetic trees used to derive , and each of the 100 trees 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 84 — using the corPagel function in the ape package85 independently for each of the 1,000 trees/models. Alternatively, 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 the subset of species with measurements of male-biased sexual selection, we conducted a phylogenetic path analysis using the phylopath R package86. 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 our rationale for each path’s directions, can be found within the along with all other analyses and the relevant R code to reproduce results.

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