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

Justin G. Cally\*, Devi Stuart-Fox, Luke Holman and Iliana Medina

\*

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 speciation or extinction and two measures of sexual selection (sexual dichromatism and a multivariate measure of male-biased sexual selection), accounting for range size and measures of environmental variability. Male-biased sexual selection, but not sexual dichromatism, predicted speciation rates () in passerines. This relationship was independent of range size or environmental variability, though species with smaller ranges had higher speciation rates. There was no association 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 has shaped diversification in songbirds.

# Introduction

Sexual selection is a fundamental evolutionary process; yet there is long-standing debate about how it shapes patterns of species diversity1–5. Sexual selection can promote speciation because it operates on traits that can create reproductive isolation when they diverge between lineages, such as signals and preferences involved in mate selection1,2,6, sperm-egg interactions7, or genital morphology8. Sexual selection could also promote speciation or prevent extinction by purging deleterious mutations9, fixing beneficial ones10, and accelerating adaptation in different environments11–13. Conversely, sexual selection might hinder speciation or make extinction more likely by favouring traits that improve mating success but reduce population fitness14–17. For example, species with costly sexual signals may be less resilient to environmental change18. Sexual selection might also promote extinction by causing maladaptation (‘gender load’) in female traits that are genetically correlated with sexually-selected male traits19–23. Although numerous studies have examined the relationship between sexual selection and speciation or extinction rates4,24–28, the availability of more complete phenotypic, ecological and phylogenetic data29, together with significant advances in phylogenetic methods30,31, present new opportunities to test whether and how sexual selection drives diversification.

The relationship between sexual selection and diversification may depend 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 ones32,33. In stable environments, consistent selection depletes genetic variation at sexually concordant loci (i.e. loci where the same allele is fittest for both sexes). In these environments, genetic variation remains disproportionately at sexually antagonistic loci, leading to stronger gender load and reduced net benefits of sexual selection33. By contrast, in spatially or temporally variable environments, sexual selection can enhance local adaptation. For example, in Darwin’s finches (*Geospiza fortis*) divergent beak morphology is an adaptation to local food availability that has been maintained through assortative mating34. Despite the potential interaction between sexual selection and environmental variability in diversification, comparative tests are currently lacking.

Birds have been a popular focus of macroevolutionary studies of sexual selection and diversification4,24,25,27,28 because their biology and 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 fish26. 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, Huang & Rabosky28 found no association between sexual dichromatism and speciation (*n* = 918 species) in a study using spectrophotometric measurements of museum specimens35 and tip-rate estimates from a molecular-only phylogeny29. Similarly, Cooney et al.36 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 dichromatism37, as well as an index of male-biased sexual selection37, which captures (co)variation in sexual size dimorphism, social polygyny and paternal care. We use these two measures because sexual dichromatism does not always signal the presence of strong sexual selection and *vice versa*37. For example, male and female dunnocks (*Prunella modularis*) are similarly coloured yet sexual selection appears to be strong38. 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 intensity5. Additionally, our analysis includes multiple ecological and environmental variables, 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 predicts33. We use multiple approaches for quantifying speciation and extinction rates at the tips of phylogenetic trees, including BAMM (Bayesian Analysis of Macroevolutionary Mixtures)39–42, as well as older but reliable tip-rate statistics, namely diversification rate () and node density ()29.

# Results

We examined the effect of sexual selection on speciation and extinction rate in 97% of passerines (*n* = 5,812 species; 58% of all birds). We calculated three different tip-rate metrics of speciation and one of extinction for a maximum clade credibility (MCC) tree and, to account for phylogenetic uncertainty, 1,000 trees for and and 100 trees for 30. is a measure of speciation rate more heavily weighted to recent speciation events while measures speciation across the root-to-tip path. Alternatively, uses a Bayesian approach to assess the probability of evolutionary rate-shift configurations, from which it generates tip-rate speciation and extinction estimates.

To test the association between speciation/extinction and sexual selection, environmental variability and their interaction, we fitted phylogenetic least squares (PGLS) models with , , or as the response variable. Predictors included one measure of sexual selection (one of two measures of sexual dichromatism or the index of male-biased sexual selection), five environmental measures, and 2-way interactions between the measure of sexual selection and each of the environmental measures, with subsequent model simplification using AIC model selection.

The two measures of sexual dichromatism were from previously published data, one based on RGB (red-green-blue) values from images in *Handbook of the Birds of the World*43 (*n* = 5,983), and the other based on spectrophotometry and avian colour space (*n* = 581)35. The index of male-biased sexual selection is associated with greater sexual size dimorphism, social polygyny and lack of paternal care (*n* = 2,465).

The five environmental variables were (*i*) the log-transformed range size; (*ii*) the average Net Primary Productivity (NPP) in each species’ range; (*iii*) mean temperature seasonality (BIO4) for each range; (*iv*) variation in temperature across a species’ range and (*v*) long-term climate variation, which primarily reflects temperature differences between the last interglacial and current climates. We included an estimate of climate variability during recent evolutionary history as it may be a better indicator of environmental effects on speciation than present-day environmental variability.

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

We found a significant positive association between the index of 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 (highest posterior density (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; ).

In contrast to male-biased sexual selection, we found no evidence that species with increased sexual dichromatism have higher or lower rates of speciation. Sexual dichromatism showed no association with ( = -1.279e-03, p = 0.147; a, ), ( = -5.745e-05, p = 0.078; a) or ( = -1.429e-05, p = 0.872; a). PGLS analyses using sexual dichromatism (*n* = 581) measured by spectrophotometry35 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 ().

No interaction terms were present in the top models ( AICc > 4) for any measure of speciation (, , ) or sexual selection (RGB values, spectrophotometry and the index of 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 (, ).

## 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 species with an index of 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, , ).

## Variability across phylogenetic trees and speciation rate measures

Estimates of the effect of predictor variables on speciation rates varied across phylogenetic trees, especially in the BAMM rates ( and ), where the 95 % HPD interval across 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 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 ( - : *r*=0.75, - : *r*=0.65, - : *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.

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 an index of male-biased sexual selection (n = 2,465) and shows the effect of log-range size and male-biased sexual selection on speciation and extinction rates. Both datasets were used for analyses with three measures of speciation (, , ) 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 an index of 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 an index of 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 spectrophotometry28 or human observers36. 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 . 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 selection24,25,27,28,44. Given our findings, and the modest correlation between dichromatism and the sexual selection index37, we suggest that sexual dichromatism may not be a robust proxy for sexual selection. Although dichromatism clearly reflects sexual selection to some extent, it may be too indirect a measure to detect any association with speciation rate, even with large 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 niches45–48 or experience different selective pressures in contexts other than competition for mates49. For example, in superb fairy-wrens (*Malurus cyaneus*) female colouration has probably evolved in response to spatial variation in predation pressure, increasing dichromatism50. 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 selection13,51. 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 species5. 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 success52. 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 studies26 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 environment33. 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 speciation53. 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 size54. Intuitively, large range size should promote speciation by creating more opportunities for geographic barriers to form55,56. 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 rates57–59. 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 species49,55,60. 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 diversity40. 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 debated39–42. 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 bias61. Although extinction rates can be inferred from alternative sources, such as the fossil record62, direct observation extinction, or IUCN red list status54, 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 taxa42,63. 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 differently63. 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, that the magnitude of this effect is modest, 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 conservation16 and captive breeding programs for threatened species64. 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 size65 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 passerines37. Briefly, Dale et al.37 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*43. 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 data35. 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 selection37, 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 maps66. Because of taxonomic changes to 1,230 species in the Birdlife database67 we manually matched these taxa with the names used in the sexual dichromatism dataset37. 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 resolution68. 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)69. 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)70. 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 adaptation13, 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 (BIO4 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.org29. We used a maximum clade credibility (MCC) tree from 2,500 samples of the posterior distribution (*n* = 5,965) as the main phylogenetic hypothesis in our comparative analysis. Additionally, a random draw of full trees (including species without genetic data) from the posterior distribution of phylogenetic trees was used for diversification analyses using tip-rate measures (1,000 trees) and BAMM (100 trees)30. These trees used a ‘Hackett backbone’71 and were constructed using a pure birth (Yule) model. We calculated three different tip-rate metrics of speciation and one of extinction across all trees.

Firstly, we obtained two tip-rate metrics of speciation using statistics derived from the properties of the nodes and branches along root-to-tip paths of the phylogeny. Node density (ND) is a simple statistic calculating the density of nodes from the phylogenetic root to the tip, while the log-transformed equal splits (logES), also known as diversification rate (DR)29,72,73, 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 speciation63,74. 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) models31.

Secondly, we used BAMM to model the dynamics of speciation and extinction across the 100 phylogenetic trees30. This software uses a Bayesian approach (reversible-jump Markov Chain Monte Carlo) to generate probability distributions of evolutionary rate-shift configurations with variable speciation and extinction rates. Importantly, these models provide tip-rate estimates of speciation and extinction rate. The parameters of the 100 BAMM runs are detailed in full in the ; 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 package75. 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 birds76. 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 package77. 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 distribution29). 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 function78. 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 79 — using the corPagel function in the ape package80 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 index of male-biased sexual selection (*n* = 2,465).

Finally, using the subset of species with an index of male-biased sexual selection, we conducted a phylogenetic path analysis using the phylopath R package81. 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.

# Acknowledgements

We would like to acknowledge Adnan Moussalli for his assistance in conducting BAMM runs across 100 phylogenetic trees.

# References

1. Lande, R. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences* **78**, 3721–3725 (1981).

2. Lande, R. Rapid origin of sexual isolation and character divergence in a cline. *Evolution* **36**, 213–223 (1982).

3. West-Eberhard, M. J. Sexual selection, social competition, and speciation. *Quarterly Review of Biology* **58**, 155–183 (1983).

4. Seddon, N., Merrill, R. M. & Tobias, J. A. Sexually selected traits predict patterns of species richness in a diverse clade of suboscine birds. *American Naturalist* **171**, 620–631 (2008).

5. Cooney, C. R., MacGregor, H. E. A., Seddon, N. & Tobias, J. A. Multi-modal signal evolution in birds: Re-examining a standard proxy for sexual selection. *Proceedings of the Royal Society of London B: Biological Sciences* **285**, (2018).

6. Safran, R. J., Scordato, E. S., Symes, L. B., Rodrı'guez, R. L. & Mendelson, T. C. Contributions of natural and sexual selection to the evolution of premating reproductive isolation: A research agenda. *Trends in Ecology & Evolution* **28**, 643–650 (2013).

7. Swanson, W. J. & Vacquier, V. D. Concerted evolution in an egg receptor for a rapidly evolving abalone sperm protein. *Science* **281**, 710–712 (1998).

8. Sloan, N. S. & Simmons, L. W. The evolution of female genitalia. *Journal of Evolutionary Biology* **in press**, (2019).

9. Whitlock, M. C. & Agrawal, A. F. Purging the genome with sexual selection: Reducing mutation load through selection on males. *Evolution* **63**, 569–582 (2009).

10. Whitlock, M. C. Fixation of new alleles and the extinction of small populations: Drift load, beneficial alleles, and sexual selection. *Evolution* **54**, 1855–1861 (2000).

11. Lorch, P. D., Proulx, S., Rowe, L. & Day, T. Condition-dependent sexual selection can accelerate adaptation. *Evolutionary Ecology Research* **5**, 867–881 (2003).

12. Candolin, U. & Heuschele, J. Is sexual selection beneficial during adaptation to environmental change? *Trends in Ecology & Evolution* **23**, 446–452 (2008).

13. Cally, J. G., Stuart-Fox, D. & Holman, L. Meta-analytic evidence that sexual selection improves population fitness. *Nature communications* **10**, 2017 (2019).

14. Rankin, D. J., Dieckmann, U. & Kokko, H. Sexual conflict and the tragedy of the commons. *American Naturalist* **177**, 780–791 (2011).

15. Kokko, H. & Jennions, M. D. Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology* **21**, 919–948 (2008).

16. Holman, L. & Kokko, H. The consequences of polyandry for population viability, extinction risk and conservation. *Philosophical Transactions of the Royal Society B-Biological Sciences* **368**, (2013).

17. Fromhage, L. & Jennions, M. D. Coevolution of parental investment and sexually selected traits drives sex-role divergence. *Nature Communications* **7**, 12517 (2016).

18. Kokko, H. & Brooks, R. Sexy to die for? Sexual selection and the risk of extinction. *Annales Zoologici Fennici* **40**, 207–219 (2003).

19. Pischedda, A. & Chippindale, A. K. Intralocus sexual conflict diminishes the benefits of sexual selection. *PLOS Biology* **4**, e356 (2006).

20. Harano, T., Okada, K., Nakayama, S., Miyatake, T. & Hosken, D. J. Intralocus sexual conflict unresolved by sex-limited trait expression. *Current Biology* **20**, 2036–2039 (2010).

21. Berger, D. *et al.* Intralocus sexual conflict and environmental stress. *Evolution* **68**, 2184–2196 (2014).

22. Bonduriansky, R. & Chenoweth, S. F. Intralocus sexual conflict. *Trends in Ecology & Evolution* **24**, 280–8 (2009).

23. Pennell, T. M. & Morrow, E. H. Two sexes, one genome: The evolutionary dynamics of intralocus sexual conflict. *Ecology and Evolution* **3**, 1819–1834 (2013).

24. Barraclough, T. G., Harvey, P. H. & Nee, S. Sexual selection and taxonomic diversity in passerine birds. *Proceedings of the Royal Society B-Biological Sciences* **259**, 211–215 (1995).

25. Morrow, E. H., Pitcher, T. E. & Arnqvist, G. No evidence that sexual selection is an ’engine of speciation’ in birds. *Ecology Letters* **6**, 228–234 (2003).

26. Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Maan, M. E. Sexual selection and speciation: The comparative evidence revisited. *Biological Reviews* **86**, 367–377 (2011).

27. Seddon, N. *et al.* Sexual selection accelerates signal evolution during speciation in birds. *Proceedings of the Royal Society B: Biological Sciences* **280**, (2013).

28. Huang, H. T. & Rabosky, D. L. Sexual selection and diversification: Reexamining the correlation between dichromatism and speciation rate in birds. *American Naturalist* **184**, E101–E114 (2014).

29. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).

30. Rabosky, D. L. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLOS ONE* **9**, e89543 (2014).

31. Harvey Michael, G., Rabosky Daniel, L. & Cooper, N. Continuous traits and speciation rates: Alternatives to state‐dependent diversification models. *Methods in Ecology and Evolution* **9**, 984–993 (2017).

32. Long, T. A. F., Agrawal, A. F. & Rowe, L. The effect of sexual selection on offspring fitness depends on the nature of genetic variation. *Current Biology* **22**, 204–208 (2012).

33. Connallon, T. & Hall, M. D. Genetic correlations and sex-specific adaptation in changing environments. **70**, 2198 (2016).

34. Huber, S. K., De Leon, L. F., Hendry, A. P., Bermingham, E. & Podos, J. Reproductive isolation of sympatric morphs in a population of darwin’s finches. *Proceedings of the Royal Society of London B: Biological Sciences* **274**, 1709–1714 (2007).

35. Armenta, J. K., Dunn, P. O. & Whittingham, L. A. Quantifying avian sexual dichromatism: A comparison of methods. *Journal of Experimental Biology* **211**, 2423 (2008).

36. Cooney, C. R., Tobias, J. A., Weir, J. T., Botero, C. A. & Seddon, N. Sexual selection, speciation and constraints on geographical range overlap in birds. *Ecology Letters* **20**, 863–871 (2017).

37. Dale, J., Dey, C. J., Delhey, K., Kempenaers, B. & Valcu, M. The effects of life history and sexual selection on male and female plumage colouration. *Nature* **527**, 367–370 (2015).

38. Davies, N. & Houston, A. Reproductive success of dunnocks, *Prunella modularis*, in a variable mating system. II. Conflicts of interest among breeding adults. *Journal of Animal Ecology* **55**, 139–154 (1986).

39. Beaulieu, J. M. & O’Meara, B. C. Extinction can be estimated from moderately sized molecular phylogenies. *Evolution* **69**, 1036–1043 (2015).

40. Rabosky, D. L. Challenges in the estimation of extinction from molecular phylogenies: A response to Beaulieu and O’Meara. *Evolution* **70**, 218–228 (2016).

41. Moore, B. R., Hohna, S., May, M. R., Rannala, B. & Huelsenbeck, J. P. Critically evaluating the theory and performance of bayesian analysis of macroevolutionary mixtures. *Proceedings of the National Academy of Sciences* **113**, 9569–9574 (2016).

42. Rabosky, D. L., Mitchell, J. S. & Chang, J. Is BAMM flawed? Theoretical and practical concerns in the analysis of multi-rate diversification models. *Systematic biology* **66**, 477–498 (2017).

43. Del Hoyo, J., Elliott, A. & Christie, D. *Handbook of the birds of the world*. **8-16**, (Lynx Edicions 2003-2011, 2011).

44. Owens, I. P. F., Bennett, P. M. & Harvey, P. H. Species richness among birds: Body size, life history, sexual selection or ecology? *Proceedings of the Royal Society B-Biological Sciences* **266**, 933–939 (1999).

45. Wallace, A. R. Colours and ornaments characteristic of sex. in *Darwinism, an exponent of the theory of natural selection, with some of its applications* (Macmillan; Company, 1889).

46. Kottler, M. J. Darwin, Wallace, and the origin of sexual dimorphism. *Proceedings of the American Philosophical Society* **124**, 203–226 (1980).

47. Slatkin, M. Ecological causes of sexual dimorphism. *Evolution* **38**, 622–630 (1984).

48. Shine, R. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *The Quarterly Review of Biology* **64**, 419–461 (1989).

49. Price, J. J. & Eaton, M. D. Reconstructing the evolution of sexual dichromatism: Current color diversity does not reflect past rates of male and female change. *Evolution* **68**, 2026–2037 (2014).

50. Medina, I. *et al.* Habitat structure is linked to the evolution of plumage colour in female, but not male, fairy-wrens. *BMC evolutionary biology* **17**, 35 (2017).

51. Miles, M. C. & Fuxjager, M. J. Synergistic selection regimens drive the evolution of display complexity in birds of paradise. *Journal of Animal Ecology* **87**, 1149–1159 (2018).

52. Weaver, R. J., Santos, E. S., Tucker, A. M., Wilson, A. E. & Hill, G. E. Carotenoid metabolism strengthens the link between feather coloration and individual quality. *Nature Communications* **9**, 73 (2018).

53. Maan, M. E. & Seehausen, O. Ecology, sexual selection and speciation. *Ecology Letters* **14**, 591–602 (2011).

54. Greenberg, D. A. & Mooers, A. Ø. Linking speciation to extinction: Diversification raises contemporary extinction risk in amphibians. *Evolution Letters* **1**, 40–48 (2017).

55. Rosenzweig, M. L. *Species diversity in space and time*. (Cambridge University Press, 1995).

56. Castiglione, S. *et al.* Diversification rates and the evolution of species range size frequency distribution. *Frontiers in Ecology and Evolution* **5**, 147 (2017).

57. Birand, A., Vose, A. & Gavrilets, S. Patterns of species ranges, speciation, and extinction. *American Naturalist* **179**, 1–21 (2012).

58. Claramunt, S., Derryberry, E. P., Remsen, J. V. & Brumfield, R. T. High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proceedings of the Royal Society B: Biological Sciences* **279**, 1567 (2012).

59. Jablonski, D. & Roy, K. Geographical range and speciation in fossil and living molluscs. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**, 401–406 (2003).

60. Weir, J. T. & Price, T. D. Limits to speciation inferred from times to secondary sympatry and ages of hybridizing species along a latitudinal gradient. *American Naturalist* **177**, 462–469 (2011).

61. Davis, M. P., Midford, P. E. & Maddison, W. Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evolutionary Biology* **13**, 38 (2013).

62. Martins, M. J. F., Puckett, T. M., Lockwood, R., Swaddle, J. P. & Hunt, G. High male sexual investment as a driver of extinction in fossil ostracods. *Nature* **556**, 366 (2018).

63. Title, P. O. & Rabosky, D. L. Diversification rates and phylogenies: What are we estimating, and how good are the estimates? *bioRxiv* 369124 (2018).

64. Charge, R., Teplitsky, C., Sorci, G. & Low, M. Can sexual selection theory inform genetic management of captive populations? A review. *Evolutionary Applications* **7**, 1120–1133 (2014).

65. Harris, G. & Pimm, S. L. Range size and extinction risk in forest birds. *Conservation Biology* **22**, 163–171 (2008).

66. BirdLife International and Handbook of the Birds of the World. *Bird species distribution maps of the world*. (<http://datazone.birdlife.org/species/requestdis>, 2017).

67. Hoyo, J. del & Collar, N. J. *HBW and birdlife international illustrated checklist of the birds of the world*. **1**, (Lynx Edicions; BirdLife International, 2016).

68. Fick, S. E. & Hijmans, R. J. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**, 4302–4315 (2017).

69. Otto-Bliesner, B. L. *et al.* Simulating arctic climate warmth and icefield retreat in the last interglaciation. *Science* **311**, 1751–1753 (2006).

70. Zhao, M., Heinsch, F. A., Nemani, R. R. & Running, S. W. Improvements of the modis terrestrial gross and net primary production global data set. *Remote Sensing of Environment* **95**, 164–176 (2005).

71. Hackett, S. J. *et al.* A phylogenomic study of birds reveals their evolutionary history. *Science* **320**, 1763–1768 (2008).

72. Quintero, I. & Jetz, W. Global elevational diversity and diversification of birds. *Nature* **555**, 246 (2018).

73. Rabosky, D. L. *et al.* An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392 (2018).

74. Belmaker, J. & Jetz, W. Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecology Letters* **18**, 563–571 (2015).

75. Rabosky, D. *et al.* BAMMtools: An R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods in Ecology and Evolution* **5**, 701–707 (2014).

76. Harvey, M. G. *et al.* Positive association between population genetic differentiation and speciation rates in new world birds. *Proceedings of the National Academy of Sciences* **114**, 6328–6333 (2017).

77. Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. *nlme: Linear and nonlinear mixed effects models*. (2018).

78. Bartoń, K. *MuMIn: Multi-model inference*. (2017).

79. Pagel, M. Inferring the historical patterns of biological evolution. *Nature* **401**, 877 (1999).

80. Paradis, E., Claude, J. & Strimmer, K. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290 (2004).

81. Bijl, W. van der. *Phylopath*: Easy phylogenetic path analysis in R. *PeerJ* **6**, e4718 (2018).