A global analysis reveals the dynamic relationship between sexual selection and population abundance in space and time

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Abstract

Sexual selection leads to the evolution of extravagant weaponry or ornamental displays, with the bearer of these traits gaining a reproductive advantage, potentially at a cost to the individual’s survival. The consequences of sexual selection can therefore impact species demographic processes and overall abundance. Currently, evidence connecting the effects of sexual selection to demography and abundance is conflicting. This study aims to rectify this issue by assessing the relationship between sexual selection and abundance in Passerines across the globe, importantly, accounting for migration and seasonality. We integrate a global citizen science dataset of bird observations with Passerine trait data to show that migration and seasonality are key moderators in the relationship between sexual selection and abundance. For resident Passerines, the relationship is consistently positive across the year, whereas for migrant Passerines, the relationship is overall neutral, with a significant negative dip during pre-breeding migration (for Northern Hemisphere Passerines). Our results suggest that sexual selection bolsters populations that experience less intense natural selection.

Main

Introduction

Abundant evidence suggests that sexual selection leads to the evolution of sex specific weaponry and ornaments (*1*), as well as other sexually dimorphic traits (*2, 3*). The bearers — usually, but not always, males — of larger weaponry and more brilliant ornaments (see Fig. 1) gain a reproductive advantage. Yet possessing such sexually selected traits can impose a cost to the survival of the individual, potentially affecting the overall demographic rates at both the population and species levels (*4*). Thus far, empirical results have been mixed both among and within different taxa: sexual selection has been shown to correlate with both increased and reduced extinction risk in comparative studies (*5*). There is also experimental evidence that, because sexual selection is associated with mate choice, it improves both population persistence (*6*) and male longevity across multiple taxa (*7*), resulting in better survival (i.e., good genes hypothesis) (*8*). The impact sexual selection has on population demographics is contentious and resolving this remains a challenge.

Previous studies on sexual selection and demographic parameters in birds have also been inconclusive. Some studies suggest that there is no correlation between sexual selection and extinction risk (*9*), and further, that sexual selection does not have any impact on population trends (*10*). On the other hand, sexual selection can result in local extinction of bird communities (*11*). These contradicting studies, however, have been limited by in some cases the number of bird species included (i.e., $N = 1030$ (*9*), $N = 320$ (*11*)) or in others by the limited geographic extent of the investigations (i.e., only Central Europe (*10*) or North America (*11*)). This means that significant effects of migration and species' ranges, which have been shown to impact population trends (*12*), are downplayed or ignored, potentially leading to the conflicting results.

Migration is a profound life-history trait which has significant impacts on population dynamics in birds and other taxa across the world. For migratory taxa, breeding and migration are linked in a particular seasonal cycle, and, in birds, this involves breeding in the months following a poleward migration. Moreover, mortality rates are higher during migratory periods (*13, 14*), likely a result of migration enforcing pressures which select for higher quality individuals (*15*). Some migratory bird species display intense competition for early arrival to the breeding grounds (*16*) in which higher-quality males outcompete lesser-quality males for mating territories which females prefer, resulting in higher reproductive success(*17*). Sexual selection in the form of male competition may therefore be another factor which increases mortality during migration, as migrants reduce stopover duration in order to arrive first (*18*). In that sense, sexual selection coupled with natural selection can impose a clear negative pressure on bird populations during migration. Migration is observed in a wide range of taxa (*19*), but despite readily available data, migration has not been investigated as a key component in the relationship between sexual selection and population dynamics. By discerning how migration interacts with sexual selection and population abundance, we will ultimately advance our broader understanding of eco-evolutionary processes connecting sexual selection, migration, and population dynamics.

We investigate how sexual selection impacts population dynamics in Passerines by integrating global citizen science data with trait data. First, we quantify the relationship between sexual dichromatism (used as a surrogate for strength of sexual selection; see Methods) and relative abundance in Passerine birds. Second, we assess how migration and seasonality influence the relationship between sexual selection and relative abundance. We predict that migration (i.e., residents versus migrants) could be the key moderator in this relationship. Specifically, we predict that migration will cause sexual dichromatism to have a negative effect on relative abundance due to the added stresses of migration.

Results & Discussion

We found that, in Passerines, the overall relationship between sexual dichromatism and relative abundance was significantly positive ($b = 0.013$, $p = 0.002$), yet heterogeneous across the world (N [number of species] = 5330, Fig. 2). The relationship appears, in general, negative or neutral in the Northern Hemisphere and positive in the Southern Hemisphere. The global scope of our analysis reconciles previous, apparently conflicting, studies by reproducing their results and displaying that they were limited by their range; i.e. sexual dichromatism (as a surrogate of sexual selection) has no negative impact on Passerine populations in Central Europe (*10*) while it has a negative impact on bird populations in North America (*11*). Essentially, the relationship shows strong geographic heterogeneity, and thus, the geographic scope of previous studies limited the ability to fully understand the relationship between sexual selection and abundance.

By investigating the relationship of sexual dichromatism and relative abundance in the context of both temporal and migratory patterns, where residents and migrants were considered separately ($N = 4520$, $N = 810$ respectively), we showed that migration and seasonality are important moderators in the relationship between sexual selection and population dynamics. The geographic heterogeneity in the relationship (Fig. 2) was reduced when the relationship was stratified temporally and by migration patterns (Fig. 3, Supplementary Fig. S1). For resident species, the relationship was relatively stable and significantly positive across all months (Fig. 4). But for migratory species, the relationship was dynamic, displaying temporal variation with the greatest peaks during January and February, and dips in the strength of the relationship during May and June (Fig. 4). Global migration systems in Passerines are highly variable across the globe due to seasonality differences, particularly between the Northern and Southern Hemispheres, but also between the Western and Eastern Hemispheres. We found that during the first months of the year, when migratory species are at the southern side of their travels, sexual selection has a positive impact on the relative abundance of migrant species. During the peak migratory period, between May and June, where birds in the Northern Hemisphere migrate to temperate zones for breeding and birds in the Southern Hemisphere migrate to the tropics for wintering (*20, 21*), sexual dichromatism has a negative impact on relative abundance of migrant species. For the remainder of the year, the relationship remains neutral. Only the peaks (January and February) and the troughs (May and June) were found to be significantly different to zero (Fig. 4).

Natural selection on mortality can have direct impacts on population dynamics and indirect effects on the evolution of sexual selection and sex roles in birds. Sex-biased adult mortality has a significant effect on adult sex ratio (*22*). For instance, higher male adult mortality would lead to a female-biased adult sex ratio (*22*). Sexually dichromatic species may experience this effect (higher male adult mortality) due to the greater visibility of colourful males (*23, 24*). The resultant female-biased adult sex ratio would then promote certain sex roles (e.g., female care and male competition) and further promote sexual selection on males (*25*). Migration entails more intense natural selection, along with other threats that lead to an increased mortality rate (*13, 14*). Birds may experience greater predation rates during migration (*26*); predation risk is likely to be greater for more colourful birds due to their greater visibility. In that sense, the cost of being sexually dichromatic (or having, in general, a more colourful male) is greater for migrants than residents as the risk of predation is higher. Therefore, in conjunction with the effects that adult sex ratios may have on a population, the cost of mortality may be too high for migrant populations to reap the benefits of sexual selection as resident populations do.

Interestingly, the impact of sexual selection upon migratory species appears to become less negative in the months after the pre-breeding dip in May and June (Fig. 4). This phenomenon would occur if the male population bore the cost of sexual selection (i.e. male biased mortality), allowing the resultant female-biased population to persist and repopulate (*27*). As such, the large decrease in the relationship between sexual selection and relative abundance during April-May migration may be caused by a potential male-biased mortality due increased migratory pressures on sexually selected birds (*16, 18, 24*). The reason the large decrease is not repeated during the October-November migration (Fig. 4), is that 657 of the total 812 migrant species were, on average, observed in the Northern Hemisphere (a result of eBird citizen science data bias) and thus would experience these added pressures during pre-breeding migration (*20*) only. It is likely that our results were driven by this group of migrant Passerines.

For resident Passerines, the benefits of sexual selection appear to outweigh the cost, leading to more abundant populations (Fig. 4). Sexual selection entails indirect benefits by allowing choosy females to acquire ‘good genes’ which are passed on to high quality offspring (*8*). Sexual selection may also help to reduce inbreeding (*28*) and mutation load (*29, 30*). Moreover, sexual selection via female choice can have direct benefits such as increased fertility and fecundity. However, there are many more factors besides male honest signalling that may attribute to these benefits (*31*). Indeed, both indirect and direct benefits of sexual selection would lead to a larger population. Meta-analytical data shows that individuals in a population evolved under sexual selection had higher fitness than those without it (*32*). Similar conclusions were found in laboratory experiments on beetles (*30*) and mites (*33*) (both of which are not part of the meta-analysis). Our results also support the notion that sexual selection bolsters populations, though only for resident Passerines (Fig. 4). For both resident populations and populations of any system studied under controlled conditions, such as those in laboratory experiments, selective pressures are fewer or at least less detrimental than those experienced by migrant populations. It is in these conditions where sexual selection appears to be most beneficial for populations, though, with our findings, we cannot infer what the exact benefits may be. In that case, is there a reason that more, if not all, resident species should not become dichromatic? We speculate that this may be because the relative impacts of the costs and benefits of being dichromatic may depend on other aspects of a species' ecologies, such as the abundance and foraging traits of predatory species.

Migration entails natural selective pressures across all migratory birds. We have shown that these selective pressures are likely to be more detrimental for dichromatic species as they tend to be less abundant during pre-breeding migration (Fig. 4). This is probably a result of the cost of displaying sexual selected ornamentation, in this case, colour (*1*). Why, then, are migrant species as dichromatic as resident species, even accounting for phylogeny (Supplementary Fig. S2), and what benefits, besides those previously discussed, may oppose the cost? First, all major aspects of migration (timing, direction, and duration) are under genetic control (*1, 34, 35*), and as such, have the potential to be selected upon within a species. Plumage colour, for example, indicates 'good genes', which could influence migration (*36*). Sexual dichromatism may, therefore, act as an honest signal of a male's genetic quality (*37*), which allows females to choose males better suited for migration. This notion, however, seems backwards, as clearly dichromatic species, or species with colourful males, fair worse during pre-breeding migration than monochromatic species (Fig. 4). Our results indicate that male colouration may be a condition-dependent trait that signals for quality in migration. The natural selection on migration may lead to the survival of higher quality males, which may be those displaying a more colourful plumage considering colour is an indicator of 'good genes' (*36*). This would result in a more colourful male population from which females may choose even more colourful males, consequently leading to the evolution of exaggerated colouration in males. This process can be described under eco-evolutionary dynamics as a feedback loop between the effects of natural selection through migration and sexual selection through female choice (*38*). Hence, the exaggeration of male colour paired with the evolutionary loss of female colour (*39*) (particularly in migrant species such as wood-warblers (*40*)) may have driven the evolution of sexual dichromatism in migrant species. This is likely an example of sexual dimorphism (in the form of sexual dichromatism) evolving as a condition-dependent trait (*41*).

These results offer significant findings that improve our understanding and direct future research into the relationship between sexual selection and population dynamics. Investigating the presence of adult sex ratios in dichromatic Passerines would aid in understanding the impacts that adult sex ratios have on sexual selection. Finding a potential male bias in mortality, along with a correlation between colour (or visibility) and predation, during migration would be crucial in supporting the notion that there is a cost of sexual selection for dichromatic species. Furthermore, we recommend the following points to be considered for future studies. More studies are required to confidently label male colouration as condition-dependent (*42*). We also recognise that migration in birds is a complex system and cannot be authentically summarised by a single pattern, but our results clearly highlight that future research investigating the relationships between sexual selection and population dynamics should incorporate changes over the full annual cycle. A more robust integration of global migration systems would significantly bolster our results.

Conclusion

In this study, we demonstrated a consistent positive relationship between sexual dichromatism and relative abundance in resident Passerines. For these species the benefits of sexual selection appear to outweigh any potential costs (*8*). While our data cannot specifically address what these benefits may be, by comparing resident species to migrant species, our results suggest that the costs, potentially that of predation risk, is higher for migrant species.

We have further shown that the relationship between sexual dichromatism and relative abundance in migrant Passerines is dynamic across the year but overall, seems to be neutral. This is likely a result of condition-dependent sexual selection. Migratory Passerines face declining populations due to climate change (*43*) and our results suggest that migratory species which exhibit strong sexual selection may be at a greater risk of diminishing populations during pre-breeding migration. However, as our data was largely based on resident species, we conclude that sexual dichromatism has a net positive relationship with relative abundance in Passerine birds. Our results have reconciled conflicting evidence of previous studies (*10, 11*) by offering a quantitative explanation as to how these contradictions came to be. Furthermore, migration and seasonality were both key moderators in this relationship. As such, future investigations on sexual selection, particularly in birds, should consider migration and seasonality as variables that influence results or conclusions.

Methods

Measures of Passerine Traits

Within Passerine birds sexual dichromatism is thought to be an appropriate surrogate of sexual selection (*39*) . While the use of sexual dichromatism as a measure of sexual selection has been argued against (*44*), many previous studies have similarly used this method to investigate the relationship between sexual selection and demographics (*9-11, 45*). Further, sexual dichromatism entails a clear cost in increased predation risk (*23, 24*), thereby demonstrating how sexual selection can put individual survival at risk. Body mass was included in our investigation to control for its effect on abundance as larger birds are often more colourful (*39*), influencing both sexual selection (*46*) and predation risk (*47*).

Measures of sexual dichromatism, mass, and migration patterns of Passerine birds were taken from a published data set (*48*). Briefly, in this dataset, sexual dichromatism was quantified for nine colour patches (forehead, crown, nape, back, throat, upper breast, lower breast, belly, and vent) for both males and females of each species ($N = 5809$) from colour plates within the Handbook of the Birds of the World Alive (HBWA) (*49*). Sexual dichromatism for a single species was then calculated as the mean Euclidean distance between male and female RGB scores of each patch. Migration patterns were assigned to species ($N = 5808$) as resident, partial migrant and complete migrant using range maps in HBWA. From this original data set, we grouped partial migrants and complete migrants into one migration type, resulting in two types of migration patterns, 'residents' and 'migrants'. Body mass was obtained for 5875 species from various sources (see McQueen et al. (*48*) for more details), 391 of which body mass was estimated using the genus average. For species in which multiple body masses were given, a mean of the values was used.

Relative Abundance Data

Relative abundance data of Passerines was derived from eBird, a database which uses citizen science to effectively and reliably collect avian abundance data from across the world (*50*) . Volunteer birdwatchers submit data by completing a 'checklist' of all the bird species they've seen and/or heard. Filling out a checklist requires information about the observation such as location, date, time, distance travelled, and duration spent birdwatching. A rare or unusual species is reviewed first by an automated system, which compares the entry to previous checklists made in the region, and then by a human moderator (*51*). This process allows for a high level of quality control which ensures that the data gathered is scientifically accurate. For our analysis, we further filtered the eBird checklists by removing any instance where species abundance data was missing, only included complete checklists, only included checklists which travelled < 5km, and only included checklists which were >5 minutes and <240 minutes in duration (*52*). This process helps to ensure the best-quality lists for inclusion and minimizes the undue leverage of potential outliers on our analyses. We acknowledge that not all birds are equally detected, and that detection probability can influence abundance (*53*). However, the biases in detection probability are systematic in space and time – i.e., more detectable birds would consistently be recorded more in the eBird data. Therefore, the differences in relative abundances among species should remain comparable. Furthermore, detectability is constrained by body size and phylogeny (*54*), both of which were included in our models, thus making the relationship between relative abundance and sexual selection at specific levels of detectability (i.e., body size or phylogenetic clade).

The data was taken as the average monthly abundance of species from data spanning from January 2010 to May 2019. The abundances of the Passerine species were then aggregated into 2592 equal-area 5-degree grid cells of the world. We then calculated the relative abundance of each species by dividing its mean abundance across all checklists recorded in a grid cell, including zeros (i.e., the checklists on which it did not occur). The dataset was again filtered by removing grid cells with less than a total of 50 eBird checklists (per month) to avoid poorly sampled parts of the world. The abundance dataset was then merged with the published dataset of passerine traits (*48*) by matching taxonomically correct species names. The final dataset had complete data for 5330 species from 565 grid cells where enough data were available.

Statistical analysis

We employed a phylogenetic linear mixed-effects model incorporating sampling error (i.e., phylogenetic multilevel meta-analytic model; (*55, 56*)), implemented in the function *rma.mv* in the R package *metafor* (*57*), to investigate the relationship between sexual selection and abundance, and how it varied across the world. In this model, we had average yearly relative abundance of Passerine species for each 5-degree grid cell as the response variable with the square of standard errors for relative abundance estimates as sampling variance (for this meta-analytic model). As fixed effects, we fitted sexual dichromatism and body mass and as random effects, we had species and phylogeny from Jetz et al. (*58*) (cf. (*56*)). From this model, we obtained the slope estimate (the relationship between abundance and sexual dichromatism) and the associated standard error for each 5-degree grid cell.

We ran the same model with 50 different phylogenetic trees and combined model results (slopes) using Rubin's rules to account for phylogenetic uncertainty (*59*). The merged (overall) slopes, we obtained for each 5-degree grid cell, were graphed in the cells against a map of the world to examine geographical variation, using R packages *sf* (*60*), *rnaturalearth* (*61*), and *ggplot2* (*62*).

The phylogenetic linear mixed-effects model of relative abundance for each 5-degree grid cell of the world was repeated using the average monthly relative abundance of Passerine species. The relationship between sexual dichromatism and relative abundance was calculated for each month across the two migration patterns. The results of this test were graphed as the regression value in each 5-degree grid cell against time (months) for migrants and residents. Again, the regression value for each grid cell was graphed in the cells against a map of the world for each month and migration patterns, finalizing in 24 separate heat maps.

Furthermore, to understand the overall trends of the relationship between sexual dichromatism and relative abundance, we statistically summarise all the slopes across the 5-degree grid cells for all the data, migrant data, and resident data. To achieve this, we used multilevel meta-analytic models with a spatial correlation matrix, implanting the model with the *rma.mv* function in the R package *metafor* (*57*). We assumed the Gaussian process for spatial dependency; the relationship between distances (d) and spatial correlations (ρ) is modelled as $\exp(d^2/ \rho^2)$ (cf. (*63*)).

In addition, we conducted phylogenetic comparative analysis using R packages *phylolm* (*64*), and *ape* (*65*) to compare sexual dichromatism between migrant and resident species. We used phylogenetic generalised least square (GLS) model using the *phylolm* function and 1000 phylogenetic trees (*58*). We fitted sexual dichromatism (ln-transformed) as the response, and the categorical variable, migration status (residents = 0, migrants = 1), as a predictor with a phylogenetic tree. We repeated the same model 999 more times with a different phylogenetic tree each time. Then, we obtained a distribution of regression estimates from the 1000 estimates. This procedure accounted for the uncertainty in phylogenetic trees (*59*).

Data Availability

Raw Passerine trait data used in this study was sourced from Alexander McQueen (*48*). All relevant datasets generated in the study are available at the GitHub repository: (https://github.com/itchyshin/abundance_sexual_selection).

Code Availability

All relevant R (version 4.0.2) code used in the study is available for access and download at the GitHub repository: (https://github.com/itchyshin/abundance_sexual_selection)

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Figures

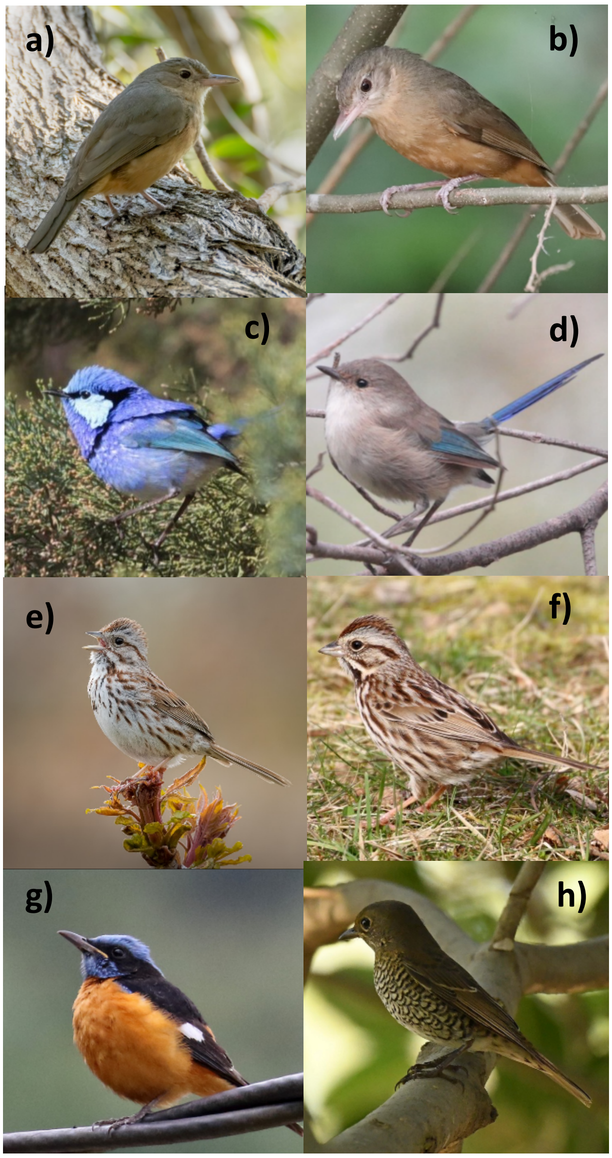


Figure 1. Pictures of sexually dichromatic and monochromatic Passerine species: a-b) male and female Little Shrikethrush (Colluricincla megarhyncha), c-d) male and female Splendid Fairywren (Malurus splendens), e-f) male and female Song Sparrow (Melospiza melodia), and g-h) male and female Blue-capped Rock-Thrush (Monticola cinclorhyncha). Species a-d) are residents and species e-h) are migrants. Photo credits: a) Richard Simmonds, b) Lorix Bertling, c-d) Corey Callaghan, e) Andy Wilson, f) Bill Brown, g) Myles McNally, and h) Subhadra Devi

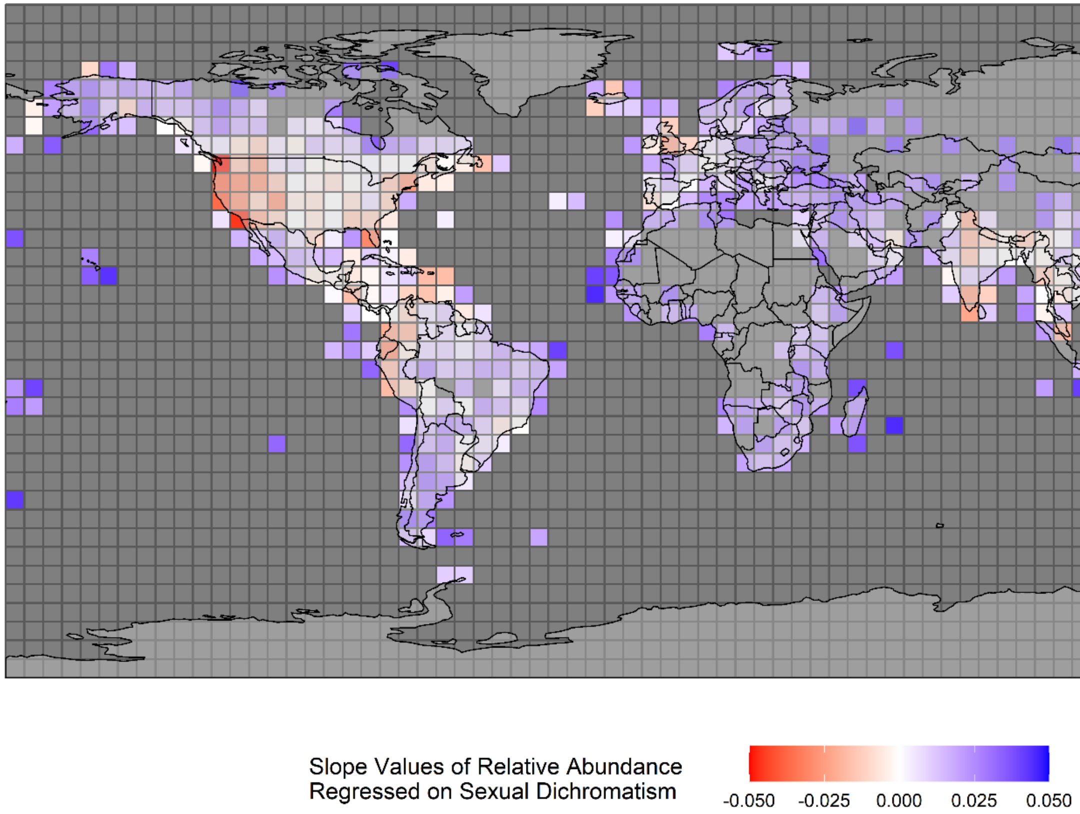


Figure 2. Global map of slope values quantifying the relationship between sexual dichromatism and relative abundance of Passerines species (N = 5330) in 5-degree grid cells. Regression values were found using sexual dichromatism scores and body mass of Passerine species as predictor variables, and the average yearly relative abundance of each species for every 5-degree grid cell they were observed in as the independent variable.

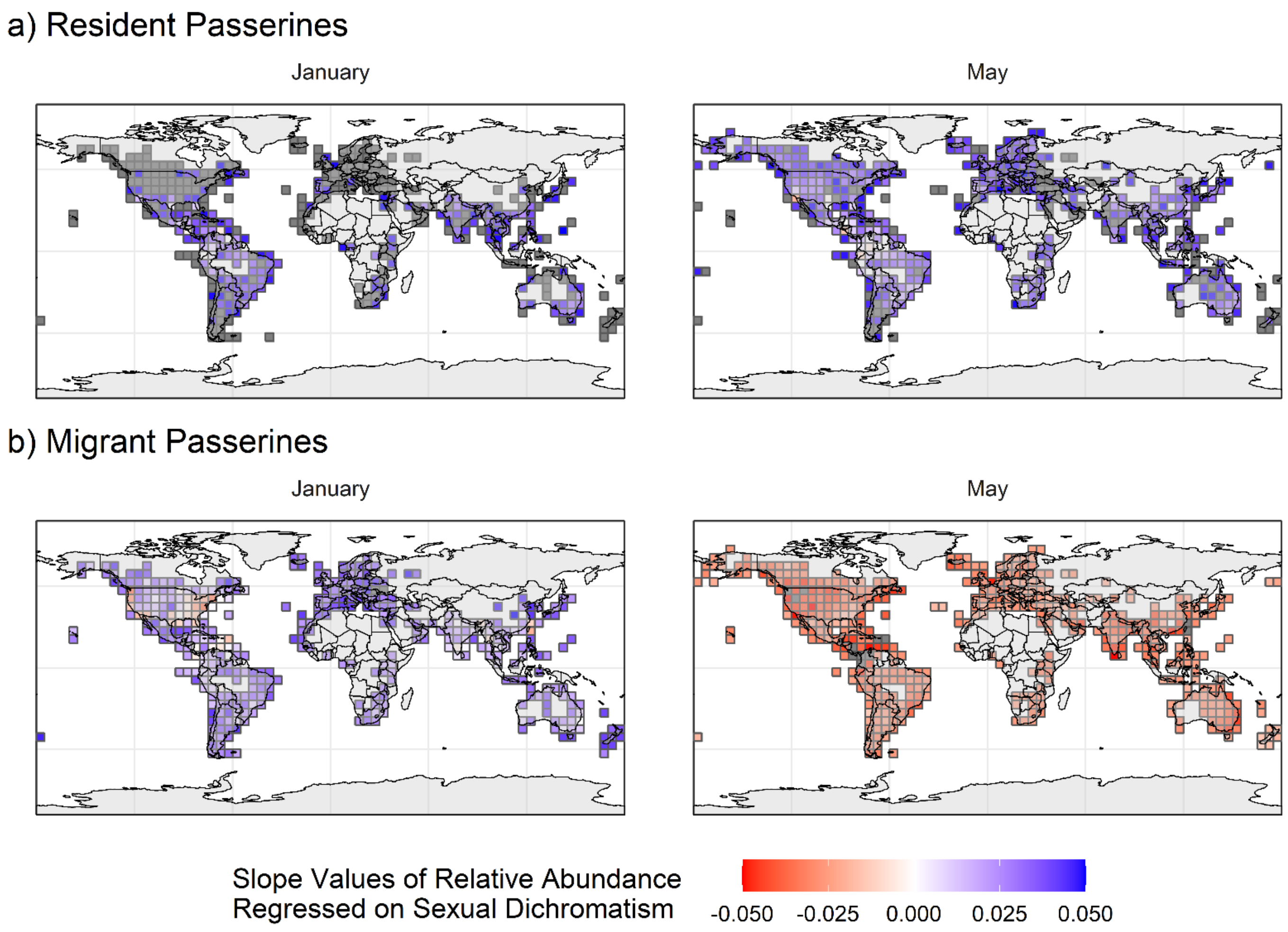


Figure 3. Global maps of slope values quantifying the relationship between sexual dichromatism and relative abundance of (a) resident (N = 4520) and (b) migrant (N = 810) Passerines species in 5-degree grid cells. Regression values were found using sexual dichromatism scores and body mass of Passerine species as predictor variables, and the monthly (January and May) average relative abundance of each species for every 5-degree grid cell they were observed in as the independent variable. See Supplementary Fig. S1 for global maps of all twelve months across both migration patterns.

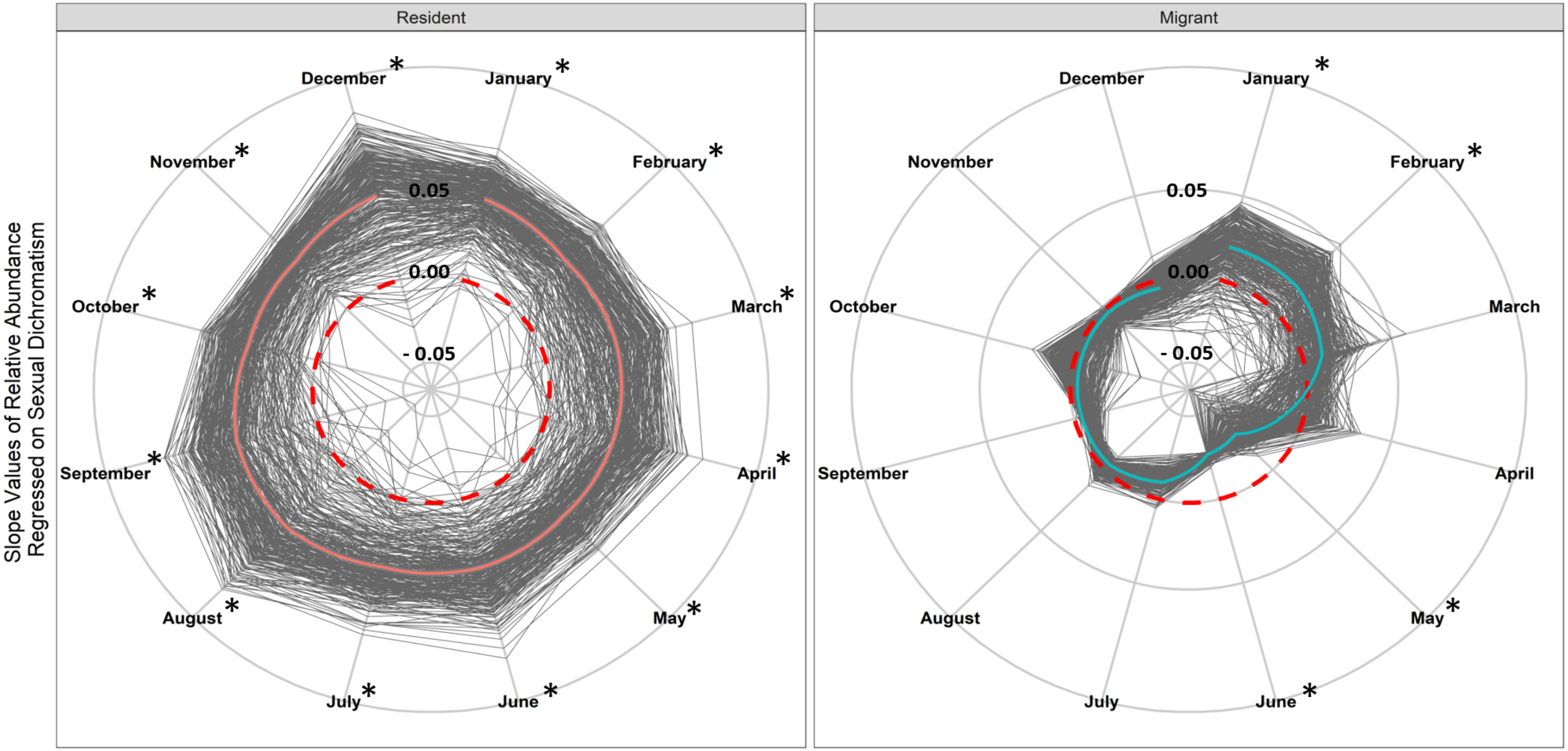
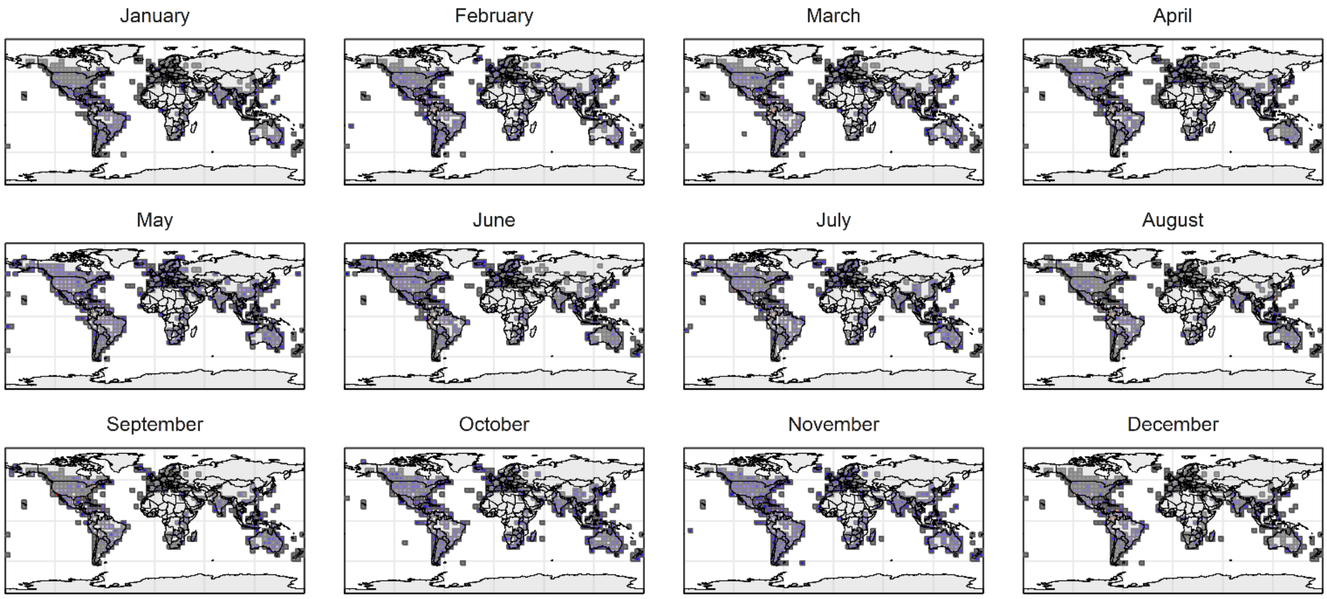


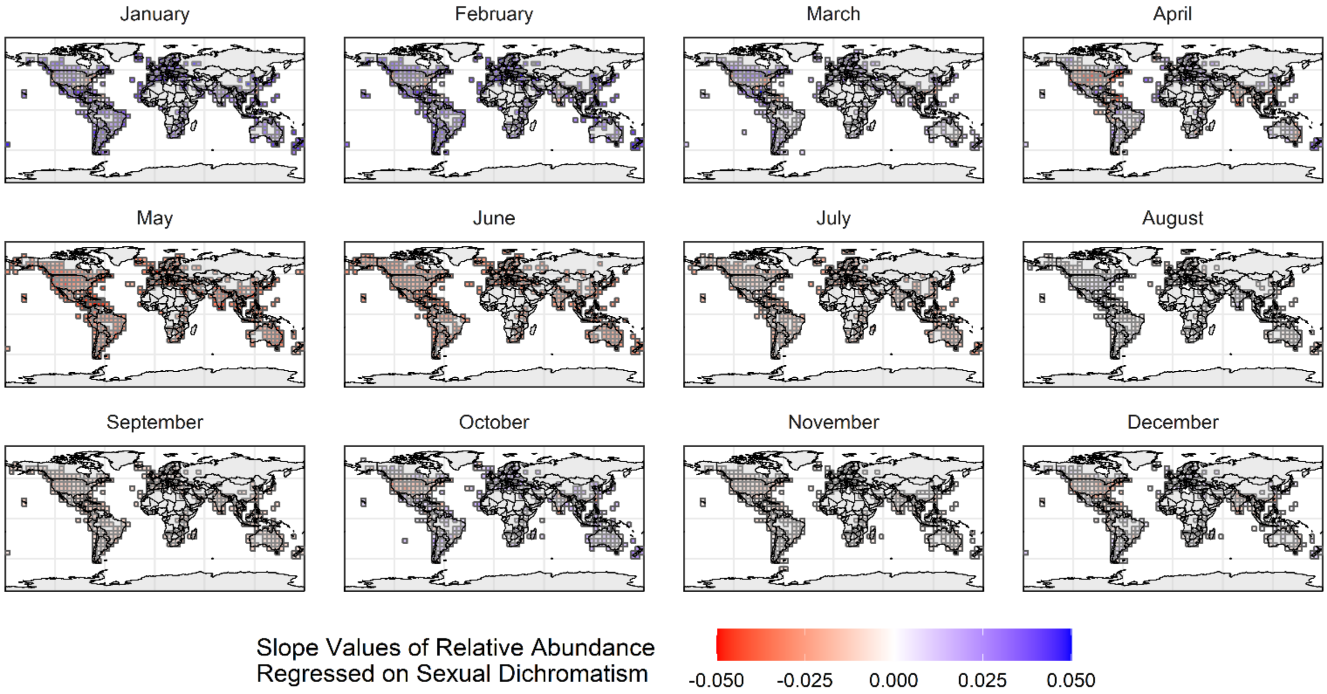
Figure 4. Line graph of slope values quantifying the relationship between sexual dichromatism and relative abundance of resident (N = 4520) and migrant (N = 810) Passerine species across twelve months of the year. Each line represents a 5-degree grid cell of the world in which the regression values were calculated using sexual dichromatism scores and body mass of Passerine species as predictor variables, and the monthly average relative abundance of each species for every 5-degree grid cell they were observed in as the independent variable. For the majority of migrant species (N = 657), pre-breeding migration occurs during March and April, and wintering migration occurs during September and October. *Months in which the average regression value is statistically different to zero.

Supplementary Results

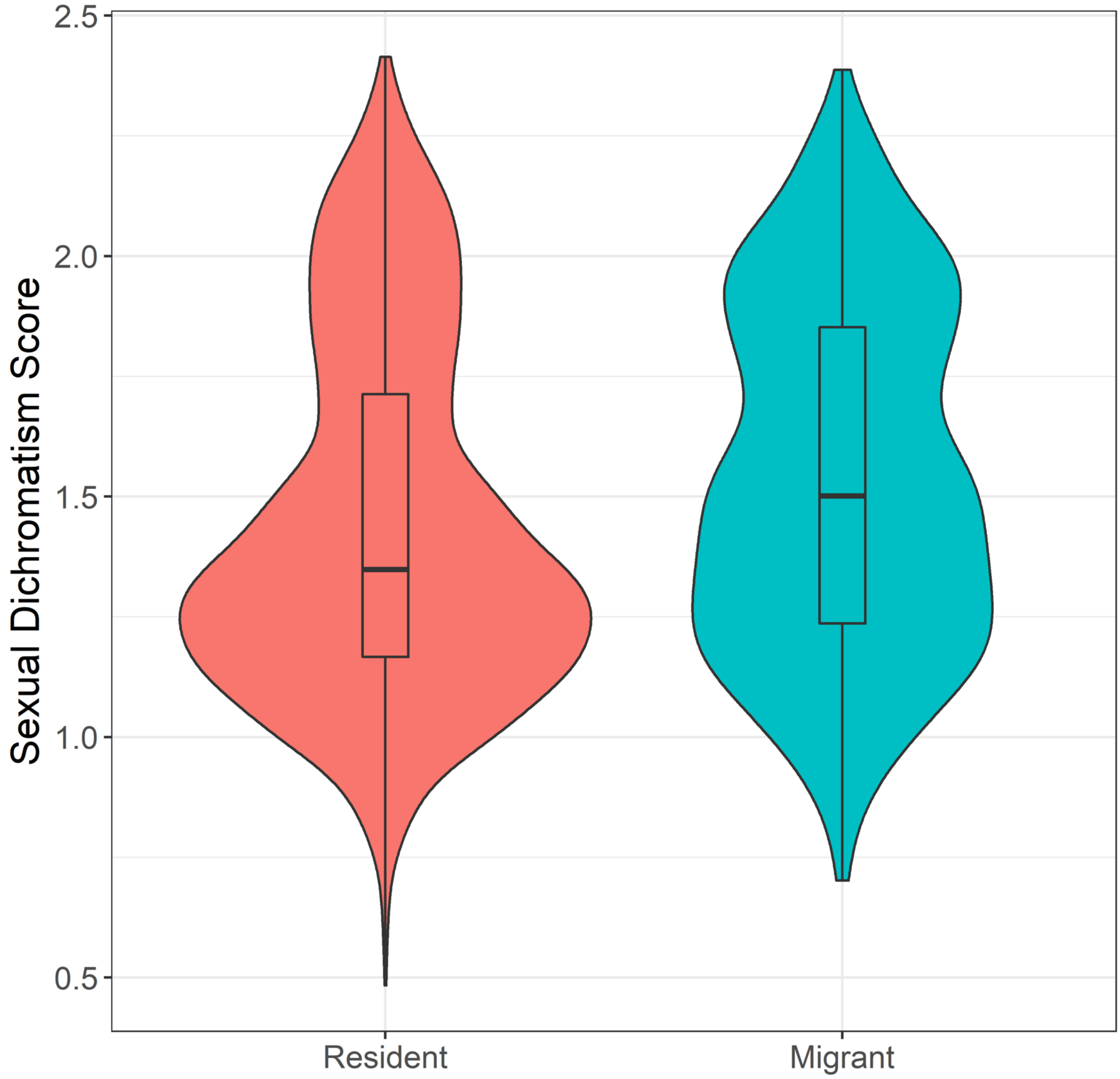
a) Resident Passerines



b) Migrant Passerines



Supplementary Figure S1. Global maps of slope values quantifying the relationship between sexual dichromatism and relative abundance of (a) resident (N = 4520) and (b) migrant (N=810) Passerines species in 5-degree grid cells. Regression values were found using sexual dichromatism scores and body mass of Passerine species as predictor variables, and the monthly average relative abundance of each species for every 5-degree grid cell they were observed in as the independent variable. Maps were separated into twelve months.



Supplementary Figure S2. Violin and boxplot comparing the sexual dichromatism scores of resident species (N = 4520) and migrant species (N=810) in Passerines. Phylogenetic comparative analysis, where sexual dichromatic was the response variable and migration status the predictor variable, using 1000 phylogenetic trees showed that there is no statistical difference between sexual dichromatism scores of resident and migrant Passerines (Estimate = 95%, CI = -0.287 to 0.206).