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ORIGINAL RESEARCH

Sexual dichromatism increases with altitude in birds with ultraviolet sensitive vision

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Abstract

The harsher environment of higher altitudes increases selection for biparental care and increases extrinsic mortality, both of which are expected to reduce the strength of sexual selection. The intensity of sexual selection is often studied using sexual dimorphism as a proxy, especially sexual dichromatism. In birds, multiple studies have shown that sexual dichromatism decreases with increasing altitude. However, those studies have either used small datasets or have used human scoring of sexual dichromatism, potentially missing out on significant levels of cryptic dichromatism. This study includes the measure of subjective sexual dichromatism of the Vorobyev-Osorio colour discrimination model of sexual dichromatism in 758 species of bird with UV-sensitive visual systems and tests whether a relationship exists between altitude and sexual dichromatism. We found a significant positive relation between altitude and sexual dichromatism when accounting for the UV-sensitive vision of Passeriformes, Charadriiformes, Psittaciformes and Struthioniformes, but not when dichromatism is measured using human scoring. This suggests that there might be a greater selection pressure for females to select high-quality males in harsher, higher altitude, environments and that this signalling is primarily done in the ultraviolet range. We suggest that macroecologists should pay closer attention to the receiver psychology of signals even when studying a large number of species and that not doing so could lead to misleading or spurious macroecological and/or macroevolutionary patterns.

Introduction

Biologists and naturalists have studied bird feathers since antiquity (Aristoteles [Peck, trans.], 2007) and evolutionary biologists have focused on bird feathers for their studies since the days of Darwin and Wallace (Darwin, 1871; Wallace, 1889). The study of feathers has helped lay the foundations of various fields within evolutionary biology (Hill & McGraw, 2006), such as sexual selection (Andersson, 1994) and signalling theory (Maynard Smith & Harper, 2003). Despite this long-standing interest from many biologists in the evolution and purpose of avian plumage, it is only in recent decades that the study of colouration has fully integrated the importance of understanding the receiver sensitivity, psychology and *umwelt*, i.e. the subjective experience of the world (von Uexküll, 1934), of the animals in question (Endler et al., 2005; Guilford & Dawkins, 1991; Partan & Marler, 2002), a change facilitated by the greater affordability and portability of spectrophotometers (Bennett & Théry, 2007; Burns et al., 2017).

Although both humans and birds are visually oriented species, fundamental differences exist in the physiology of vision that differentiates the *umwelt* of vision between them. While most humans possess three spectrally distinct single-cone cell photoreceptors (Jacobs, 2018), many bird species, including Passeriformes, Charadriiformes, Psittaciformes and Struthioniformes possess four (Hart, 2001; Hart & Hunt, 2007). Consequently, birds in these four orders, which constitute more than half of all known bird species (Billerman et al., 2022), are able to see into the ultraviolet spectrum. Furthermore, unlike humans, birds possess double-cone cells whose function is primarily to detect luminescence (Hart & Hunt, 2007; Osorio & Vorobyev, 2005). These differences in visual system mean that many examples exist of differences in colouration between birds of the aforementioned Orders, which cannot be seen by humans (Benites et al., 2010; Burns & Shultz, 2012; Cuthill et al., 2000; Eaton, 2005; Eaton, 2007; Eaton & Lanyon, 2003; Hart & Hunt, 2007; Hofmann et al., 2006; Mays et al., 2004; Mennill et al., 2003; Mullen & Pohland, 2007; Santos Sico et al., 2007; Tubaro et al., 2005). Despite these differences in visual system, most work on avian colouration has used human observers to quantify colour (Carballo et al., 2020; Cooney et al., 2018, 2019, 2022; Dale et al., 2015; Stevens & Merilaita, 2009; Webb et al., 2016). This has been justified by studies demonstrating that human assessments of bird colouration are comparable to those made by spectrophotometers (Armenta et al., 2008; Bergeron & Fuller, 2018; Seddon et al., 2010). However, there remains no *a priori* reason to assume that human and avian assessments of colouration are comparable (Eaton, 2005; Eaton et al., 2022), and new examples continue to be found of cryptic, to human eyes, colouration in birds (Barreira et al., 2012; Burns & Shultz, 2012; Hung et al., 2017; Lou et al., 2022; Rull et al., 2016; Wilson et al., 2012). Thus, we consider it still necessary to assess avian colouration using avian visual systems as models, rather than relying on the assessments of human observers.

Many hypotheses around avian sexual dichromatism, that is, differences in colouration between males and females, focus on sexual selection (Badyaev & Hill, 2003; Baker & Parker, 1979; Darwin, 1871; Price, 1998). Sexual selection is known to be an important evolutionary driver of sexual dichromatism within many species (Cooney et al., 2019). Avian dichromatism has also been used as a proxy for sexual selection intensity in several studies (Iglesias-Carrasco et al., 2019; Sorci et al., 1998). Identifying cryptic (to humans) sexual dichromatism was one of the first posited functions for ultraviolet vision in birds (Bennett & Cuthill, 1994; Guilford & Harvey, 1998), and such cryptic dichromatism has been found to be the object of sexual selection in some species (Andersson et al., 1998; Galván et al., 2016; Hunt et al., 1999; Pearn et al., 2001; Sirkiä & Laaksonen, 2009). Work on the macroecology and macroevolution of avian sexual dichromatism has linked more sexual dichromatism to higher rates of extra-pair paternity (Valcu et al., 2023), with polygynous mating systems (Dale et al., 2015) and to female-biased adult sex ratios (Gonzalez-Voyer et al., 2022), though all these studies used scores of sexual dichromatism assessed by human observers.

The study of the macroecology and biogeography of sexual selection is an actively growing field (Bacon et al., 2023; Machado et al., 2016; Macías-Ordóñez et al., 2013). Within this field, avian sexual dichromatism has received more attention than many other traits related to sexual selection, with work suggesting both a latitudinal (Badyaev & Hill, 2003; Bailey, 1978; Cooney et al., 2022) and altitudinal gradient in sexual dichromatism (Badyaev, 1997a, 1997b; Beltrán et al., 2022; Fang et al., 2022; Tobias & Seddon, 2009). Sexual dichromatism appears to decline with both latitude (Cooney et al., 2022) and altitude (Badyaev, 1997a). The hypothesis offered for the apparent altitudinal gradient is that in harsher higher altitude environments, it is costlier to raise a chick, leading to selection for biparental care (Lyon & Montgomerie, 1987), which is negatively correlated with sexual dichromatism (Ekanayake et al., 2015). However other aspects of the high-altitude environment, such as higher extrinsic mortality rate increasing the cost of high acceptance thresholds for mates (Reeve, 1989) or higher degrees of ultraviolet light intensity (Fang et al., 2022) could also be responsible for a declining rate of sexual dichromatism.

Latitude would likely be an important confounding factor which might hide an altitudinal gradient for birds. It is well established that the effect of altitude interacts with latitude (Janzen, 1967; Sheldon et al., 2018), as the same altitude at a different latitude can impose substantially different selective pressures. These include the effect of altitude and latitude on traits which are assumed to be primarily influenced by sexual selection rather than natural selection (Bonier et al., 2014; Friedman & Remeš, 2016; Valcu et al., 2021). The mechanism by which altitude is thought to influence traits under sexual selection is that increasing environmental harshness imposes greater selection for both cooperative breeding and lower acceptance thresholds of potential mates.

Despite these studies on the effect of altitude on avian sexual dichromatism, showing that sexual dichromatism decreases with altitude (Badyaev, 1997a, 1997b), we consider the time ripe to return to the question of altitude and avian dichromatism while addressing the shortcomings of earlier studies. As stated, previous work failed to account for the difference between human and many avian visual systems, thus potentially missing cryptic dichromatism (Badyaev, 1997a, 1997b; Tobias & Seddon, 2009). However, many focused on variation in sexual dichromatism within a single species (Cornuault et al., 2015; Fang et al., 2022) or family (Badyaev, 1997a; Beltrán et al., 2022), or focused on a small number of species but used only human perception to score dichromatism (Badyaev, 1997a, 1997b). This study is the first to use Vorobyev-Osorio Sexual Dichromatism Scores from a large number of species across multiple families to test the hypothesis that sexual dichromatism decreases with altitude. Whilst focusing on the correlation between altitude and sexual dichromatism, we also consider how justified is the standard methodology of assuming human visual scoring is equivalent to spectrophotometer scoring for the assessment of avian visual systems.

Materials and methods

Included variables

In addition to altitude and latitude, we included other variables in our analyses that are known to impact the degree of sexual dichromatism, for which data are readily available for the majority of species. Unlike latitude, which directly interacts with altitude, we excluded the interaction effects of these variables with altitude in our model. The non-altitude and non-latitude variables included are body mass, parental care and habitat preference. Before being included in the overall model, all variables were checked for multicollinearity using the variance inflation factor (Akinwande et al., 2015), using the function *vif* from the package *car* (Fox & Weisberg, 2019) with a cutoff of 2.5 (Zuur et al., 2010).

Data collection

Data on altitude for the species was copied from the BirdLife International Data Zone. Data on avian dichromatism came from Armenta et al. (2008). This includes a dataset of 987 species, representing 9.8% of the world's bird species, across 91 families and 20 orders. We trimmed the dataset to include only members of Orders where UV-sensitive vision is widespread, that is, Passeriformes, Charadriiformes, Psittaciformes and Struthioniformes, leaving us with 758 species. This dataset includes both measures of absolute dichromatism, such as Principal component analysis (PCA), segment classification and colour discrimination. However, we opted to use the Vorobyev–Osorio colour discrimination model measurements (Vorobyev et al., 1998), which attempt to model the degree of colour discrimination as perceived by a conspecific. Data on latitude, body mass and habitat preference were obtained from the AVONET database (Tobias et al., 2022), with the latitude data being obtained from the absolute latitude centroids in said database. Data on parental care come from Cockburn (2006) and Lavaniegos-Puebla et al. (2024). We used the habitat preference typology of AVONET and the parental care typology of Cockburn (2006).

The Vorobyev-Osorio colour discrimination model measures the observed subjective difference in colour by calculating the quantum catch photoreceptors in the eye and incorporating information such as ambient light, transmission spectrum of oil droplets in the colour cones in the eye, sensitivity of individual opsins and photoreceptor noise, and returns distance in colour space in units of just noticeable differences (JNDS). The Vorobyev-Osorio colour discrimination model assumes that colour discrimination is determined by the noise within the photoreceptors and the relative abundance of photoreceptors. The calculation accrues parameters as the number of cones increases, but in its simplest form, in a species with dichromatic vision, can be calculated as

$$\frac{(\Delta q_i - \Delta q_2)^2}{e_1^2 + e_2^2}$$

Where Δq_i is the difference in the quantum catch between threshold stimuli, and e_i is the standard deviation of the noise in receptor channel i. Full details both on the mathematical model used the Vorobyev-Osorio colour discrimination model and the physiological and physical variables that are measured to get Δq_i and e^{i} ^{c} can be found in Vorobyev et al. (1998).

Because of these variables, while the Vorobyev–Osorio methodology is useful to study perceived subjective colour difference in an objective fashion, it is highly sensitive to the parameters being used, such as the visual system being modelled and ambient light (Bitton et al., 2017; Lind et al., 2017; Maia & White, 2018). For that reason, we have opted to use one dataset which used one standard approach (Armenta et al., 2008), rather than amalgamate data from other sources which have also used the Vorobyev–Osorio colour discrimination model, but with slightly different spectral sensitivity function measures of ambient light, or other parameters in the model (i.e. Beltrán et al., 2022; Eaton et al., 2022; Luro & Hauber, 2022).

Ideally, the Vorobyev–Osorio colour discrimination model would use unique spectral sensitivity functions for each species and its natural environment, but these remain unknown for most bird species (Martin, 2021, 2022). Thus, instead, we have followed the approach of other studies (Armenta et al., 2008; Eaton et al., 2022; Luro & Hauber, 2022) in using a representative UVS-type visual system. While this is far from ideal, UVS-type visual systems are widespread amongst birds of the Orders Passeriformes, Charadriiformes, Psittaciformes and Struthioniformes (Hart & Hunt, 2007; Ödeen & Håstad, 2013), making them the most reasonable to use in multispecies studies. Full details can be found in Armenta et al. (2008).

The Vorobyev–Osorio colour discrimination model provides a measure of observed subjective difference in colour, but it is generally agreed that any difference of less than 1 JND is not perceptible (Kelber et al., 2003; Olsson et al., 2015; Siddiqi et al., 2004). While the minimum difference of 1 JNDS has been criticized for not being sufficiently conservative, especially in ecological settings where vision is less than in lab environments (Caves et al., 2018; Maia & White, 2018), it remains the standard threshold for the creation of testable hypotheses in the study of vision (Benites et al., 2010; Eaton et al., 2022).

In addition to this global analysis of 758 species, we also compared our results with those of previous studies, conducted using human-scored dichromatism, which had reported an altitudinal or latitudinal gradient in sexual dichromatism in birds (Badyaev, 1997a, 1997b; Cooney et al., 2022). This required us to trim the dataset to include only species present in both the original analysis and in the dataset of subjective avian dichromatism, (Cooney et al., 2022). The trimmed dataset contained 596 species: all in the Passeriformes.

The following statistical analyses were performed using both the human dichromatism scores and the Vorobyev–Osorio colour discrimination scores.

Statistical methods

We downloaded 100 species trees from the Bird Tree of Life (Jetz et al., 2012, 2014), using the higher taxa backbones from Hackett et al. (2008). We then developed a strict consensus tree (Felsenstein, 2004), with branch lengths derived using the method in Grafen (1989), using the *consensus* and the *compute.brlen* functions from the package ape (Paradis & Schliep, 2019). We used a consensus tree, rather than running the analysis over distribution of trees since a consensus tree has been found to provide the same result as running the analysis over multiple trees, and then averaging (Rubolini et al., 2015), and because the use of consensus trees remains a widespread practice in comparative phylogenetic work which uses data from the Bird Tree of Life (i.e. Deakin et al., 2024; Hatfield et al., 2018). Trees were then trimmed, using the *keep.tip* function from the *ape* package, to include only data on species for which we had both Vorobyev–Osorio colour discrimination data and altitudinal data for the global analysis,

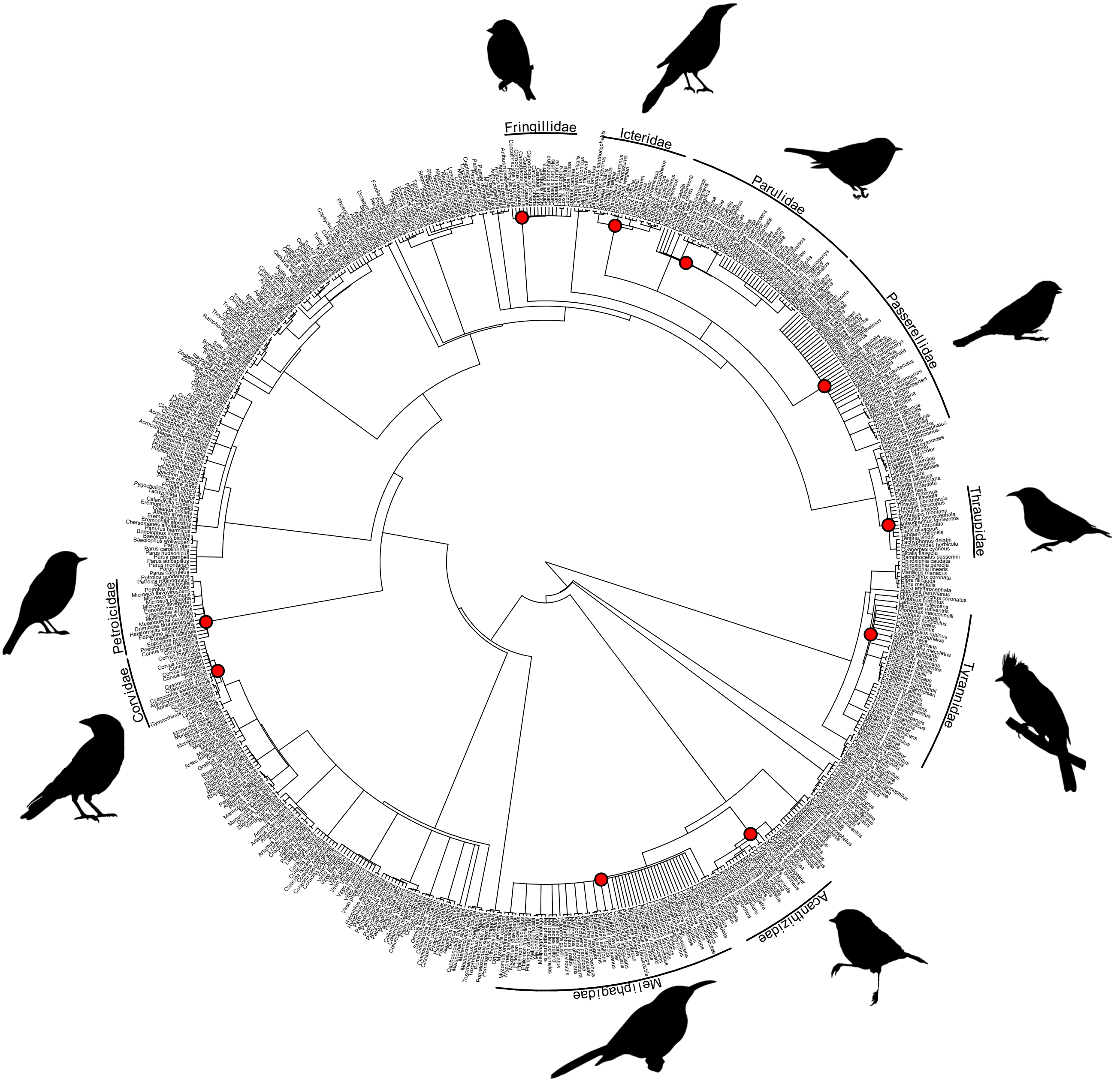

Figure 1 Phylogeny of species included in both the Armenta and the Cooney datasets. Only the 10 most speciose families are labelled to ensure legibility.

and the subset of this global dataset for comparisons between human-scored and Vorobyev–Osorio colour discrimination scores of dichromatism.

Normal statistical techniques cannot be used when working with interspecific data, since the relatedness of species violates the assumption of independence of datapoints found in most statistical tests (Harvey & Pagel, 1991). To correct for the relatedness of species, multiple techniques have been developed, including Phylogenetic Independent Contrasts (PICs) (Felsenstein, 1985), phylogenetic generalized estimating equations (PGEE) (Paradis & Claude, 2002) and phylogenetic generalized least-squares (PGLS) regression (Martins & Hansen, 1997). Due to the difficulty of getting data to meet the residual normality assumption required for the PGLS, and of Brownian trait evolution required for PICs, we opted to use a PGEE, implemented through the *compar.gee* function of the ape package, which does not impose these assumptions. Generalized Estimating Equations (GEEs) are an extension of Generalized Linear Models (GLM) which permits GLMs to be fitted to clustered data (Liang & Zeger, 1986), and PGEEs are GEEs

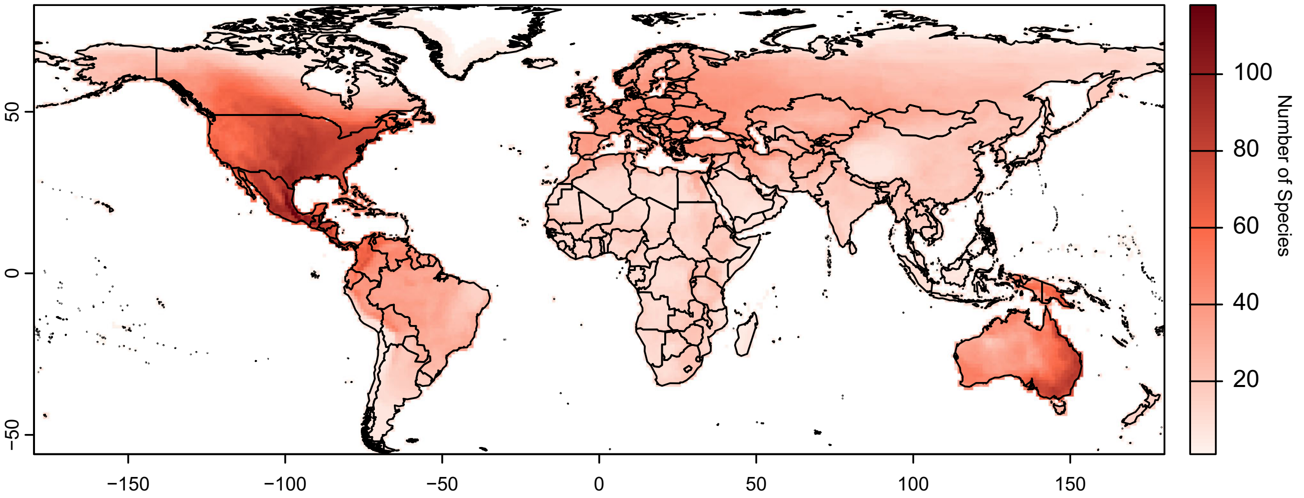

Figure 2 Species richness map of all species included in this study.

which include phylogenetic relatedness within its correlation matrix (Paradis & Claude, 2002). We ran two PGEEs with the Armenta et al. (2008) data, one including data on all species and one including data only for species which had visible sexual dichromatism (JNDS >1). We also ran PGEEs on the direct comparison datasets, where we had data on both human scoring on Vorobyev-Osorio colour discrimination scores. We ran these on both the complete and the trimmed datasets. PGEEs run on both the complete and the trimmed dataset, with one exception (see below) included altitude, latitude, mass, habitat type, parental care and the interaction between altitude and latitude as potential explanatory variables. We used absolute dichromatism, rather than accounting for the direction of dichromatism, as the measure of dichromatism. In order to maintain sufficient degrees of freedom to calculate *P*-values, the PGEEs on species found in both the Badyaev (1997a) and Armenta et al. (2008) lists included only altitude, latitude and their interaction. To correct for multiple testing, we performed Holm-Bonferroni Corrections (Holm, 1979) on all *P*-values of PGEE analyses. *P*-values presented in the rest of the paper are the Holm-Bonferroni corrected *P*-values.

All statistical analysis was carried out using R. In addition to the functions and libraries which have already been mentioned, data were imported and PGLSs and PICs and testing for the assumptions of PGLSs and PICs were done using the readxl, writexl, geiger, nlme, phytools, caper and evobiR packages (Pinheiro & Bates, 2000; Revell, 2012; Pennell et al., 2014; Jonika et al., 2023; Orme et al., 2023; Ooms, 2023; Wickham & Bryan, 2023). Graphs were drawn using the ggplot2, ggeffects, letsR and ggtree libraries, with images from rphylopic (Gearty et al., 2018; Lüdecke, 2017; Vilela & Villalobos, 2015; Wickham, 2016; Yu et al., 2017).

Results

Data for the Vorobyev-Osorio Sexual Dichromatism scores were available for 758 species, and had data on both Vorobyev-Osorio Sexual Dichromatism scores and human scoring from Cooney et al., 2022, from 596 species. The 758 species for which data were available on Vorobyev-Osorio Sexual Dichromatism (the full dataset) included 90 Charadriiformes, 11 Psittaciformes, 654 Passeriformes and three Struthioniformes. The 596 species of the trimmed dataset included in both the Cooney and the Armenta datasets included 76 families of Passeriformes (Fig. 1). While species from every continent were included in the dataset, they were biased towards North and Central America and Australia (Fig. 2). We found a statistically significant positive correlation between sexual dichromatism and altitude when analysing the Vorobyev-Osorio Sexual Dichromatism Scores of the 758 species in the full dataset (Table 1) (Fig. 3), and when using the Vorobyev-Osorio Sexual Dichromatism Scores of the trimmed. However, we found a negative correlation between the interaction between altitude and latitude amongst the 596 passerine species of the trimmed dataset (Table 1), and no significant impact of altitude on sexual dichromatism. We found that male-only, female-only and cooperative parental care all increase sexual dichromatism measured by Vorobyev-Osorio Sexual Dichromatism Scores amongst the 758 species of the full dataset, but not in the trimmed dataset, perhaps due to the taxa used in our analysis. Due to the small number ($N = 11$) of species available with Vorobyev-Osorio Sexual Dichromatism Scores from the original Badyaev, 1997b dataset we have excluded the results of the PGEEs of those species. They are, however, included in the Supporting Information for interest. Nevertheless, our comparison of the results of human and Vorobyev-Osorio Sexual Dichromatism scores is based on both the trimmed and complete datasets.

Discussion

While Badyaev found a decreasing altitudinal gradient in sexual dichromatism using human scoring, we could find no evidence of any gradient, positive or negative, in sexual

Table 1 Statistically significant results of the generalized estimating equations run in this analysis

Model	Variable	Estimate	SE	*t*	Raw *P*-values	Helm-Bonferroni corrected *P*-values	Phylogenetic degrees of freedom (Pdf)	*N*
Model 1	Altitude	5.63E-05	5.87E-06	9.580	8.90E-06	5.00E-05	27.321	758
Model 1	Mass	-5.40E-06	7.21E-07	−7.486	5.71E-05	3.00E-03	27.321	758
Model 1	Habitat Forest	1.54E-01	2.99E-02	5.148	7.74E-04	4.10E-2	27.321	758
Model 1	Habitat Riverine	6.09E-01	3.78E-02	16.129	1.44E-07	9.00E-6	27.321	758
Model 1	Habitat Woodland	2.09E-01	2.99E-02	6.992	9.39E-05	5.00E-03	27.321	758
Model 1	Parental Care Cooperation	−7.74E-01	7.48E-02	−10.347	4.91E-06	3.00E-04	27.321	758
Model 1	Parental Care Female Only	−9.24E-01	7.54E-02	−12.257	1.30E-06	8.00E-05	27.321	758
Model 1	Parental Care Male Only	−1.09E+00	9.60E-02	−11.319	2.43E-06	1.00E-04	27.321	758
Model 1	Parental Care Pair	−9.19E-01	7.45E-02	−12.337	1.23E-06	8.00E-05	27.321	758
Model 3	Altitude	1.10E-04	7.89E-06	13.925	2.18E-07	1.00E-05	24.986	596
Model 3	Latitude	5.60E-03	4.64E-04	12.083	7.36E-07	5.00E-05	24.986	596
Model 3	Mass	8.92E-04	9.18E-05	9.715	4.60E-06	3.00E-04	24.986	596
Model 3	Habitat Human Modified	5.64E-01	6.52E-02	8.644	1.20E-05	7.00E-04	24.986	596
Model 3	Habitat Riverine	1.12E+00	7.38E-02	15.147	1.05E-07	7.00E-06	24.986	596
Model 3	Habitat Rock	3.58E-01	7.23E-02	4.952	7.93E-04	4.10E-02	24.986	596
Model 3	Habitat Woodland	3.15E-01	6.57E-02	4.792	9.89E-04	4.90E-02	24.986	596
Model 3	Altitude × Latitude	−1.48E-06	2.70E-07	−5.471	3.97E-04	2.10E-02	24.986	596
Model 4	Latitude	4.58E-03	3.03E-04	15.120	1.07E-07	7.00E-06	24.986	596
Model 4	Mass	−4.24E-04	5.99E-05	−7.077	5.86E-05	3.00E-03	24.986	596
Model 4	Habitat Desert	−4.16E-01	7.06E-02	−5.885	2.35E-04	1.30E-02	24.986	596
Model 4	Habitat Riverine	−3.71E-01	4.82E-02	−7.706	3.01E-05	2.00E-03	24.986	596
Model 4	Parental Care Female Only	2.34E-01	1.19E-02	19.745	1.04E-08	7.00E-07	24.986	596
Model 4	Parental Care Pair	3.21E-02	6.66E-03	4.821	9.50E-04	4.80E-02	24.986	596

Model 1 refers to Generalized Estimating Equation of all Vorobyev-Osorio Sexual Dichromatism Scores of all species with ultraviolet species included in Armenta et al. (2008). Model 2 refers to Generalized Estimating Equation of Vorobyev-Osorio Sexual Dichromatism Scores of all species with ultraviolet species included in Armenta et al. (2008) with a JNDS >1. Model 3 refers to Phylogenetic Generalized Estimating Equation of Species included in both Cooney et al. (2022) and Armenta et al. (2008), with the Vorobyev-Osorio Sexual Dichromatism Scores as the dependent variable. Model 4 refers to Phylogenetic Generalized Estimating Equation of Species included in both Cooney et al. (2022) and Armenta et al. (2008), with the Human Scores as the dependent variable.

dichromatism, using human scoring. However, in both models of sexual dichromatism using Vorobyev-Osorio Sexual Dichromatism scores, we found a positive correlation between altitude and sexual dichromatism. This runs counter to most previous work and theory on macroecology of bird colouration in recent years, which has found that bird and human scoring is roughly equivalent (Bergeron & Fuller, 2018; Seddon et al., 2010). It also suggests precisely the opposite correlation between altitude and sexual dichromatism which Badyaev posited. While this can be for a variety of reasons, one possible one is that the harsher, higher altitude, environments make it more important for females to select high-quality mates, which in turn requires greater sexual signalling by males to attract partners. This signalling in turn is primarily done in the ultraviolet range at these higher altitudes.

While our results suggest the presence of an altitudinal gradient in sexual dichromatism amongst birds with UV-sensitive visual systems, it is not conclusive that such a gradient exists across all birds. That conclusion would require a wider study of the subjective dichromatism of all, or at least most, bird orders, including those that lack the UV-sensitive visual system of the Passeriformes, Charadriiformes, Psittaciformes and Struthioniformes. Ideally, such subjective measures of sexual dichromatism would include detailed information on the sensory physiology and typical ecological atmospheric light conditions of the birds in question. However, despite significant advances in global databases for many other aspects of bird biology (Santini et al., 2023; Tobias et al., 2022), no published database exists for avian sensory parameters of species where that information is known and the sensory parameters for most species remain unknown (Martin, 2021, 2022).

Our results differed depending on whether we used human or Vorobyev–Osorio colour discrimination scores, contradicting previous literature which has shown which human visual scoring and modelling the avian visual system should lead to equivalent results across a large range of species (Armenta et al., 2008; Bergeron & Fuller, 2018; Seddon et al., 2010). We doubt that this is an artefact of trimming the dataset for our study, but rather suggest that this reflects the difference in methodology. This greatly strengthens the arguments made by some (Eaton et al., 2022) that studies of dichromatism should default to incorporating avian visual systems. We suggest that using models that incorporate avian visual systems when studying avian colouration is more likely to lead to accurate assessments of macroecological patterns than are the more commonly used human assessments since divergences between human and avian assessment in dichromatism remain

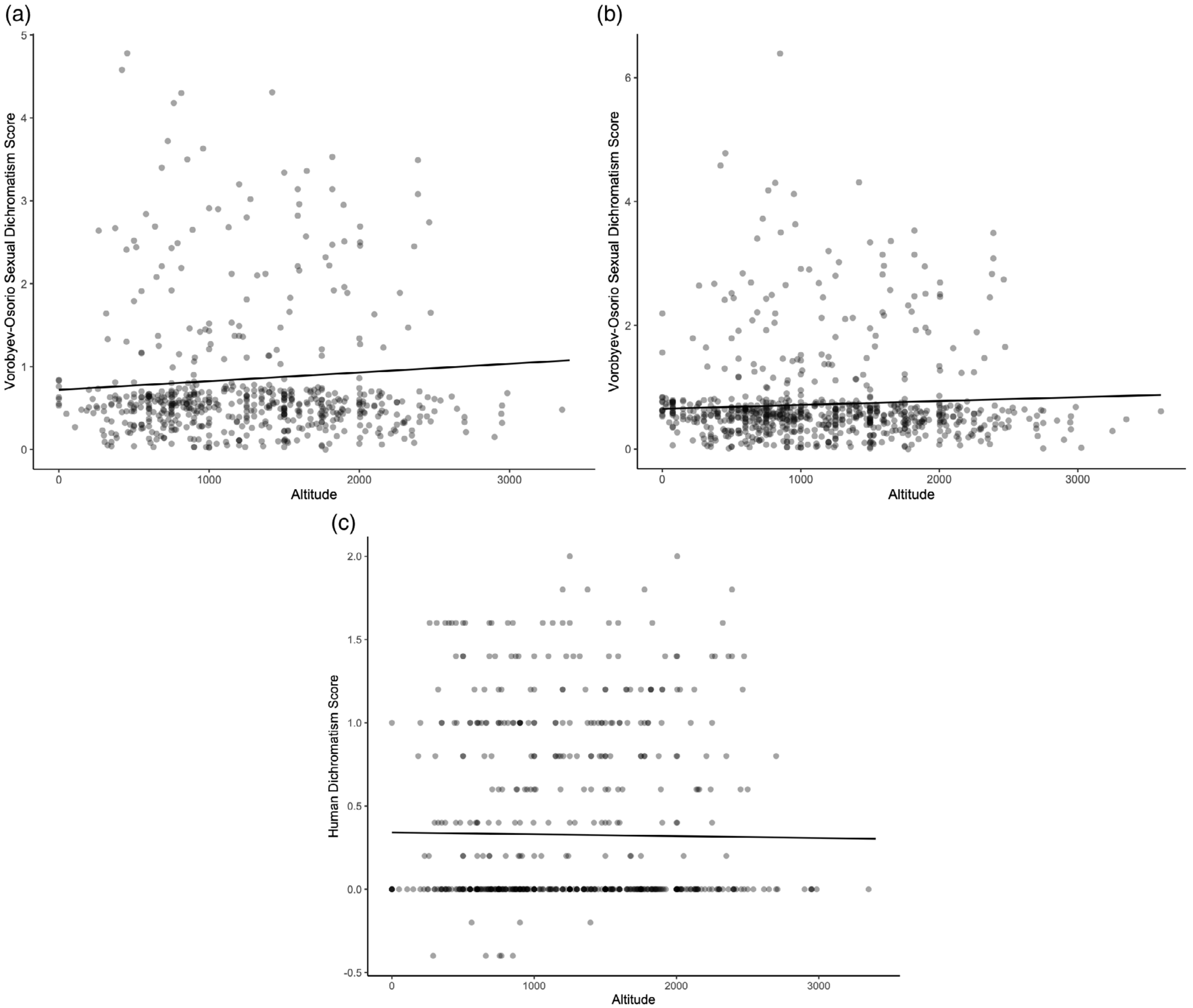

Figure 3 Relation between altitude and sexual dichromatism. (a) The Vorobyev-Osorio Sexual Dichromatism scores of species from Armenta et al., 2008 which are in Orders which customarily see into the ultraviolet spectrum, (b) The Vorobyev-Osorio sexual dichromatism scores of sexual dichromatism of species included in both Armenta et al. (2008) and Cooney et al. (2022). (c) Human scores of sexual dichromatism of species included in both Armenta et al. (2008) and Cooney et al. (2022). Trend lines show the effect of altitude in PGEE models used in this study.

impossible to predict *a priori*. Using avian visual systems as a model also allows us to test the hypothesis more accurately about the role of the environment in influencing the intensity of sexual selection, and in turn in influencing sexually dimorphic traits such as sexual dichromatism. We suggest that macroecologists should work more closely with behavioural ecologists, animal psychologists and ethologists who research the receiver psychology of animals (Guilford & Dawkins, 1991), in order to make comparisons which are biologically relevant to the taxa at hand. Our results suggest that failure to do so, and using human perception as the measure of signals, can lead to a misreading of macroevolutionary patterns.

We found a positive correlation between altitude and sexual dichromatism when using Vorobyev-Osorio Sexual Dichromatism Scores. It is possible that the result found by Badyaev et al. (1997b) is due to it being a single taxon study, focused on cardueline finches. It is also consistent with the work of Beltrán et al. (2022), who found that sexual dichromatism increases with altitude in hummingbirds. These findings combined suggest that the sexual dichromatism of species in higher altitudes are more likely to be in the ultraviolet range which humans cannot see with the naked eye. Ideally, we would be able to include information on the strength of sexual selection across the birds in these datasets to determine whether sexual selection or natural selection, is driving this pattern. Although

Bateman Gradients of these species would be ideal as a measure of sexual selection, they are only available for 66 species (Janicke et al., 2016). Other measures, which are often used as proxies of the strength of sexual selection, such as sexual dimorphism (Iglesias-Carrasco et al., 2019; Sorci et al., 1998), we consider would be an instance of 'begging the question', while social mating systems have been found to be a poor guide to the strength of sexual selection in birds given the commonality of extra-pair paternity (Valcu et al., 2023). It is also possible that this altitudinal sexual dichromatism gradient is unrelated to sexual selection and instead caused by natural selection, as has been shown for other dimorphic traits (Price, 1998; Rico-Guevara & Hurme, 2019).

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Data Availability

R Code and data needed to recreate this analysis are deposited at Dryad: https://datadryad.org/stash/share/7Cr9-9rtTi8h-JmAHZsOkv7-aFnXPd6ThX7qRRx6Pd4.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. All species from Armenta et al. (2008).

Table S2. Species from Armenta et al. (2008) with jns > 1.

Table S3. Species from Badyaev et al. (1997), spectrophotometer scores.

Table S4. Species from Badyaev et al. (1997), human scores.

Table S5. Species from Cooney et al. (2022), spectrophotometer scores.

Table S6. Species from Cooney et al. (2022), human scores.