Sex differences in avian plumage evolution: stronger effects of natural selection and social competition on females

Robert A. Barber[1,2], Jingyi Yang[1], Rafael Marcondes[3,4], Robb Brumfield[3], Joseph A. Tobias[1]

[1]Department of Life Sciences, Imperial College London, Silwood Park, Ascot, SL5 7PY, UK

[2]Ecosystem Stewardship Directorate, Royal Botanic Gardens, Kew, London, UK

[3]Museum of Natural Science and Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana, 70803, USA

[4]Department of Biosciences, Rice University, Houston, Texas, USA

Corresponding author

Robert A. Barber[1,2]; r.barber@kew.org; 0000-0001-6735-5250

Running title: Plumage ornamentation in suboscines

Keywords: sexual selection, natural selection, social selection, signal ornamentation, mating system, nest visibility, predation, territoriality, habitat density, body mass

ABSTRACT

Sexual dichromatism in birds may evolve via sexual selection for increased elaboration in male plumage (Darwin hypothesis) or, alternatively, by natural selection for increased crypsis in female plumage (Wallace hypothesis). Both these effects may be counteracted by social competition promoting ornamentation in females. However, the relative roles of sexual, natural, and social selection in shaping patterns of plumage dichromatism have proved difficult to disentangle. To test these hypotheses in conjunction, we estimated the strength of sexual selection on males, the level of predation risk on females and the intensity of social selection across 1283 species of suboscine passerines. We then used phylogenetic analyses to evaluate the drivers of sex differences in plumage elaboration and brightness. The results confirm that sexual selection increases plumage elaboration in males but not females, driving overall dichromatism. In contrast, predation risk more strongly affected female plumage, limiting brightness in species with exposed nests and female-only incubation. Similarly, social competition for year-round territories predicted greater plumage elaboration in both sexes, particularly in females. Our findings show that sexual dichromatism arises not only through sexual selection on male ornamentation, but also via natural and social selection pressures, which have greatest effect on female plumage evolution.

INTRODUCTION

Sexual dichromatism – the difference between males and females in plumage elaboration or conspicuousness – is widely considered a hallmark of sexual selection in birds (Dale *et al.* 2015; Dunn *et al.* 2001; Owens & Hartley 1998). Indeed, examples of plumage dichromatism featured prominently in Charles Darwin's initial proposal of sexual selection theory (Darwin 1871) while modern comparative studies often find that dichromatism correlates with mating strategies such as polygyny, extra-pair paternity, and lekking displays, suggesting a key role for female choice or male–male competition. However, this association is inconsistent across avian taxa. Many polygynous species are monochromatic (Bleiweiss 1997; Trail 1990), while substantial dichromatism also occurs in socially monogamous lineages (Badyaev & Hill 2003; McGraw *et al.* 2001; Surmacki *et al.* 2015). Furthermore, widespread mutual ornamentation, in which plumage is elaborate in both sexes, challenges the view that ornamentation arises exclusively from sexual selection acting on males and highlights the importance of understanding selection in females (Clutton-Brock 2009; Kraaijeveld *et al.* 2007; Rosvall 2011; Tobias *et al.* 2012b).

The earliest challenge to Darwin's hypothesis came from the co-discoverer of evolution, Alfred Russell Wallace (Fig. 1). Wallace (Wallace 1889) proposed that sex differences in plumage did not result from selection on males but instead from natural selection for crypsis in females, as a result of predation risk during nesting. According to this view, conspicuous females face higher fitness costs, favouring reduced female ornamentation in species with exposed nests or female-only incubation. Comparative studies provide mixed support for this prediction, reporting reduced brightness or lower conspicuousness of nesting females in some cases (Delhey *et al.* 2023; Drury & Burroughs 2016), but not others (Matysioková *et al.* 2017; Soler & Moreno 2012). These findings suggest that crypsis alone cannot explain the full range of plumage variation in female birds.

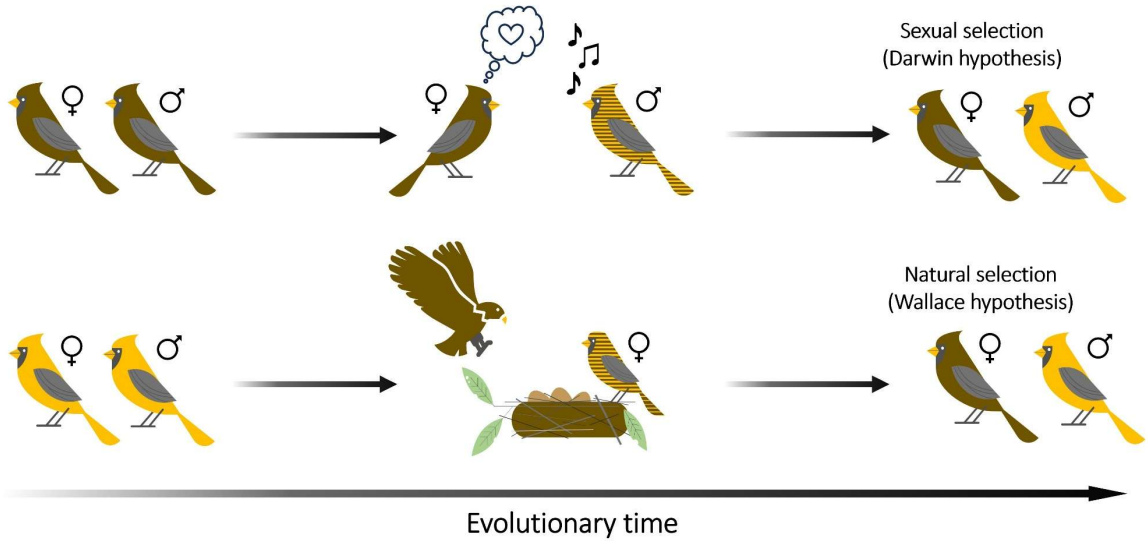

Figure 1. Opposing viewpoints on the origins of sexual dichromatism. Charles Darwin and Alfred Russel Wallace proposed two different evolutionary pathways explaining patterns of sexual dichromatism in birds. Darwin proposed that the ancestral state of avian plumage was dull monomorphism, with increased plumage ornamentation among males arising through processes such as intra-sexual competition and female choice, leading to plumage dichromatism in species with heightened sexual selection. Wallace proposed that the ancestral state of avian plumage was elaborate monomorphism, and that dichromatism arose instead because females were under natural selection for crypsis to reduce the risk of nest predation in species with visible nests and female-biased parental care. While these hypotheses assume distinct ancestral states and evolutionary mechanisms, they both theoretically converge on modern patterns of elaborate males and dull females—a prevalent characteristic observed in the majority of contemporary bird species.

A more recent hypothesis is that female ornamentation may arise through social selection via competition for ecological resources such as territories, nesting sites or social status (LeBas 2006; West-Eberhard 1983). In species with strong territoriality or frequent female–female aggression, female plumage often functions in social signalling and may evolve independently of male traits (Enbody *et al.* 2018; Macedo *et al.* 2021). Current evidence suggests that social competition may drive

ornamentation in both sexes (Amundsen 2000; Irwin 1994; Tobias *et al.* 2011), potentially explaining many cases of 'bright monomorphism', particularly in tropical birds (Tobias *et al.* 2012b).

Despite increased recognition of these alternative evolutionary drivers of plumage dichromatism, most comparative studies continue to focus narrowly on sexual selection, overlooking the complex suite of selection pressures acting on each sex. Macroevolutionary studies often treat dichromatism as a single trait, without resolving whether sex differences arise through changes in males, females, or both. Yet divergent evolutionary processes such as male elaboration, female crypsis, and mutual ornamentation can all produce similar levels of dichromatism, making it near-impossible to infer the direction or cause of effects without decomposing these outcomes (Doutrelant *et al.* 2020; García *et al.* 2022). In response, some studies have developed sex-specific metrics, including brightness (Irwin 1994; Marcondes & Brumfield 2019), colour complexity (García *et al.* 2022; Shultz & Burns 2017), and male-like appearance in females (Dale *et al.* 2015). However, while each metric captures a specific aspect of plumage variation, none offers a general framework for quantifying ornamentation across diverse species. For instance, metrics that treat high brightness as inherently more elaborate risk underestimating the signal value of extremely dark traits, such as super-black plumage (McCoy & Prum 2019). Resolving the evolutionary origins of dichromatism requires a generalisable metric that captures directional elaboration in both sexes, without presupposing which traits are ornamented.

To develop this metric, we disaggregate sexual dichromatism into sex-specific trajectories by quantifying ornamentation separately in males and females. Using colour spectrophotometry and visual models calibrated to avian perception, we estimate two key dimensions of plumage design: elaboration and brightness. We quantify elaboration as chromatic distance from the average suboscine colour, and brightness as achromatic reflectance. Unlike previous approaches, this method does not assume that ornamentation scales along a single axis of conspicuousness, but instead captures both colour and brightness changes as independent axes of plumage variation. Moreover, by quantifying elaboration as trait uniqueness or distinctiveness in multidimensional colour space, we enable consistent comparisons across lineages, independent of species-specific contexts. In other words, our system detects extreme

red and extreme black plumages as equally far from the norm, and therefore equally elaborate.

We apply this framework to the suboscine passerines (Tyranni), a diverse clade that includes manakins, cotingas, antbirds, and ovenbirds, representing around a tenth of the world's bird species. Suboscines span a wide range of ecological strategies, mating systems, and signal types, making them a powerful system for testing how sex differences in plumage evolve across environments (Tobias *et al.* 2012a). They also vary markedly in sexual dichromatism, from extreme male-biased ornamentation in lekking cotingas and manakins (Porzio & Mota 2025; Ribeiro *et al.* 2015) to dull monomorphism in monogamous ovenbirds (Marcondes & Brumfield 2019). Finally, the suboscine clade has a highly resolved species-level molecular phylogeny and rich trait datasets (Harvey *et al.* 2020; Tobias *et al.* 2022), providing an ideal template for evaluating the relative contributions of sexual, natural, and social selection.

Using phylogenetic comparative analyses, we test whether sex-specific elaboration and brightness are shaped by three major selective pressures. Under sexual selection, polygamous species are expected to show increased elaboration in males, driving stronger dichromatism (Cooney *et al.* 2019; Dale *et al.* 2015). Under natural selection, female ornamentation should be constrained in species subject to visible predation, particularly those with exposed nests and female-only incubation (Drury & Burroughs 2016; Wallace 1889). Under social selection, year-round territoriality is predicted to favour signal elaboration in both sexes, reducing dichromatism via increased female ornamentation (Tobias *et al.* 2012b; West-Eberhard 1983). To account for additional ecological factors that may shape or confound these relationships, we also include measures of habitat density, body size, and diet—traits known to influence plumage evolution through their effects on signal transmission, metabolic constraint, and trophic ecology (Beehler 1983; Carballo *et al.* 2020; Shultz & Burns 2017). In particular, a frugivorous diet has been proposed to drive the evolution of polygamy in suboscines, offering an ecological mechanism for patterns of plumage elaboration (Snow 1971). By evaluating these selective pressures on each sex independently, we test whether sex differences in ornamentation arise primarily through selection on males, females, or both.

METHODS

Quantifying plumage dichromatism

To quantify sex differences in plumage, we used two complementary approaches: human-assessed dichromatism and avian-perceived colour differences derived from spectral models. Human scores were based on illustrations published in the Handbook of the Birds of the World series (del Hoyo *et al.* 1992). We used these published versions for scoring although scanned digital versions of the same illustrations are now available online in Birds of the World (Billerman *et al.* 2025). To generate scores for all 1283 species in the suboscine phylogeny (Harvey *et al.* 2020), we adapted the standardised protocol of Irwin (Irwin 1994) and Owens & Bennett (Owens & Bennett 1994). We followed the same basic format of scoring five body regions (head; back; underparts; wings; tail) as 0 (no difference), 1 (difference in shade or intensity), or 2 (difference in colour or pattern) between males and females. In cases where only a single illustration is presented, we scored the species 0 when the text indicated that sexes are alike and 1 when the text indicated slight plumage differences between the sexes (see Supplementary Methods for details). In rare cases where different subspecies showed different levels of dichromatism, we scored the most widespread form, typically the nominate race. While human scoring is subject to potential biases in illustration and spectral sensitivity, previous analyses have shown that it is consistent between observers and highly correlated with avian-perceived dichromatism assessed using visual models (Seddon *et al.* 2010). This approach also improves sample size and captures variation in patterning—such as barring, colour blocking, or speckling—that may be overlooked by reflectance-based methods.

For avian-perceived dichromatism, we used reflectance spectra from 6,977 museum specimens representing 877 suboscine species. This dataset contained spectra published by Marcondes & Brumfield (Marcondes & Brumfield 2019), supplemented with new measurements for 292 species. Measurements were taken across seven standardised plumage patches (belly, breast, throat, crown, back, rump, and tail). Violet-sensitive visual models, calibrated to suboscine opsin data (Barreira *et al.* 2021; Ödeen & Håstad 2013), were used to convert spectra into chromatic and achromatic values in tetrahedral colour space. Male–female distances were calculated for each patch in just-noticeable differences (JNDs), yielding one chromatic and one achromatic contrast per region. To reduce dimensionality, we combined these into a

single composite dichromatism score using phylogenetic factor analysis (see below).

Quantifying elaboration and brightness

To assess the direction of sex differences in plumage, we adapted a method developed by Carballo *et al.* (Carballo *et al.* 2020), measuring elaboration as the distance between each patch and the average suboscine colour in avian colour space (Fig. S1). This approach quantifies elaboration as trait rarity (i.e., deviation from a common phenotype), supported by a recent empirical association between colour rarity and ornamental function across all birds (Delhey *et al.* 2023). The resulting metric provides a consistent measure of chromatic and achromatic elaboration across species, without assuming that ornamentation scales with brightness or any particular colour hue. As the centroid corresponds to a drab brown average, our metric also doubles as a proxy for 'distance from brownness', aligning with general perceptions of elaboration in birds.

We first calculated the centroid of suboscine plumage reflectance by averaging cone stimulation values across all patches and species, then measured chromatic and achromatic distances from this centroid for each patch in each individual (Fig. 2). Elaboration thus combines both colour and brightness distances from the centroid into a composite measure of distinctiveness, with greater distances indicating rarer, and therefore typically more elaborate, plumage traits. We used a different method for deriving absolute brightness (or luminance) from the same avian visual models, simply taking the achromatic reflectance of each plumage patch rather than a distance from the average suboscine brightness. While often correlated with elaboration, brightness captures a distinct axis of signal design, representing the total amount (intensity) of light reflected from plumage. For both elaboration and brightness, patch-level values were computed separately for males and females across seven plumage regions (belly, breast, throat, crown, back, rump, and tail). Sex-specific species-level scores were then estimated using phylogenetic factor analysis.

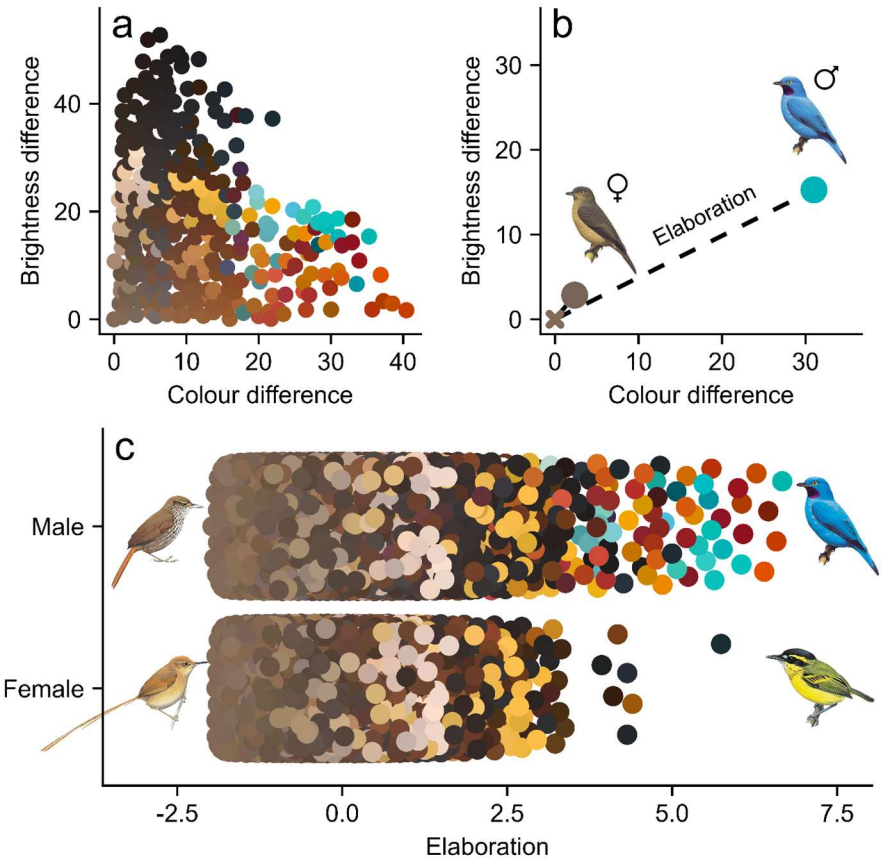

Figure 2. Inter- and intra-specific differences in plumage elaboration across suboscine passerine birds. To quantify elaboration of plumage patches, we estimated distance in colour and brightness from the most typical suboscine colour, calculated as the sample centroid within a violet-sensitive avian colourspace (*n* = 877 species). a, stratified sample of plumage patches (one patch randomly selected from each region of the elaboration space) shows how variation in both colour and brightness translates to distance from the suboscine centroid (i.e. distance from the origin). b, method for calculating sex differences in elaboration shown for a single species, *Cotinga maynana.* Combining differences in colour and brightness, male plumage is much further from the centroid (marked with an x), and therefore more elaborate. c, all 12,278 plumage patches plotted for males and females of 877 species. Colour and brightness differences were combined for each patch using a principal components analysis for visualisation purposes. Species shown at either end relate to the most and least elaborate patch for males and females, respectively: *Cotinga maynana* (top right); *Todirostrum chrysocrotaphum* (bottom right); *Syndactyla rufosuperciliata* (top left)*; Sylviorthorhynchus desmursii* (bottom left). Images are shared with permission of Birds of the World, Cornell University.

Phylogenetic factor analysis

To summarise variation across multiple plumage regions, we used phylogenetic factor analysis (PFA) to generate composite scores for each trait: human-assessed dichromatism, avian-perceived dichromatism, male elaboration, female elaboration, male brightness, and female brightness. PFA incorporates models of trait evolution, allowing latent variables to be estimated while accounting for phylogenetic non-independence among species (Hassler *et al.* 2022).

Each PFA was run separately using the maximum credibility tree from Harvey *et al.* (Harvey *et al.* 2020), extracting a single factor per trait type to retain interpretability. In nearly all instances, each patch loaded positively onto principal factor 1, indicating that species with higher values for each model were more dichromatic, elaborate, or brighter (Supplementary Methods for detailed breakdown). Models were run for 100,000 MCMC iterations using default priors, with convergence assessed using trace plots and posterior diagnostics. The resulting factor scores provided a single composite measure per species for use in phylogenetic linear models.

Predictors of plumage variation

To test how estimates of sexual, natural, and social selection shape sex-specific plumage traits, we compiled species-level data from the literature and published trait databases (Billerman *et al.* 2025; Tobias *et al.* 2016, 2022; Tobias & Pigot 2019). Our three focal predictors were coded as binary variables to reflect key ecological contrasts relevant to each hypothesis.

We estimated the intensity of sexual selection using a published ordinal scale ranging from strict monogamy (0) to extreme polygyny (4), inferred from behavioural traits and mating systems (Barber *et al.* 2024). We converted these scores to a binary variable by merging scores 0-2 and 3-4, coding the first category as monogamous (0) and the second as polygamous (1). We do this to simplify our analyses and because many suboscine passerines are relatively poorly known tropical species with limited information about mating behaviours such as extra-pair copulations (Brouwer & Griffith 2019; Griffith *et al.* 2002).

Natural selection was evaluated in the context of predation risk disparity between males and females during incubation. We generated a binary risk metric by

combining two factors: nest concealment (cavity vs. exposed) and incubation sex roles (female-only vs. biparental). Note that we expand the definition of cavity nests to include dome or globe nests, and any species in which the incubating bird is unlikely to be visible to predators approaching from any angle (see Supplementary Methods). Species with female-only incubation in exposed nests were coded as high predation disparity (1), while all other combinations—all biparental incubation and female-only incubation in cavity nests—were coded as low predation disparity (0). This coding scheme aligns with Wallace's (Wallace 1889) supposition that conspicuous females face stronger predation costs during nesting. Importantly, our low-disparity category includes cases where absolute predation may be high but is symmetrical between sexes (e.g., biparental incubation in exposed nests), which should select for crypsis in both sexes, leading to plumage monomorphism rather than dichromatism. Our definition incorporates both behavioural and structural exposure, which together determine whether females are more visually detectable to predators than males during the breeding period. Nest concealment and incubation roles were scored following standardised protocols (see Supplementary Methods), with nest types verified using species accounts, photographs, and video recordings where available.

Social selection was evaluated through territorial behaviour. Seasonal (breeding) territories can be perceived as elements of sexual selection whereas competition for territories during the non-breeding season or year-round is more closely associated with social competition for non-sexual resources (Tobias *et al.* 2012b). Since we expect female suboscine passerines to develop elaborate social signals primarily in species with year-round territories (Tobias *et al.* 2011), we dichotomised territoriality as 0 (non-territorial or seasonal) or 1 (year-round territorial). This approach distinguishes between highly territorial systems in which female–female signalling may evolve as a consequence of persistent social competition, versus those in which territoriality is absent or closely related to mating opportunities.

To account for broader ecological effects on signal evolution, we included three additional covariates. Habitat density was scored on a three-point ordinal scale (open, semi-open, dense), and then collapsed into a binary variable: dense (1) versus open or semi-open (0), reflecting the contrasting constraints of visual signal

transmission and conspicuousness in different light environments (Endler 1992; Shultz & Burns 2017). Body mass ($\log_{10}$ grams) was included as a proxy for size-based constraints or advantages in signal evolution (Carballo *et al.* 2020; Galván *et al.* 2013). Diet was coded as primary consumer (0; herbivores, frugivores, nectarivores, granivores) or secondary consumer (1; insectivores, omnivores, carnivores), on the basis that frugivory has been linked to higher sexual selection in tropical species (Beehler 1983; Snow 1971). Trait data for all three variables were sourced from AVONET (Tobias *et al.* 2022), with minor updates from Billerman *et al.* (Billerman *et al.* 2025) for specific suboscine species.

To assess data reliability, we followed the approach of Tobias *et al.* (Tobias *et al.* 2016) and Barber *et al*. (Barber *et al.* 2024) in scoring each behavioural trait on a four-point confidence scale. Species with low-confidence scores (1 or 2) for any focal predictor were excluded from a sensitivity analysis. After filtering, our final datasets comprised 1009 species for human-assessed dichromatism, and 727 species for avian-perceived elaboration and brightness.

Statistical analysis

We used phylogenetic linear models implemented in the R package *phylolm* (Tung Ho & Ané 2014) to test how each predictor influenced plumage variation. Separate models were fitted for each response variable: human-assessed dichromatism, avian-perceived dichromatism, male elaboration, female elaboration, male brightness, and female brightness. All response variables were standardised (mean = 0, SD = 1) prior to analysis. All models used Pagel's lambda as the best fit to estimate the phylogenetic signal in residual variation, based on Akaike Information Criterion (AIC) comparisons. To verify that multicollinearity would not bias parameter estimates, we confirmed that variance inflation factors (VIFs) were below 3 for all models (Zuur *et al.* 2010). To quantify parameter uncertainty while accounting for phylogenetic structure, we used the built-in bootstrap function in *phylolm*, generating 10,000 replicates per model. We then extracted bootstrapped confidence intervals for each parameter estimate to determine predictor significance. To quantify the variance explained by phylogeny versus ecological predictors, we calculated partial R^2 values using the R package *rr2* (Ives & Li 2018).

RESULTS

Dichromatism

Plumage dichromatism varied widely across suboscine species, with high values concentrated in cotingas, manakins, and some antbirds, and lower values in ovenbirds and tyrant flycatchers (Fig. 3). Human- and avian-assessed dichromatism were strongly correlated (r = 0.86, df = 875, 95% CI = 0.84–0.87), suggesting that both measures capture similar interspecific patterns (Fig. S2).

Phylogenetic linear models revealed that sexual selection was the strongest significant predictor of dichromatism (Fig. 4; Table S6), regardless of whether vision was assessed via human scores (β = 0.18, $p < 0.001$) or avian models (β = 0.39, $p < 0.001$). Trophic level was also a significant predictor for both vision models, although with a negative effect (human: β = -0.09, $p = 0.004$; avian: β = -0.20, $p = 0.025$) indicating that higher trophic levels (e.g. insectivores) are less dichromatic than lower trophic levels (e.g. frugivores). Other predictors—social selection, predation risk, body mass, and habitat density—had no significant effect on dichromatism in either vision model. The total variance explained by the full model was high (Total R^2: human = 0.98, avian = 0.87), but almost entirely attributable to phylogeny (Phylo R^2: human = 0.97, avian = 0.83). Predictors alone explained only 2-3% of the variation (Pred R^2: human = 0.03, avian = 0.02), highlighting the strong phylogenetic structuring of dichromatism in this clade.

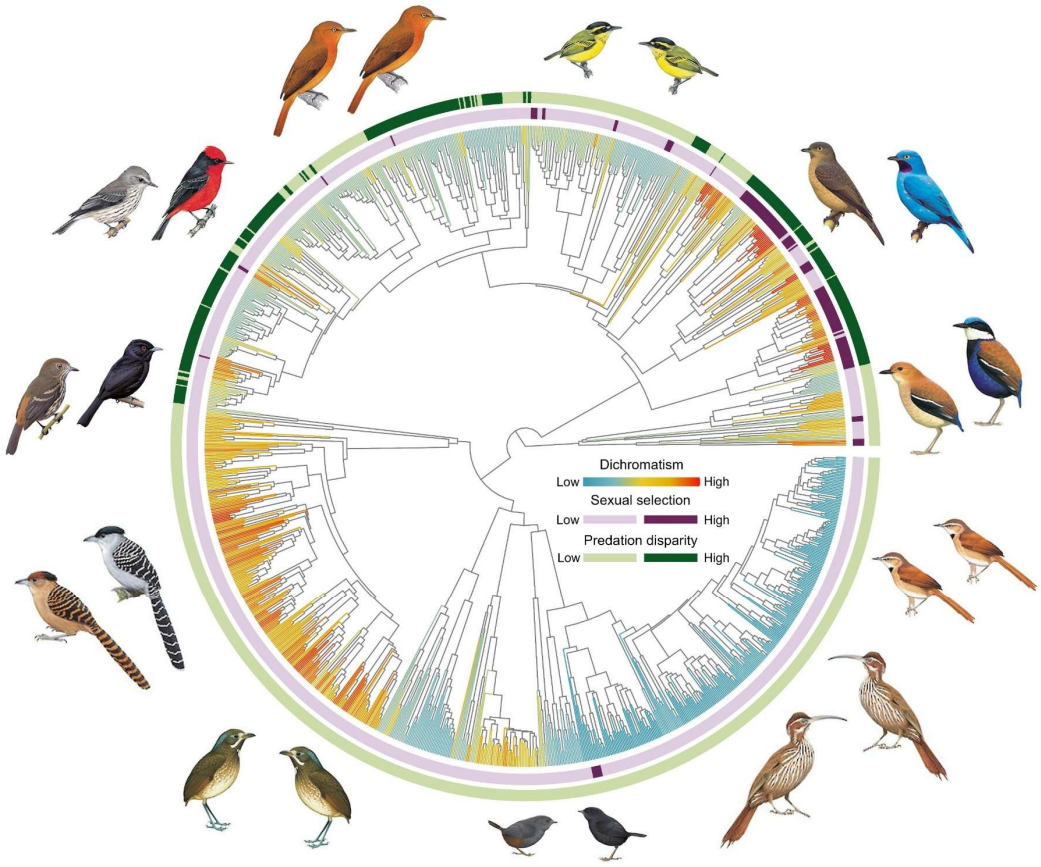

Figure 3. The distribution of plumage dichromatism and potential predictors in suboscine passerine birds. Phylogram shows a maximum-likelihood phylogenetic tree (Harvey *et al.* 2020) with branch colours representing the extent of dichromatism in suboscine species (n = 1283). Dichromatism was scored by visual assessment of standardised illustrations in the Handbook of the Birds of the World series (del Hoyo *et al.* 1992). Coloured rings encircling the phylogeny show two binary predictors: sexual selection and nest predation disparity (i.e. sex differences in predation risk). Sexual selection was inferred from mating systems, with polygamous species assumed to be under higher selection pressure. For predation risk, species with female-only incubation and exposed nests were scored as high predation disparity, whereas biparental exposed nesters and all cavity nesters were scored as low predation disparity, reflecting shared risk in exposed nests, and minimal risk of visual detection by predators in cavity-nesting species. Illustrations showcase examples of monochromatism and dichromatism across suboscines, reproduced with permission from Cornell Lab of Ornithology, Birds of the World (https://birdsoftheworld.org).

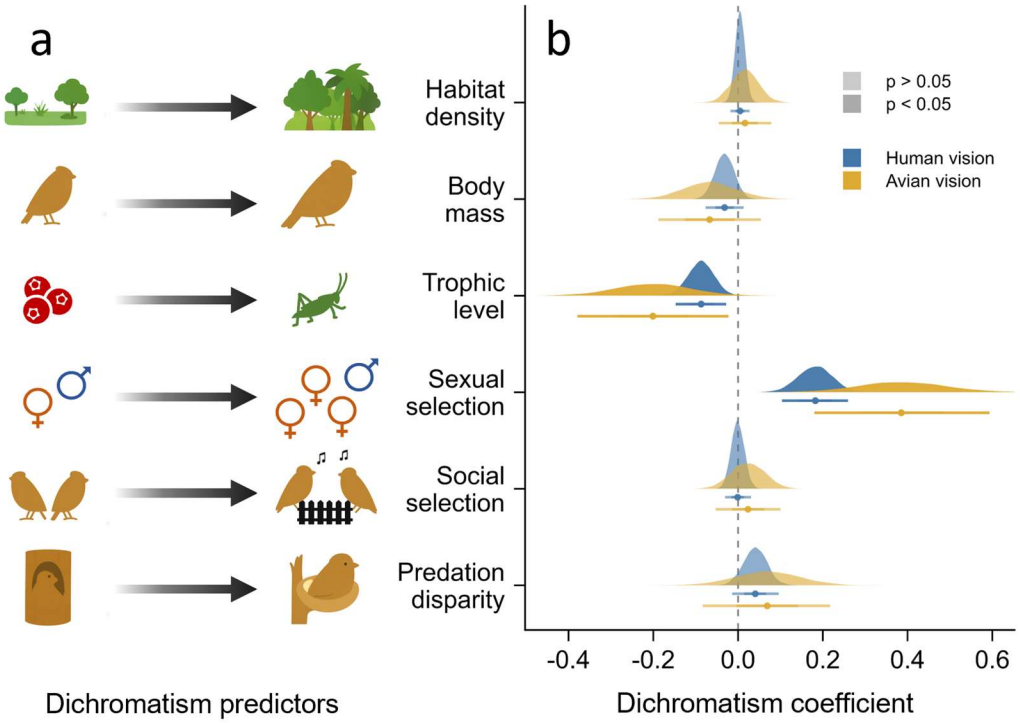

Figure 4. Predictors of sexual dichromatism in suboscine birds. a, Conceptual diagram illustrating theoretical predictors of plumage dichromatism. Six predictors are visualised as gradients: habitat density (low to high), body mass (small to large), trophic level (low/frugivore to high/invertivore), sexual selection (low to high), social selection (low/non-territorial to high/territorial), and predation disparity (low to high). b, Results of phylogenetic linear models predicting the extent of dichromatism according to human vision (n = 1283 species) and avian vision (n = 877 species). Phylogenetic information was incorporated using a maximum likelihood tree (Harvey *et al.* 2020), and each model was run with 10,000 bootstrap iterations to account for any uncertainty in branch placement. Distributions were generated from a random sample of 1,000 iterations. Points denote mean effect size estimates; bars denote 95% confidence intervals. Full statistical results in Table S6.

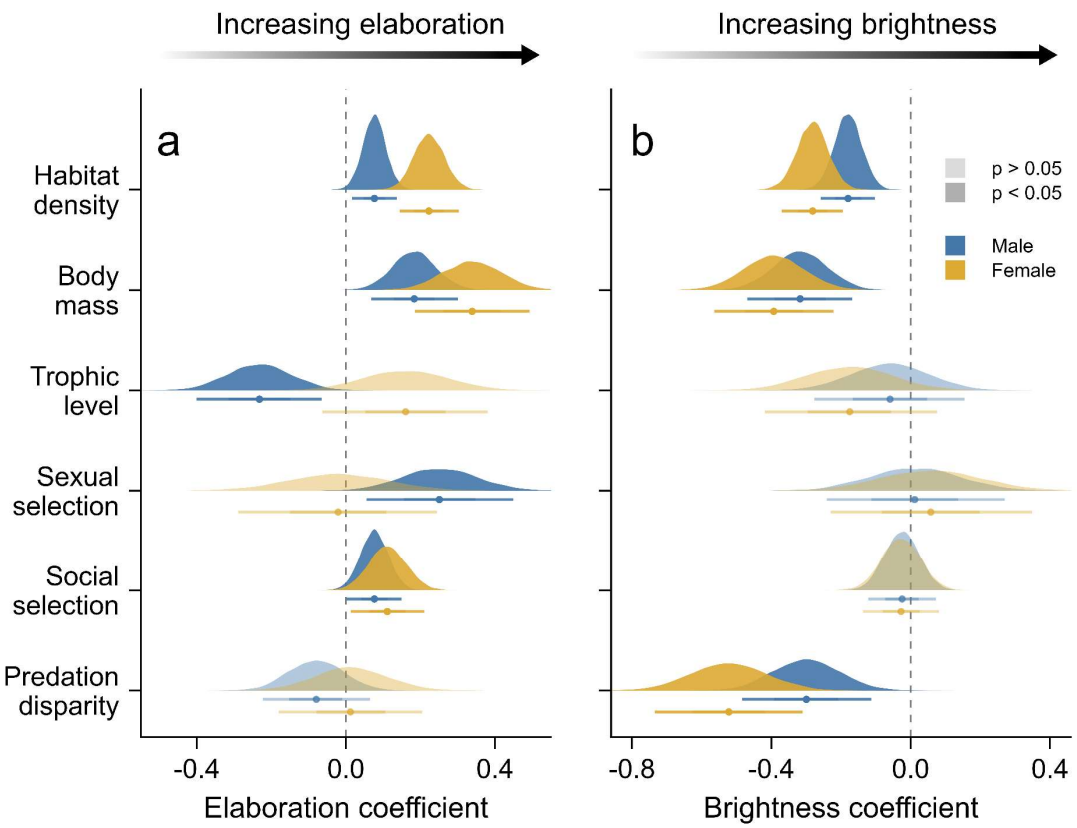

Figure 5. Predictors of plumage elaboration in male and female suboscine birds. Results shown are from phylogenetic linear models predicting plumage (**a**) elaboration and (**b**) brightness for males and females of 877 suboscine species. Phylogenetic information was incorporated using a maximum likelihood tree (Harvey *et al.* 2020), and each model was run with 10,000 bootstrap iterations to account for any uncertainty in branch placement. Distributions were generated from a random sample of 1,000 iterations. Points denote mean effect size estimates; bars denote 95% confidence intervals. Full statistical results are available in Table S6.

Elaboration and brightness

Elaborate plumage colours were most often saturated or high-contrast colours—especially red, blue, and yellow—or extremely dark or light patches. In contrast, the lowest elaboration scores were associated with dull greens and browns, which clustered around the clade-average colour (Fig. 4; Fig. S1).

Phylogenetic linear models revealed distinct selection pressures shaping elaboration in each sex (Fig. 5a; Table S6). In males, elaboration was most strongly predicted by sexual selection (β = 0.25, p = 0.013), apparently linked to trophic level (β = -0.23, p = 0.007). Weaker drivers of male elaboration included body mass (β = 0.18, p = 0.002), and to a lesser extent habitat density (β = 0.08, p = 0.012) and social selection (β = 0.08, p = 0.043). In contrast, female elaboration was unrelated to sexual selection (β = -0.02, p = 0.882) or trophic level (β = 0.16, p = 0.163), but positively related with a range of other factors including body mass (β = 0.34, p < 0.001), habitat density (β = 0.22, p < 0.001), and social selection (β = 0.11, p = 0.027). Predation risk had no significant effect on elaboration in either sex. Predictors explained more variation in female elaboration (Pred R^2 = 0.06) than male elaboration (Pred R^2 = 0.04), though most variation remained phylogenetically structured (Phylo R^2 = 0.67 female, 0.81 male).

Phylogenetic linear models indicated that brightness was significantly influenced by ecological selection rather than social or sexual selection (Fig. 5b; Table S6). Brightness decreased significantly with increasing predation risk in both females (β = -0.52, p < 0.001) and males (β = -0.30, p = 0.002). It was similarly negatively related to body mass (female: β = -0.39, p < 0.001; male: β = -0.32, p < 0.001) and habitat density (female: β = -0.28, p < 0.001; male: β = -0.18, p < 0.001). These relationships were consistently stronger for females. Neither sexual selection (female: β = 0.06, p = 0.694; male: β = 0.01, p = 0.937), trophic level (female: β = -0.17, p = 0.17; male: β = -0.06, p = 0.6), nor social selection (female: β = -0.03, p = 0.636; male: β = -0.02, p = 0.62) significantly predicted brightness in either sex. Predictors explained slightly more variation in brightness for females (Pred R^2 = 0.08) than for males (Pred R^2 = 0.05), though phylogeny again explained the majority of variance in both sexes (Phylo R^2 = 0.67 female, 0.75 male).

Sensitivity analyses

Restricting analyses to high-confidence data (n = 727 species) yielded broadly consistent results. Sexual selection remained the strongest predictor of dichromatism across both human-assessed and avian-perceived measures (Table S7). The effect of trophic level was weaker, although effects were still close to the full model (human: β = -0.08, p = 0.013; avian: β = -0.18, p = 0.06). For elaboration, the effects of habitat density, body mass, trophic level, and social selection were consistent, although social selection became marginally weaker and slightly overlapped zero in both females (β = 0.10, p = 0.054) and males (β = 0.06, p = 0.12). Brightness results remained unchanged, with predation risk, habitat density, and body mass retaining strong negative effects. Overall, these additional analyses support our main conclusions, suggesting that consistent selective pressures shape male and female plumage in suboscine birds.

DISCUSSION

Our analyses confirm that sexual selection is the dominant evolutionary force shaping sex differences in plumage across the suboscine passerine radiation. We found that species with polygamous mating systems consistently evolve greater sexual dichromatism, as measured by both human-assessed and avian-perceived metrics (Fig. 4). These findings support Darwin's longstanding prediction, and align with previous studies highlighting the important role of sexual selection as a predictor of male ornamentation and a driver of dichromatism across a wide range of taxa (Bijl *et al.* 2020; Dale *et al.* 2015; Pérez i de Lanuza *et al.* 2013). However, decomposing plumage into sex-specific traits reveals a more complex picture: natural and social selection exert stronger and more consistent effects on female ornamentation (Fig. 5). In fact, with the exception of sexual selection and trophic level, effect sizes were greater in females than in males, suggesting that female plumage evolution is directly shaped by natural selection and social competition, both of which therefore influence levels of plumage dichromatism primarily via effects on females.

The weaker effect of predation risk and territorial competition as predictors of male elaboration is roughly in line with standard expectations. By decomposing male and female traits, we show that variation in sexual dichromatism is partly driven by

an underlying positive relationship between sexual selection and male elaboration, supporting previous analyses focused on bird plumage (Cooney *et al.* 2022; Shultz & Burns 2017). However, this effect was modest compared to most effects on female elaboration (Fig. 5), suggesting that sexual selection on males alone cannot explain patterns of plumage evolution. Although some studies have concluded that sexual selection reduces female plumage ornamentation in birds, potentially due to reduced mutual mate choice in polygynous systems (Dale *et al.* 2015; Delhey *et al.* 2023), we found no evidence for this effect. Instead, female elaboration was similar in polygamous and monogamous species, suggesting that sexual selection acts predominantly on males in suboscine birds, consistent with Darwin's original hypothesis (Darwin 1871). While this male-biased effect helps to explain why mating system is a strong predictor of dichromatism in birds, we find evidence that ornamentation in females is much more sensitive to selection for crypsis or aggressive signalling in species with female territoriality.

Diet, particularly frugivory, has long been proposed to promote polygamy and thereby intensify sexual selection on male plumage traits (Beehler 1983; Snow 1971). In tropical forests, a hyperabundant, patchily distributed fruit supply can remove the need for territory defence, increasing mating opportunities for males and freeing them from parental duties (Barber *et al.* 2024; Barve & La Sorte 2016). Consistent with these ideas, we found that diet and mating system were positively correlated across suboscines (Fig. S3) and that diet predicted greater dichromatism under both vision models (Fig. 4). This effect may be slightly accentuated by factors acting in females because frugivorous species tend not to defend pair or group territories and often have female-only parental care, resulting in stronger predation disparity (i.e. selection for crypsis limited to females) or limited social signalling in females (Tobias *et al.* 2012b). However, as with mating system, diet showed no significant effect on female elaboration and was instead associated with greater male elaboration (Fig. 5).

A key result of our models is that the effect of diet on dichromatism and plumage elaboration remained significant even after accounting for the intensity of sexual selection and alternative drivers, providing comparative evidence that frugivory shapes male elaboration independent of mating system, predation and social competition. One plausible reason for this independent effect is that a high concentration of carotenoid pigments ingested by frugivores may facilitate the

production of bright yellows and reds, thus providing a direct trophic mechanism linking fruit consumption with colourful plumage (Delhey *et al.* 2023; Rincón-Rubio *et al.* 2025). In addition, the energetic surplus associated with a fruit-rich diet may also improve feather quality during moult, enhancing structural colours such as blues and ultraviolets (McGraw *et al.* 2002). Thus, frugivorous males freed from parental duties may be particularly well placed to channel dietary resources directly into plumage production, amplifying male elaboration and driving greater overall dichromatism.

Disentangling male and female plumage trends also highlights the role of social selection. This is often overlooked in studies focusing simply on dichromatism because strong social selection is predicted to drive evolution of elaborate plumage in both sexes, thus reducing dichromatism (Tobias *et al.* 2012b). Using year-round territoriality as a marker of elevated social competition for space and ecological resources, we found evidence that social selection is a key driver of ornamentation in both sexes of socially monogamous and group-living species. Year-round territorial behaviour was significantly associated with increased elaboration in both males and females, with a slightly stronger effect in females. This result supports a growing body of evidence that female ornamentation evolves in response to social competition (Tobias *et al.* 2012b; West-Eberhard 1983), rather than as a byproduct of selection on males. While previous studies have documented these dynamics within species (Enbody *et al.* 2018; Macedo *et al.* 2021; Murphy *et al.* 2009; Odreitz & Sefc 2015; Tobias *et al.* 2011), our findings provide comparative evidence that social selection contributes to patterns of female ornamentation at a macroevolutionary scale. Male elaboration also increased in year-round territorial species, suggesting that male ornamentation can also arise through multiple pathways beyond sexual selection alone. Together, these results emphasise that social competition, not just mating strategy, shapes plumage elaboration across both sexes.

In contrast to their effect on plumage elaboration, sexual and social selection had no effect on plumage brightness in either sex. This result aligns with the idea that both extremely dark and extremely light plumage can function as conspicuous signals, depending on context (Caro 2005). For example, lekking cotinga species in our dataset include both the bright-white *Procnias albus* and the jet-black *Cephalopterus ornatus*, each highly ornamented despite their opposite positions along

the achromatic spectrum. In some cases, dark and light plumage may even be used in tandem to exaggerate contrast (McCoy & Prum 2019), complicating attempts to interpret brightness as a proxy for ornamentation. These factors may help to explain why comparative studies using brightness to infer sexual selection have often produced inconsistent results (Dunn *et al.* 2015; Irwin 1994; Shultz & Burns 2017).

Natural selection emerged as one of the strongest forces shaping plumage variation, especially in females. The clearest signal was a negative association between predation risk disparity and plumage brightness, which was significant in both sexes but nearly twice as strong in females. The strength of this association is perhaps related to our use of a novel predation risk score, taking into account whether incubation is biparental or female-only. This finding suggests that exposure to predation during the incubation period imposes constraints on female conspicuousness, supporting Wallace's hypothesis that selection for crypsis drives female plumage evolution. However, Wallace predicted that a tendency for greater crypsis in females would accentuate plumage dichromatism, whereas we found no corresponding evidence to this effect. Indeed, our study adds to a growing list of analyses finding weak or inconsistent links between incubation roles and overall dichromatism (Drury & Burroughs 2016; Matysioková *et al.* 2017; Soler & Moreno 2012). One reason may be that males in biparental species suffer predation risk during nest defence or provisioning, roles often overlooked when focusing solely on incubation (Ketterson & Nolan 1994; Owens & Bennett 1994). Nonetheless, our method establishes a clear connection between predation risk and reduced plumage brightness in females, and further research is needed to assess the role of incubation and predation disparity across much larger samples of species.

Habitat density was another ecological factor with pervasive impacts on plumage of both sexes, yet stronger effects in females. We found that species in dense habitats tend to be darker and less bright, in line with the Light Environment Hypothesis predicting that signal design is shaped by trade-offs between visibility and predation across different light environments (Endler 1992; Marchetti 1993). This finding supports earlier evidence that living in forested environments leads to reduced plumage brightness in birds (Shultz & Burns 2013; Simpson *et al.* 2020), including suboscines (Marcondes & Brumfield 2019). Concurrently, we found that habitat density was positively related to plumage elaboration, particularly in females,

perhaps because denser vegetation provides more cover from predators, reducing predation risk. However, dense tropical forests also tend to be more humid, resource-rich and species-rich, factors which may alter the costs and benefits of plumage signalling (Badyaev & Hill 2003; Delhey *et al.* 2023). Incorporating further ecological parameters into future studies will be essential to disentangle the various selective pressures shaping colour signals in tropical ecosystems (Marcondes *et al.* 2021; Wu *et al.* 2024).

Body mass emerged as one of the strongest ecological predictors of plumage elaboration, especially in females, yet remains one of the least understood. Across multiple avian clades, larger species tend to be more ornamented (Carballo *et al.* 2020; Dale *et al.* 2015; Delhey *et al.* 2023), a pattern replicated in suboscines. This relationship is often attributed to reduced predation risk in larger birds, although this concept has proved difficult to demonstrate in practice (Preisser & Orrock 2012). Alternative explanations include relaxed metabolic constraints or increased mutual mate choice in larger species, both of which could also favour the evolution of elaborate plumage (Badyaev & Hill 2003). Body mass also had a weak negative effect on dichromatism, consistent with ornamentation increasing in both sexes. However, without finer-scale data on life history and physiology, these hypotheses remain difficult to disentangle.

Caveats and limitations

All large-scale comparative analyses face the problem of patchy ecological data across large samples of species. Although birds are relatively well known, making them a suitable template for macroecological studies (Tobias 2022), the quality of information is weaker for tropical species, including many suboscine passerines. Descriptions of mating systems, nest design and incubation roles are often based on sparse evidence or inferred from related species. Scoring of nest visibility was problematical in some instances because literature descriptions of cup nests often overlook highly concealed nests shielded by overhanging material (usually rock, moss, living or dead leaves, depending on the environment). We cross-checked our assignments with nest photographs and videos available in online archives, which provide an increasingly valuable insight into nest structure and visibility (see Supplementary Methods). Nonetheless, the availability of nest images and videos is

patchy, increasing uncertainty of classification in data-poor cases.

To assess the role of uncertainty in shaping our results, we ran sensitivity analyses on a subset of high-certainty data. The results were largely unchanged (Table S7), but the effect of year-round territoriality became non-significant for male and female elaboration. In both cases, effect sizes remained positive but confidence intervals marginally overlapped zero. Given the large reduction in sample size, this outcome may reflect reduced statistical power, compounded by phylogenetic conservatism. Mating systems, territoriality, and plumage traits are all strongly conserved in suboscines (Fig. 3), limiting the number of independent evolutionary transitions and reducing the power of comparative models to detect evolutionary trends (Uyeda *et al.* 2018).

Another factor reducing statistical effects may be phenotypic heterogeneity across suboscines, perhaps explaining the low variance explained by most predictors (0.02–0.08). For example, some of the most extreme dichromatism values occurred in antbirds, species that are socially monogamous and year-round territorial. This combination should favour mutual ornamentation and reduced dichromatism, yet many antbirds counter this trend, with female ornamentation highly divergent from male ornamentation. Sex-specific ornamentation in antbirds may reflect high levels of female-female competition driving female-specific social selection (Macedo *et al.* 2021; Tobias *et al.* 2011). If so, social selection may exaggerate dichromatism in some suboscine lineages via divergent ornamentation. Further work is needed to evaluate the role of social competition, incorporating more detailed behavioural data across a broader phylogenetic scope, ideally combining tropical and temperate taxa with multiple independent shifts in social behaviour.

CONCLUSIONS

Our analyses reconcile two longstanding evolutionary hypotheses (Darwin 1871; Wallace 1889). We find support for Darwin's proposal that sexual selection is the primary driver of avian plumage dichromatism. Yet we also find evidence that natural selection is a strong counterforce, particularly in females, supporting Wallace's hypothesis. Specifically, our analyses confirm a strong negative relationship between predation risk and plumage brightness in females, suggesting that females are under

selection for crypsis in species with exposed nests and female-only parental care.

Previous studies (Bijl *et al.* 2020; Dale *et al.* 2015) have generally shown strong support for Darwin's (Darwin 1871) hypothesis and rejected Wallace's hypothesis (Wallace 1889), with a few analyses producing weak support linking predation to dichromatism (Drury & Burroughs 2016; Matysioková *et al.* 2017; Soler & Moreno 2012). However, these ideas have been tested exclusively with composite scores of dichromatism based on colour differences. Our findings reveal that different patterns emerge if sex differences in plumage are decomposed into separate dimensions of elaboration and brightness for each sex, allowing sex-specific variation in different signal features to be analysed independently. By adopting this more nuanced approach, our analyses expose the tendency of composite dichromatism metrics to conflate distinct evolutionary processes, thus highlighting the importance of examining male and female traits independently to reveal asymmetric selection pressures shaping the evolution of sex-specific ornamentation (Doutrelant *et al.* 2020; Odom & Benedict 2018; Tobias *et al.* 2012b).

Our results also indicate a role for social selection in driving signal evolution. We show that year-round territory defence (associated with territoriality in both males and females) predicts increased plumage elaboration in both sexes, with effects stronger in females. This result is consistent with recent evidence that female ornamentation evolves through direct selection for social signalling (Enbody *et al.* 2018; Macedo *et al.* 2021; Murphy *et al.* 2009; Odom *et al.* 2025; Odreitz & Sefc 2015; Tobias *et al.* 2011), rather than merely as a by-product of male traits. Overall, we found that the effects of body mass, predation risk, habitat density and territoriality were greater in females than males, highlighting the adaptive nature of female signals (Irwin 1994; Odom *et al.* 2014; Tobias *et al.* 2012b). The message from suboscine birds is that broad-scale patterns of sexual dichromatism reflect a complex interplay between natural, sexual and social selection, with a wider set of mechanisms operating in females.

REFERENCES

Amundsen, T. (2000). Why are female birds ornamented? *Trends Ecol. Evol.*, 15, 149–155.

Badyaev, A.V. & Hill, G.E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annu. Rev. Ecol. Evol. Syst.*, 34, 27–49.

Barber, R.A., Yang, J., Yang, C., Barker, O., Janicke, T. & Tobias, J.A. (2024). Climate and ecology predict latitudinal trends in sexual selection inferred from avian mating systems. *PLoS Biol.*, 22, e3002856.

Barreira, A.S., Eaton, M.D., Vilacoba, E., Tubaro, P.L. & Kopuchian, C. (2021). Short-wavelength visual sensitivity and sexual differences in plumage colouration of ovenbirds (Aves: Furnariinae). *J. Ornithol.*, 162, 737–748.

Barve, S. & La Sorte, F.A. (2016). Fruiting season length restricts global distribution of female-only parental care in frugivorous passerine birds. *PLoS ONE*, 11, e0154871.

Beehler, B. (1983). Frugivory and polygamy in birds of paradise. *Auk*, 100, 1–12.

Bijl, W. van der, Zeuss, D., Chazot, N., Tunström, K., Wahlberg, N., Wiklund, C., *et al.* (2020). Butterfly dichromatism primarily evolved via Darwin's, not Wallace's, model. *Evol. Lett.*, 4, 545–555.

Billerman, S.M., Keeney, B.K., Kirwan, G.M., Medrano, F., Sly, N.D. & Smith, M.G. (2025). *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Bleiweiss, R. (1997). Covariation of sexual dichromatism and plumage colours in lekking and non-lekking birds: A comparative analysis. *Evol. Ecol.*, 11, 217–235.

Brouwer, L. & Griffith, S.C. (2019). Extra-pair paternity in birds. *Mol. Ecol.*, 28, 4864–4882.

Carballo, L., Delhey, K., Valcu, M. & Kempenaers, B. (2020). Body size and climate as predictors of plumage colouration and sexual dichromatism in parrots. *J. Evol. Biol.*, 33, 1543–1557.

Caro, T. (2005). The adaptive significance of coloration in mammals. *BioScience*, 55, 125–136.

Clutton-Brock, T. (2009). Sexual selection in females. *Anim. Behav.*, 77, 3–11.

Cooney, C.R., He, Y., Varley, Z.K., Nouri, L.O., Moody, C.J.A., Jardine, M.D., *et al.* (2022). Latitudinal gradients in avian colourfulness. *Nat. Ecol. Evol.*, 6, 1–8.

Cooney, C.R., Varley, Z.K., Nouri, L.O., Moody, C.J.A., Jardine, M.D. & Thomas, G.H. (2019). Sexual selection predicts the rate and direction of colour divergence in a large avian radiation. *Nat. Commun.*, 10, 1773.

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

Darwin, C.R. (1871). *The Descent of Man, and Selection in Relation to Sex*. John Murray, London.

Delhey, K., Valcu, M., Muck, C., Dale, J. & Kempenaers, B. (2023). Evolutionary predictors of the specific colors of birds. *Proc. Natl. Acad. Sci.*, 120, e2217692120.

Doutrelant, C., Fargevieille, A. & Grégoire, A. (2020). Chapter Four - Evolution of female coloration: What have we learned from birds in general and blue tits in particular. In: *Advances in the Study of Behavior* (eds. Naguib, M., Barrett, L., Healy, S.D., Podos, J., Simmons, L.W. & Zuk, M.). Academic Press, pp. 123–202.

Drury, J.P. & Burroughs, N. (2016). Nest shape explains variation in sexual dichromatism in New World blackbirds. *J. Avian Biol.*, 47, 312–320.
Dunn, P.O., Armenta, J.K. & Whittingham, L.A. (2015). Natural and sexual selection act on different axes of variation in avian plumage color. *Sci. Adv.*, 1, e1400155.
Dunn, P.O., Whittingham, L.A. & Pitcher, T.E. (2001). Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution*, 55, 161–175.
Enbody, E.D., Boersma, J., Schwabl, H. & Karubian, J. (2018). Female ornamentation is associated with elevated aggression and testosterone in a tropical songbird. *Behav. Ecol.*, 29, 1056–1066.
Endler, J.A. (1992). Signals, signal conditions, and the direction of evolution. *Am. Nat.*, 139, S125–S153.
Galván, I., Negro, J.J., Rodríguez, A. & Carrascal, L.M. (2013). On showy dwarfs and sober giants: body size as a constraint for the evolution of bird plumage colouration. *Acta Ornithol.*, 48, 65–80.
García, N.C., Barreira, A.S. & Tubaro, P.L. (2022). Sexual dichromatism may not be a good index of sexual or natural selection in the blue cardinalids (Aves: Passeriformes). *Ornithology*, 139, ukac008.
Griffith, S.C., Owens, I.P.F. & Thuman, K.A. (2002). Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Mol. Ecol.*, 11, 2195–2212.
Harvey, M.G., Bravo, G.A., Claramunt, S., Cuervo, A.M., Derryberry, G.E., Battilana, J., *et al.* (2020). The evolution of a tropical biodiversity hotspot. *Science*, 370, 1343–1348.
Hassler, G.W., Gallone, B., Aristide, L., Allen, W.L., Tolkoff, M.R., Holbrook, A.J., *et al.* (2022). Principled, practical, flexible, fast: A new approach to phylogenetic factor analysis. *Methods Ecol. Evol.*, 13, 2181–2197.
del Hoyo, J., Elliott, A. & Christie, D. (1992). *Handbook of the birds of the world*. Lynx Edicions, Barcelona.
Irwin, R.E. (1994). The evolution of plumage dichromatism in the New World blackbirds: social selection on female brightness. *Am. Nat.*, 144, 890–907.
Ives, A.R. & Li, D. (2018). rr2: An R package to calculate R2s for regression models. *J. Open Source Softw.*, 3, 1028.
Ketterson, E.D. & Nolan, V. (1994). Male parental behavior in birds. *Annu. Rev. Ecol. Syst.*, 25, 601–628.
Kraaijeveld, K., Kraaijeveld-Smit, F.J.L. & Komdeur, J. (2007). The evolution of mutual ornamentation. *Anim. Behav.*, 74, 657–677.
LeBas, N.R. (2006). Female finery is not for males. *Trends Ecol. Evol.*, 21, 170–173.
Macedo, G., Bravo, G.A., Marcondes, R.S., Derryberry, E.P. & Biondo, C. (2021). Differences in plumage coloration predict female but not male territorial responses in three antbird sister species pairs. *Anim. Behav.*, 182, 107–124.
Marchetti, K. (1993). Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature*, 362, 149–152.
Marcondes, R.S. & Brumfield, R.T. (2019). Fifty shades of brown: Macroevolution of plumage brightness in the Furnariida, a large clade of drab Neotropical passerines. *Evolution*, 73, 704–719.
Marcondes, R.S., Nations, J.A., Seeholzer, G.F. & Brumfield, R.T. (2021). Rethinking Gloger's rule: climate, light environments, and color in a large family of tropical birds (Furnariidae). *Am. Nat.*, 197, 592–606.

Matysioková, B., Remeš, V. & Cockburn, A. (2017). Broad-scale variation in sexual dichromatism in songbirds is not explained by sex differences in exposure to predators during incubation. *J. Avian Biol.*, 48, 1322–1330.
McCoy, D.E. & Prum, R.O. (2019). Convergent evolution of super black plumage near bright color in 15 bird families. *J. Exp. Biol.*, 222, jeb208140.
McGraw, K.J., Mackillop, E.A., Dale, J. & Hauber, M.E. (2002). Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J. Exp. Biol.*, 205, 3747–3755.
McGraw, K.J., Stoehr, A.M., Nolan, P.M. & Hill, G.E. (2001). Plumage redness predicts breeding onset and reproductive success in the House Finch: a validation of Darwin's theory. *J. Avian Biol.*, 32, 90–94.
Murphy, T.G., Hernández-Muciño, D., Osorio-Beristain, M., Montgomerie, R. & Omland, K.E. (2009). Carotenoid-based status signaling by females in the tropical streak-backed oriole. *Behav. Ecol.*, 20, 1000–1006.
Ödeen, A. & Håstad, O. (2013). The phylogenetic distribution of ultraviolet sensitivity in birds. *BMC Evol. Biol.*, 13, 36.
Odom, K.J., Araya-Salas, M., Benedict, L., Lim, K., Dale, J., Webb, W.H., *et al.* (2025). Global incidence of female birdsong is predicted by territoriality and biparental care in songbirds. *Nat. Commun.*, 16, 6157.
Odom, K.J. & Benedict, L. (2018). A call to document female bird songs: Applications for diverse fields. *Auk*, 135, 314–325.
Odom, K.J., Hall, M.L., Riebel, K., Omland, K.E. & Langmore, N.E. (2014). Female song is widespread and ancestral in songbirds. *Nat. Commun.*, 5, 3379.
Odreitz, U. & Sefc, K.M. (2015). Territorial competition and the evolutionary loss of sexual size dimorphism. *Behav. Ecol. Sociobiol.*, 69, 593–601.
Owens, I.P.F. & Bennett, P.M. (1994). Mortality costs of parental care and sexual dimorphism in birds. *Proc. R. Soc. Lond. B*, 257, 1–8.
Owens, I.P.F. & Hartley, I.R. (1998). Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proc. R. Soc. Lond. B*, 265, 397–407.
Pérez i de Lanuza, G., Font, E. & Monterde, J.L. (2013). Using visual modelling to study the evolution of lizard coloration: sexual selection drives the evolution of sexual dichromatism in lacertids. *J. Evol. Biol.*, 26, 1826–1835.
Porzio, N.S. & Mota, P.G. (2025). Evidence for the independent evolution of sex-related signals in manakins. *J. Evol. Biol.*, 38, 716–727.
Preisser, E.L. & Orrock, J.L. (2012). The allometry of fear: interspecific relationships between body size and response to predation risk. *Ecosphere*, 3, art77.
Ribeiro, R.D., McCormack, J.E., Álvarez, H.G., Carrasco, L., Grether, G.F., Mena-Olmedo, P., *et al.* (2015). Loss of sexual dimorphism is associated with loss of lekking behavior in the green manakin Xenopipo holochora. *J. Avian Biol.*, 46, 307–314.
Rincón-Rubio, V.A., Zenil-Ferguson, R. & Gonzalez-Voyer, A. (2025). The macroevolutionary consequences of the association between frugivory and carotenoid-dependent plumage coloration in passerine birds. *Evolution*, 79, 1643–1657.
Rosvall, K.A. (2011). Intrasexual competition in females: evidence for sexual selection? *Behav. Ecol.*, 22, 1131–1140.
Seddon, N., Tobias, J.A., Eaton, M. & Ödeen, A. (2010). Human vision can provide a valid proxy for avian perception of sexual dichromatism. *Auk*, 127, 283–292.
Shultz, A.J. & Burns, K.J. (2013). Plumage evolution in relation to light environment in a novel clade of Neotropical tanagers. *Mol. Phylogenet. Evol.*, 66, 112–125.

Shultz, A.J. & Burns, K.J. (2017). The role of sexual and natural selection in shaping patterns of sexual dichromatism in the largest family of songbirds (Aves: Thraupidae). *Evolution*, 71, 1061–1074.
Simpson, R.K., Mistakidis, A.F. & Doucet, S.M. (2020). Natural and sexual selection shape the evolution of colour and conspicuousness in North American wood-warblers (Parulidae). *Biol. J. Linn. Soc.*, 130, 89–100.
Snow, D.W. (1971). Evolutionary aspects of fruit-eating by birds. *Ibis*, 113, 194–202.
Soler, J.J. & Moreno, J. (2012). Evolution of sexual dichromatism in relation to nesting habits in European passerines: a test of Wallace's hypothesis. *J. Evol. Biol.*, 25, 1614–1622.
Surmacki, A., Stępniewski, J. & Stępniewska, M. (2015). Juvenile sexual dimorphism, dichromatism and condition-dependent signaling in a bird species with early pair bonds. *J. Ornithol.*, 156, 65–73.
Tobias, J.A. (2022). A bird in the hand: Global-scale morphological trait datasets open new frontiers of ecology, evolution and ecosystem science. *Ecol. Lett.*, 25, 573–580.
Tobias, J.A., Brawn, J.D., Brumfield, R.T., Derryberry, E.P., Kirschel, A.N.G. & Seddon, N. (2012a). The importance of suboscine birds as study systems in ecology and evolution. *Ornitol. Neotrop.*, 23, 261–274.
Tobias, J.A., Gamarra-Toledo, V., García-Olaechea, D., Pulgarín, P.C. & Seddon, N. (2011). Year-round resource defence and the evolution of male and female song in suboscine birds: social armaments are mutual ornaments. *J. Evol. Biol.*, 24, 2118–2138.
Tobias, J.A., Montgomerie, R. & Lyon, B.E. (2012b). The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Philos. Trans. R. Soc. B*, 367, 2274–2293.
Tobias, J.A. & Pigot, A.L. (2019). Integrating behaviour and ecology into global biodiversity conservation strategies. *Philos. Trans. R. Soc. B*, 374, 20190012.
Tobias, J.A., Sheard, C., Pigot, A.L., Devenish, A.J.M., Yang, J., Sayol, F., *et al.* (2022). AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.*, 25, 581–597.
Tobias, J.A., Sheard, C., Seddon, N., Meade, A., Cotton, A.J. & Nakagawa, S. (2016). Territoriality, social bonds, and the evolution of communal signaling in birds. *Front. Ecol. Evol.*, 4, 74.
Trail, P.W. (1990). Why should lek-breeders be monomorphic? *Evolution*, 44, 1837–1852.
Tung Ho, L. si & Ané, C. (2014). A linear-time algorithm for gaussian and non-gaussian trait evolution models. *Syst. Biol.*, 63, 397–408.
Uyeda, J.C., Zenil-Ferguson, R. & Pennell, M.W. (2018). Rethinking phylogenetic comparative methods. *Syst. Biol.*, 67, 1091–1109.
Wallace, A.R. (1889). *Darwinism: An Exposition of the Theory of Natural Selection With Some of Its Applications.* Macmillan & Co., London.
West-Eberhard, M.J. (1983). Sexual selection, social competition, and speciation. *Q. Rev. Biol.*, 58, 155–183.
Wu, S., Zhang, K., Wang, B., Que, P., Yang, B. & Xu, Y. (2024). Disentangling ecological drivers of interspecific achromatic plumage variation in birds. *Global Ecol. Biogeogr.*, 33, e13892.
Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.*, 1, 3–14.

SUPPLEMENTARY MATERIALS

CONTENTS

Supplementary Methods

Human-assessed dichromatism

We compiled plumage scores for all 1283 suboscine passerine species included in the phylogeny of Harvey *et al.* (2020), using illustrations and species accounts from the Handbook of the Birds of the World series (del Hoyo *et al.* 1992 - 2013). Scanned digital versions of the same illustrations are available for viewing in Birds of the World (Billerman *et al.* 2025). Following Irwin (1994) and Owens & Bennett (1994), we quantified dichromatism across five body regions (head, back, underparts, wings, and tail) on an ordinal scale: 0 (monomorphic), 1 (difference in shade or intensity), and 2 (difference in colour or pattern).

For species with a single illustration (typically depicting a generic adult), we cross-referenced the visual data with textual descriptions. A score of 0 was assigned only if the species account explicitly stated "sexes similar" or "sexes alike." When text described sexual differences not visible in the illustration (e.g., females slightly duller, lacking a concealed crown patch, or having a less distinct throat pattern), we assigned a score of 1 to the relevant body regions. Similarly, where only a female head was illustrated alongside a full male, we consulted the text to confirm no additional differences existed in other body regions. For polytypic species, we scored the most widespread subspecies (typically the nominate race) to ensure trait values reflected the predominant phenotype of the species lineage.

Reflectance data

Bird plumage varies in colour wavelengths invisible to human vision (Cuthill 2006), so we relied on measurements of plumage elaboration generated using a database of spectrophotometry. Our colour database contained reflectance spectra in the 300-700nm range for 6977 museum specimens. All measurements were generated using methods and equipment described in detail by Marcondes & Brumfield (2019). Because feathers show significant degeneration in colour intensity approximately 50 years after collection (Armenta *et al.* 2008), we selected specimens collected after to 1965 wherever possible. Reflectance spectra were measured in seven plumage patches: belly, breast, throat, crown, back, rump, and dorsal surface of the tail. We took 3–5 replicate readings per patch, with slight adjustment to the probe to account

for intra-patch variation.

Reflectance data was cleaned and processed using R version 4.2.1 (R Core Team 2022) and the R package *pavo* (Maia *et al.* 2019). We first used the function *procspec* to remove electrical noise produced during measurement by smoothing spectral curves with a span of 0.4. We then removed any patch with a reflectance reading below zero or above 100 percent, as these measurements were caused by miscalibration of optical equipment. Excessively dark measurements can skew colour measurements, because small amounts of noise are relatively large in comparison, and therefore generate random hues. To address this issue, we plotted individual measurements in a tetrahedral colourspace (described below) and discarded any individual measurement with both single colour intensity above 0.25, and relative brightness below 0.01. Visual inspection of the colour space, spectral curves and illustrations of species confirmed that this removed erroneous measurements, whilst still preserving plumage that was truly black.

After cleaning spectral data there was an average of 3.14 replicate readings per patch, and 3.02 individuals per sex. We then averaged reflectance spectra so that the sex of each species had a single measurement for each patch. Lastly, we discarded any species that no longer had a complete set of patches for both sexes, to leave 877 species.

Visual models

We used an avian visual model to convert raw reflectance data into relative cone stimulation. Unlike humans, birds possess tetrachromatic vision, with a fourth cone that is either violet or ultra-violet sensitive due to mutations on the SWS1 opsin gene (Hart 2001). We used an average avian visual model with violet sensitivity because previous evidence has shown that UV sensitivity is highly conserved, and all genetic sequencing of the SWS1 gene to date within suboscines has demonstrated violet sensitive vision (Barreira *et al.* 2021; Ödeen *et al.* 2011; Ödeen & Håstad 2013; Seddon *et al.* 2010). Because a model of achromatic stimulation does not currently exist for suboscines, we used an achromatic model based on another passerine, the Blue Tit (*Cyanistes caeruleus*), in line with previous research on similar neotropical passerines (Shultz & Burns 2017).

Using the avian visual model, we were able to plot each plumage patch within a 3D avian colour space (Figure S1). To quantify both dichromatism and elaboration, we measured both chromatic and achromatic distances between patches using just-noticeable distances (JND) with a weber fraction of 0.05. Because photo-receptor estimates were unavailable for suboscine species, we averaged the photo-receptor density across all passerines (Hart 2001).

Phylogenetic factor analysis

To combine patch measurements, we ran six PFA models in total. For human assessed dichromatism, we ran a single PFA combining all five body regions, with ranks treated as discrete data. All five patches loaded positively onto principal factor 1 (PF1), with dorsal patches contributing more variation than ventral patches (Table S1). To summarise avian dichromatism, we combined chromatic and achromatic differences for all seven patches. Both chromatic and achromatic differences loaded positively, and all patches explained a similar level of variation (Table S2).

To summarise elaboration, we performed the same steps as with avian dichromatism, substituting sex differences for distance from the suboscine centroid patch. For males, nearly each patch loaded equally for chromatic and achromatic differences, however achromatic differences in belly patches were an insignificant contribution to overall variation (Table S3). For females, the pattern was more complex (Table S4); all chromatic and achromatic patch differences had equally positive loadings, except for achromatic differences in ventral patches, which loaded negatively. We retained female PF1 as a composite measure of elaboration because 11 of the 14 patch differences loaded on positively, so overall, females with a high PF1 tended to be further from the typical suboscine colour. Lastly, we also combined overall brightness differences for each sex, which all loaded positively (Table S4), indicating males and females with higher PF1 values maintained overall brighter plumage.

Nest concealment and incubation scoring

Nest concealment was scored as a binary variable: cavity (1) vs. exposed (0). Cavity nests included natural cavities (tree holes, burrows, rock crevices) and constructed cavities such as domed or globe nests where the incubating bird was not visible to

predators. Constructed cavities were particularly common in ovenbirds (Furnariidae), including oven-shaped mud nests (e.g., *Furnarius*) and elaborate stick structures with tunnel entrances (e.g., *Anumbius*, *Phacellodomus*). Incomplete domes, domes with large side-entrances, or nests with partial roofs were treated as exposed. Open cup nests were scored as exposed even when placed in recesses or under overhangs if the incubating bird remained visible from any angle. However, cup nests are scored as cavity nests if they are habitually placed under a dense screen of overhanging vegetation, making the incubating bird invisible to any approaching predator.

Literature descriptions of nest structure can be ambiguous, particularly for cup nests that may be deeply concealed by overhanging vegetation, moss, or rock. To verify nest type, we cross-referenced species accounts with photographs and videos from online databases (e.g., Macaulay Library) and primary literature. In cases where images revealed greater concealment than described in text, we adjusted scores accordingly, with justification documented in the dataset notes column.

Incubation sex roles were scored as a binary variable: 0 (female-only) or 1 (biparental). Male incubation was only counted as biparental if it represented >10% of total incubation time, as brief male contributions are common in suboscines but functionally negligible. For species without direct observational data, we inferred incubation roles from closely related species within genera or families where the behaviour was highly conserved. Each trait was assigned a certainty score (1-4, highest to lowest) reflecting data quality and the degree of inference required (see Main Methods). Species with low-confidence scores (1 or 2) for nest type or incubation were excluded from sensitivity analyses.

2. Supplementary Tables

Table S1. Phylogenetic factor analysis results for human-assessed dichromatism in suboscine birds. Results shown are the output of a phylogenetic factor analysis on human-assessed dichromatism, using all birds in our dataset (*n* = 1283). The analysis integrated data from five body regions (head; under: throat, chest, and belly; upper: nape, back and rump; wings; and tail), treating ranks as discrete variables. Models were run for 100,000 iterations, and outputs were restricted to a single principal factor, which explained 93.9% of the total variation in plumage dichromatism.

Patch	Loading	Lower CI	Upper CI
Head	1.80	1.52	2.06
Under	1.86	1.59	2.11
Upper	3.32	2.84	3.70
Wing	3.30	2.83	3.71
Tail	2.20	1.84	2.60

Table S2. Phylogenetic factor analysis results for avian assessed dichromatism in suboscine birds. Results shown are the output of a phylogenetic factor analysis on avian assessed dichromatism, using all birds with available reflectance data (*n* = 877). The analysis integrated data from seven plumage patches (belly, breast, throat, crown, back, rump, and dorsal surface of the tail). Models were run for 100,000 iterations, and outputs were restricted to a single principal factor, which explained 29.1% of the total variation in plumage dichromatism.

Patch	**Colour**			**Brightness**		
	Loading	Lower CI	Upper CI	Loading	Lower CI	Upper CI
Belly	0.66	0.59	0.73	0.68	0.60	0.75
Breast	0.69	0.62	0.75	0.70	0.64	0.77
Throat	0.62	0.55	0.68	0.68	0.62	0.76
Back	0.69	0.62	0.75	0.63	0.57	0.70
Crown	0.69	0.62	0.75	0.60	0.53	0.66
Rump	0.60	0.53	0.67	0.60	0.53	0.66
Tail	0.60	0.54	0.67	0.68	0.62	0.76

Table S3. Phylogenetic factor analysis results for male plumage elaboration in suboscine birds. Results shown are the output of a phylogenetic factor analysis on male plumage elaboration, using all birds with available reflectance data (*n* = 877). The analysis integrated data from seven plumage patches (belly, breast, throat, crown, back, rump, and dorsal surface of the tail). Models were run for 100,000 iterations, and outputs were restricted to a single principal factor, which explained 18.3% of the total variation in male elaboration.

Patch	**Colour**			**Brightness**		
	Loading	Lower CI	Upper CI	Loading	Lower CI	Upper CI
Belly	0.48	0.42	0.56	0.01	-0.07	0.08
Breast	0.52	0.45	0.60	0.37	0.30	0.44
Throat	0.41	0.34	0.49	0.35	0.28	0.42
Back	0.62	0.55	0.68	0.48	0.41	0.56
Crown	0.55	0.48	0.62	0.32	0.25	0.40
Rump	0.58	0.51	0.65	0.48	0.41	0.55
Tail	0.58	0.51	0.65	0.50	0.44	0.56

Table S4. Phylogenetic factor analysis results for female plumage elaboration in suboscine birds. Results shown are the output of a phylogenetic factor analysis on female plumage elaboration, using all birds with available reflectance data (*n* = 877). The analysis integrated data from seven plumage patches (belly, breast, throat, crown, back, rump, and dorsal surface of the tail). Models were run for 100,000 iterations, and outputs were restricted to a single principal factor, which explained 14.9% of the total variation in female elaboration.

Patch	**Colour**			**Brightness**		
	Loading	Lower CI	Upper CI	Loading	Lower CI	Upper CI
Belly	0.28	0.19	0.35	-0.54	-0.46	-0.61
Breast	0.33	0.25	0.40	-0.24	-0.16	-0.32
Throat	0.15	0.08	0.22	-0.24	-0.16	-0.32
Back	0.44	0.37	0.51	0.60	0.67	0.53
Crown	0.27	0.20	0.35	0.43	0.51	0.35
Rump	0.46	0.39	0.54	0.61	0.68	0.53
Tail	0.52	0.45	0.59	0.37	0.45	0.29

Table S5. Phylogenetic factor analysis results for plumage brightness in suboscine birds. Results shown are the output of a phylogenetic factor analysis on male and female plumage brightness, using all birds with available reflectance data (*n* = 877). The analysis integrated data from seven plumage patches (belly, breast, throat, crown, back, rump, and dorsal surface of the tail). Models were run for 100,000 iterations, and outputs were restricted to a single principal factor, which explained 28% of the total variation in perceived brightness for females, and 28.1% for males.

Patch	**Female**			**Male**		
	Loading	Lower CI	Upper CI	Loading	Lower CI	Upper CI
Belly	0.73	0.65	0.79	0.77	0.70	0.83
Breast	0.72	0.66	0.79	0.75	0.68	0.81
Throat	0.64	0.56	0.71	0.67	0.60	0.74
Back	0.70	0.64	0.77	0.63	0.56	0.70
Crown	0.49	0.42	0.55	0.28	0.20	0.35
Rump	0.63	0.57	0.71	0.66	0.58	0.72
Tail	0.36	0.29	0.44	0.46	0.39	0.52

Table S6. Phylogenetic linear model estimated effect sizes. Results are derived from phylogenetic linear models predicting plumage variation in suboscine birds. Separate models were run predicting the extent of dichromatism according to human vision (n = 1283 species) and avian vision (n = 877 species), as well as male and female brightness and elaboration (n = 877 species). Phylogenetic information was incorporated using a maximum likelihood tree (Harvey *et al.* 2020), and each model was run with 10,000 bootstrap iterations to account for any uncertainty in branch placement.

Predictor	**Estimate**	***p* value**	**Estimate**	***p* value**
Dichromatism	Human		Avian	
Habitat density	0.00	0.68	0.02	0.607
Body mass	-0.03	0.163	-0.07	0.275
Trophic level	-0.09	0.004	-0.20	0.025
Sexual selection	0.18	< 0.001	0.39	< 0.001
Social selection	0.00	0.979	0.02	0.549
Predation risk	0.04	0.143	0.07	0.367
Elaboration	Female		Male	
Habitat density	0.22	< 0.001	0.08	0.012
Body mass	0.34	< 0.001	0.18	0.002
Trophic level	0.16	0.163	-0.23	0.007
Sexual selection	-0.02	0.882	0.25	0.013
Social selection	0.11	0.027	0.08	0.043
Predation risk	0.01	0.901	-0.08	0.275
Brightness	Female		Male	
Habitat density	-0.28	< 0.001	-0.18	< 0.001
Body mass	-0.39	< 0.001	-0.32	< 0.001
Trophic level	-0.17	0.170	-0.06	0.595
Sexual selection	0.06	0.694	0.01	0.937
Social selection	-0.03	0.636	-0.02	0.618
Predation risk	-0.52	< 0.001	-0.30	0.002

Table S7. Phylogenetic linear model estimated effect sizes from a conservative dataset. Results are derived from phylogenetic linear models predicting plumage variation in suboscine birds for species with moderate and high data certainty scores (scored 3–4). Separate models were run predicting the extent of dichromatism according to human vision (n = 1009 species) and avian vision (n = 727 species), as well as male and female brightness and elaboration (n = 727 species). Phylogenetic information was incorporated using a maximum likelihood tree (Harvey *et al.* 2020), and each model was run with 10,000 bootstrap iterations to account for any uncertainty in branch placement.

Predictor	**Estimate**	***p* value**	**Estimate**	***p* value**
Dichromatism	Human		Avian	
Habitat density	0.00	0.696	0.03	0.401
Body mass	-0.02	0.383	-0.04	0.512
Trophic level	-0.08	0.013	-0.18	0.056
Sexual selection	0.22	< 0.001	0.36	0.004
Social selection	0.00	0.972	0.01	0.828
Predation risk	0.01	0.752	0.08	0.340
Elaboration	Female		Male	
Habitat density	0.25	< 0.001	0.08	0.021
Body mass	0.32	< 0.001	0.20	0.003
Trophic level	0.19	0.142	-0.21	0.025
Sexual selection	0.03	0.867	0.31	0.011
Social selection	0.10	0.054	0.06	0.120
Predation risk	-0.01	0.964	-0.09	0.278
Brightness	Female		Male	
Habitat density	-0.31	< 0.001	-0.19	< 0.001
Body mass	-0.35	0.001	-0.29	0.001
Trophic level	-0.26	0.07	-0.11	0.394
Sexual selection	0.01	0.974	-0.10	0.535
Social selection	-0.02	0.742	-0.02	0.734
Predation risk	-0.54	< 0.001	-0.28	0.011

3. Supplementary Figures

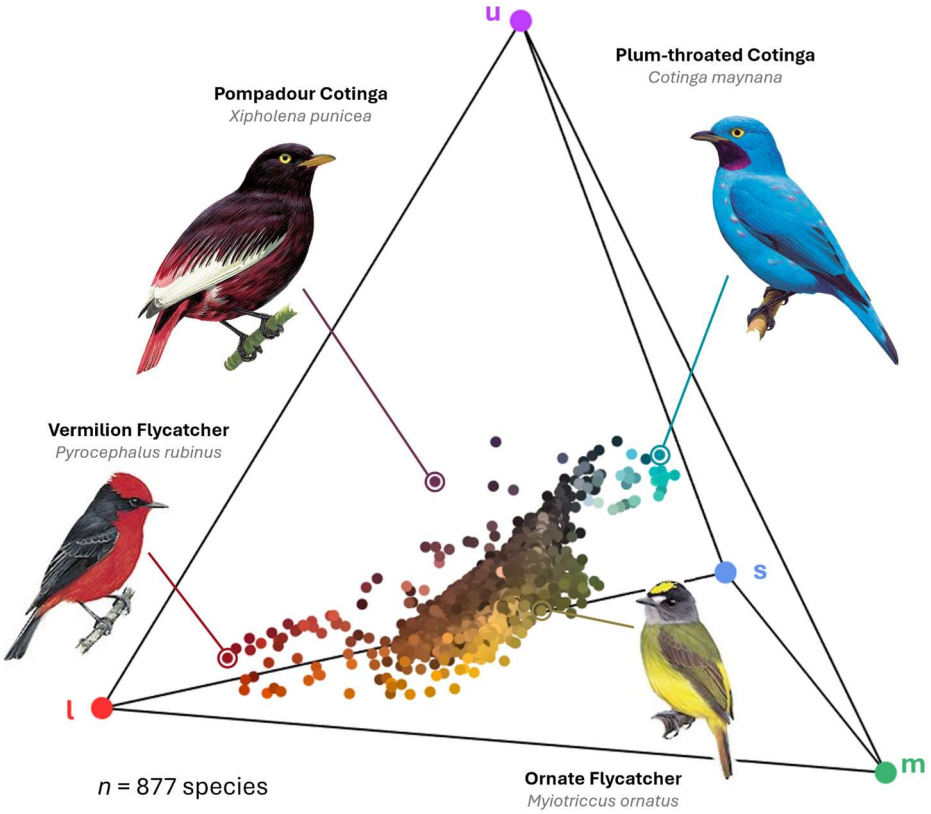

Figure S1. Suboscine plumage patches in a tetrahedral avian colourspace. A 3D representation of a tetrahedral colourspace, generated from an average violet-sensitive avian visual system. Each point represents a single patch for each sex for 877 species of suboscine birds (12,278 patches in total). Vertices of the tetrahedral represent the four cones birds use to perceive colour (red, green, blue and UV/violet). The centre of the colourspace is achromatic: plumage patches near this region are typically perceived as white, grey, or black. Illustrations showcase examples of plumage variation across suboscines, reproduced with permission from Cornell Lab of Ornithology, Birds of the World (https://birdsoftheworld.org).

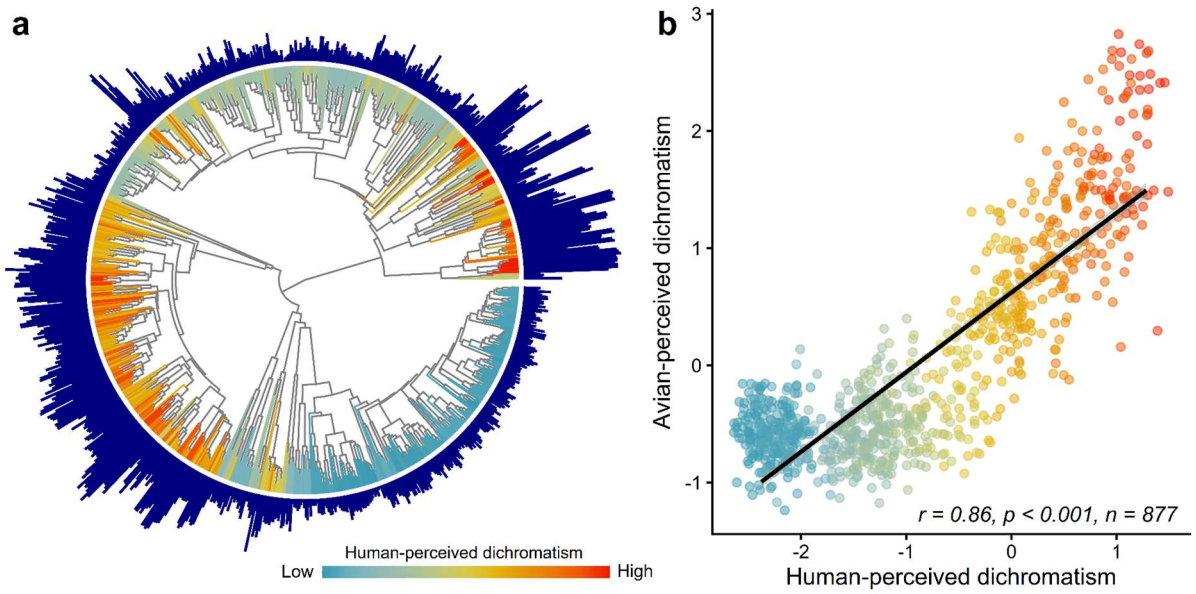

Figure S2. Suboscine plumage dichromatism according to human and avian vision. (**a**) Phylogram shows a maximum-likelihood phylogenetic tree (Harvey *et al.* 2020) representing the extent of dichromatism in suboscine species with available reflectance data (*n* = 877). Branches are coloured according to human ranks of dichromatism, scored through a visual assessment of illustration in the Handbook of the Birds of the World series (del Hoyo *et al.* 1992 - 2013). External bars represent relative dichromatism according to avian vision, measured as just noticeable differences within an avian colourspace. To create specific-specific composite scores for each vision method, we combined individual patches using phylogenetic factor analysis (see section above). (**b**) The correlation between human-perceived and avian-perceived dichromatism scores. Both scores were highly correlated (Pearson's *r* = 0.87, df = 875, 95% CI = 0.85–0.88), suggesting that human assessments are a valid proxy for avian vision.

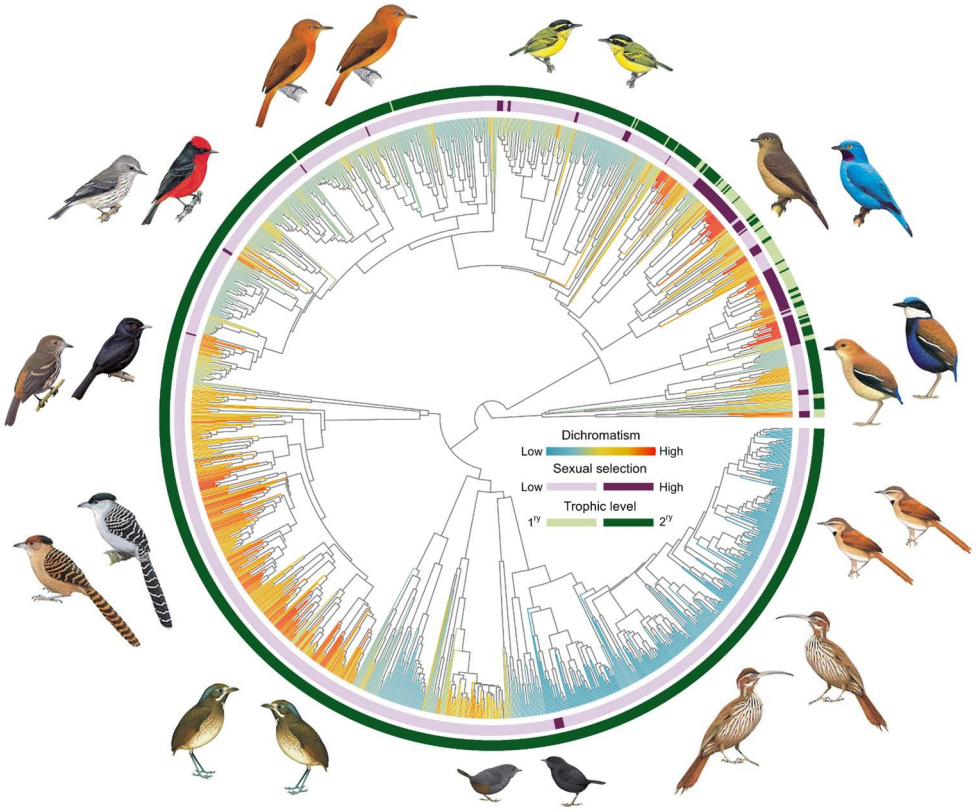

Figure S3. The influence of sexual selection and diet on suboscine dichromatism. Phylogram shows a maximum-likelihood phylogenetic tree (Harvey et al. 2020) with branch colours representing the extent of dichromatism in 1283 suboscine species. Dichromatism was scored through a visual assessment of colour illustrations in the Handbook of the Birds of the World series (del Hoyo *et al.* 1992-2013). Coloured rings encircling the phylogeny show the distribution of two binary factors: sexual selection and trophic level (1^{ry} = primary consumer, 2^{ry} = secondary consumer). Most primary consumers are frugivores; most secondary consumers are insectivores. Omnivores (*n* = 101) were grouped with secondary consumers for analysis. The bird illustrations featured in the figure showcase examples of monochromatism and dichromatism across suboscines, reproduced with permission from Birds of the World (https://birdsoftheworld.org).

4. Supplementary References

Armenta, J.K., Dunn, P.O. & Whittingham, L.A. (2008). Quantifying avian sexual dichromatism: a comparison of methods. *J. Exp. Biol.*, 211, 2423–2430.

Barreira, A.S., Eaton, M.D., Vilacoba, E., Tubaro, P.L. & Kopuchian, C. (2021). Short-wavelength visual sensitivity and sexual differences in plumage colouration of ovenbirds (Aves: Furnariinae). *J. Ornithol.*, 162, 737–748.

Billerman, S.M., Keeney, B.K., Kirwan, G.M., Medrano, F., Sly, N.D. & Smith, M.G. (2025). *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA.

Cuthill, I. (2006). Color Perception. In: *Bird Coloration. Volume 1. Mechanisms and Measurement* (eds. Hill, G.E. & McGraw, K.J.). Harvard University Press, pp. 3–40.

Hart, N.S. (2001). The visual ecology of avian photoreceptors. *Prog. Retin. Eye Res.*, 20, 675–703.

Harvey, M.G., Bravo, G.A., Claramunt, S., Cuervo, A.M., Derryberry, G.E., Battilana, J., *et al.* (2020). The evolution of a tropical biodiversity hotspot. *Science*, 370, 1343–1348.

del Hoyo, J., Elliott, A. & Christie, D. (1992). *Handbook of the birds of the world*. Lynx Edicions, Barcelona.

Maia, R., Gruson, H., Endler, J.A. & White, T.E. (2019). pavo 2: New tools for the spectral and spatial analysis of colour in r. *Methods Ecol. Evol.*, 10, 1097–1107.

Marcondes, R.S. & Brumfield, R.T. (2019). Fifty shades of brown: Macroevolution of plumage brightness in the Furnariida, a large clade of drab Neotropical passerines. *Evolution*, 73, 704–719.

Ödeen, A. & Håstad, O. (2013). The phylogenetic distribution of ultraviolet sensitivity in birds. *BMC Evol. Biol.*, 13, 36.

Ödeen, A., Håstad, O. & Alström, P. (2011). Evolution of ultraviolet vision in the largest avian radiation - the passerines. *BMC Evol. Biol.*, 11, 313.

Seddon, N., Tobias, J.A., Eaton, M. & Ödeen, A. (2010). Human vision can provide a valid proxy for avian perception of sexual dichromatism. *The Auk*, 127, 283–292.

Shultz, A.J. & Burns, K.J. (2017). The role of sexual and natural selection in shaping patterns of sexual dichromatism in the largest family of songbirds (Aves: Thraupidae). *Evolution*, 71, 1061–1074.