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Original Article

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Evaluating the light environment as a contributor to colour differences among related bird species

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ABSTRACT

Understanding the diversity of colour in nature has been one of the more elusive evolutionary problems. In the terrestrial environment, comparative analyses have associated differences in colour between species to light environment, background, and receiver perception. However, these account for only a small fraction of colour diversity, and it has been difficult to explain why a certain species is the colour it is. Here we examine colour variation across 12 very similar species of warblers belonging to the genus *Phylloscopus,* whose general brightness along an achromatic axis has previously been related to light intensity in their habitat. Many of these species also show variation in the colour of several plumage regions, including the wing bar, belly, and white vs. green in the outer tail feathers. We ask if these differences can be connected to the spectrum of light found in the habitat of each species. We find little evidence that contrast between patches and adjacent plumage or colour per se is affected by light environment. We argue that the heterogeneity of light environments experienced within a habitat and throughout the day make it unlikely that downwelling irradiance alone has a direct influence on colour variation. Accordingly, other features must have driven colour evolution. Diversification may be driven by environmental characteristics, such as background, or unrelated to environment altogether, reflecting the possibility that many different variants may effectively stimulate a receiver, and those that appear in a certain species reflect stochastic processes (e.g. mutation) and contingency (form of the ancestor).

Keywords: colour distance; irradiance; *Phylloscopus*; receptor noise model; relational colour constancy; sensory drive

INTRODUCTION

Understanding what drives diversification in animal signals has proved to be a particularly challenging topic (Price 2017, Delhey *et al.* 2023). Why, for example, does the Wilson's bird-of-paradise (*Cicinnurus respublica*) possess a feather-less blue head, while its closest relative, the magnificent bird-of-paradise (*Cicinnurus magnificus*), have a feathered, rufous head? Substantial differences in animal colours may result from the many possible colour variants that can elicit favourable responses from receivers (Arak and Enquist 1993). Given the relentless pressure of social selection (West-Eberhard 1983), even small colour differences may become exaggerated, leading to dramatic differences between species that can be uncorrelated with environmental features (Lande 1981, Schluter and Price 1993, Mendelson *et al.* 2014). This reasoning probably contributes to differences among males in strongly sexually selected radiations, such as the birds-of-paradise. However, despite the innumerable possibilities for diversification, ecological factors do make it more likely that some signals are favoured over others. For example, in the birds-of-paradise, display repertoires are more complex in species dwelling near the forest floor (Ligon *et al.* 2018, Miles and Fuxjager 2018), while acoustic repertoires increase for species in higher forest strata (Ligon *et al.* 2018), probably due to different transmission pressures along a vertical gradient in tropical forests. Delhey *et al.* (2023) conducted a near-global analysis of birds, and found significant correlations for several ecological factors, albeit with low explanatory power (R^2 values). Ecological factors include body size, nesting ecology, predation pressure (see also Bliard *et al.* 2020), thermoregulation (Rogalla *et al.* 2022), camouflage (Mason *et al.* 2023), and light environment (Gomez and Théry 2004, Beco *et al.* 2021).

In this paper, we address the role of a habitat's light environment in contributing to colour differences across a sexually monomorphic, generally dull coloured, group of birds, the Phylloscopidae warblers. Many avian families, including the Phylloscopidae, contain bird species that differ relatively slightly in coloration. Further, males and females are often very similar or even identical in their colours (Dale *et al.* 2015, Dunn *et al.*

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2015). Species exhibiting minimal sexual dichromatism are considered to be subject to weak sexual selection, and diversification in social signals is correspondingly limited (Seddon *et al.* 2013, Dale *et al.* 2015). Accordingly, we predict that a relatively large fraction of a species' colour and pattern variation should be correlated with ecological factors. Studying clades in which there is relatively little variation between species is therefore a promising route to develop a more predictive theory of colour evolution and to elucidate the role of ecology in these processes (Marcondes and Brumfield 2019). Comparative and experimental studies assessing the association of colour and ecology in such groups provide a baseline model against which arbitrary divergence in more sexually selected groups can be evaluated.

We frame our study around the concept of sensory drive (Endler 1992), defined as signal evolution that results from biases that arise from 'known and predictable properties of the environment, signals and neural systems' (Endler and Basolo 1998). Since its proposal, evidence has accumulated showing an important role for sensory drive (reviewed by Cummings and Endler 2018). However, in the visual modality the strongest support comes from aquatic environments, which experience stark gradients in the light spectra due to differential scattering and absorption of wavelengths at different depths. Differences also arise from variation in water turbidity or the presence of organic matter. These variable optical environments influence both the colours aquatic species have evolved to perceive (Cummings and Partridge 2001, Carleton *et al.* 2005, Fuller *et al.* 2005, Maan *et al.* 2006, Veen *et al.* 2017) and the colours species carry (Endler 1991, Boughman 2001, Fuller 2002, Maan *et al.* 2006, Cummings 2007, Seehausen *et al.* 2008).

While the importance of irradiance (the spectrum of incident light on an object) has been most clearly shown in the aquatic environment, some broadscale comparative analyses have suggested a role in the terrestrial environment. Within forests, a stratification in both the chromatic (colour) and achromatic (brightness) axes occurs along a gradient from canopy to understorey, with a decrease in overall light intensity and in the proportion of low-wavelength ('blue') light as one moves to the understorey (Endler 1993, Théry 2001). Species in the canopy have, on average, higher within-plumage chromatic diversity and more UV reflectance than species occurring in the understorey (Gomez and Théry 2004, Shultz and Burns 2013, 2017). Species in 'closed' environments, such as forests, are also on average 'redder' (McNaught and Owens 2002) or at least more rufous (Delhey *et al.* 2023), and show a higher diversity of within-plumage coloration (Shultz and Burns 2013, 2017) than species in open habitats. However, in closed environments, plumage diversity has often been attributed to camouflage, because of the greater diversity of background objects against which more complex plumage can appear cryptic (Shultz and Burns 2013, 2017, Delhey *et al.* 2023).

Variation in the spectral shape of downwelling irradiance is determined largely by differences in forest geometry and these geometries have been found to remain consistent across different forest locations and tree compositions (Endler 1993). Consequently, most analyses assign representative spectra based on broad habitat categories that capture the dominant geometry, such as 'large gap' in open habitat, 'forest shade' in closed, lower strata habitats, and 'woodland shade' in closed-canopy habitats. However, the sensory environment experienced by an animal is spatially and temporally heterogeneous, especially in forests, which have both horizontal and vertical variation in light (Matsuo *et al.* 2021, Helbach *et al.* 2022). Finer-scale evaluations of light environments in the microhabitats are needed for more detailed tests of sensory drive (Marcondes and Brumfield 2019, Scott *et al.* 2024) but are largely unavailable to accommodate the scale of most macroevolutionary studies. Here, we empirically test variation in light environment experienced by 12 species of *Phylloscopus* warbler across five forested breeding habitats.

The *Phylloscopus* warblers are monomorphic. Species are similar in appearance, with the most striking difference being the number of pale plumage patches (generally yellowish) on olive, brown, or greenish upperparts, with yellow to white underparts (Fig. 1; Price and Pavelka 1996). Variation in the quantity of patches (on the wing, crown, rump, and tail in the most patterned species) has been attributed to sensory drive along an achromatic (bright–dark) axis (Marchetti 1993). Species living in dark habitats, notably conifer, have more pale patches than species living in open woodlands or high alpine scrub (Marchetti 1993). We studied 12 species of *Phylloscopus* warbler that breed across an altitudinal range of 2000–4000 m within the west Indian Himalayan region of Himachal Pradesh (Price 1991, Price *et al.* 2003). Species have restricted altitudinal distributions, closely tied to specific habitats (Price 1991, Ghosh-Harihar and Price 2014).

We analyse colour variation of five plumage regions that serve different but intersecting functions: the back, belly, greater covert feathers (wing bar and adjacent area), and rectrices (tail feathers). The back and belly plumage encompass the largest area of the bird and the contrast between them is responsible for countershading, a feature important in camouflage (Thayer 1896, Cuthill *et al.* 2016). While the relatively dull back plumage probably functions in camouflage (Friedman and Remeš 2024), the ventral plumage of different *Phylloscopus* species varies in colour considerably, from white to yellow (Fig. 1). Many Phylloscopus species have lighter portion at the distal end of the greater covert feathers that forms a distinct patch due to an absence of melanin and deposition of carotenoid (Price and Pavelka 1996),called the wing bar (Fig. 1), which functions as a signal in aggressive interactions (Marchetti 1993). The rest of the feather is darker, often brown or olive green in coloration and we refer to this as the area adjacent to the wing bar. Darker areas adjacent to signalling patches can increase the contrast of the focal patch, making it appear brighter or more conspicuous (Gomez and Théry 2007, Jones *et al.* 2017, McCoy and Prum 2019). Lastly, some species also have varying extents of white in the outer tail feathers (Supporting Information Fig. S1). Unlike the belly and wing bar, the tail patch is concealed during normal foraging but exposed during displays and in flight (Fig. S1). We study these three patch pairs (contrasting belly to back, wing bar to adjacent area, and for those species with white tail feathers, white to adjacent nonwhite feathers).

To ask whether differences in signalling environment influence differences in colour across species and plumage patch types, we characterized the light environment during the breeding season by measuring irradiance. Because light spectra in forests are strongly influenced by geometry (Endler 1993),

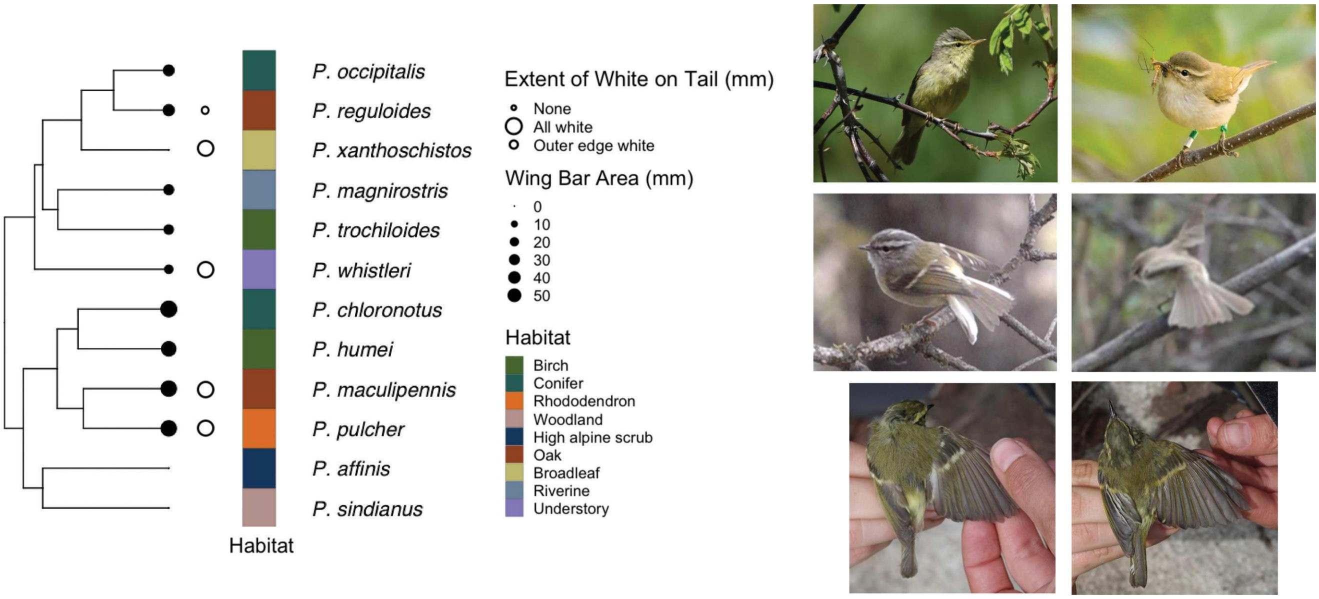

Figure 1. Left: evolutionary relationships for 12 *Phylloscopus* species in the west Himalaya. Filled circles at the tips of the phylogeny correspond to the wing bar size of each species and open circles correspond to the extent of white on the outer tail feather. The coloured squares represent the primary habitat of each species during the breeding season. Phylogeny is pruned from Alström *et al.* (2018). Right: examples of colour variation in *Phylloscopus*. Top row: variation in belly and back plumage of *P. affinis* and *P. trochiloides*. Middle row: variation in the extent of white in the tail for *P. maculipennis* and *P. sindianus*. Bottom row: variation in wing bar coloration for *P. chloronotus* and *P. pulcher*. *Phylloscopus trochiloides* photo taken by Chayant Goncalves; all others by K.F.

different characteristics of tree species may affect which light regimes are possible. Achieving a 'forest shade' spectrum, for example, requires an extremely dense canopy with no ambient light from the sky or sun (Endler 1993, Théry 2001). Therefore, if certain tree species form a discontinuous canopy, then both 'forest shade' and 'small gap light' environments (Endler 1993) would be rare in that habitat. We focus on five habitats, four characterized by their dominant tree species (birch, conifer, oak, and rhododendron) and one, understorey, as the layer of vegetation found between the canopy and forest floor at lower elevations. We first ask whether these habitats present distinct chromatic light environments and then use avian visual models to investigate whether plumage colour and adjacent plumage contrasts differ under different light regimes.

MATERIAL AND METHODS

Plumage measurements

We quantified plumage characteristics from specimens at the Field Museum of Chicago. We used an Ocean Insight Flame spectrometer with a PX-2 pulsed xenon light source to measure plumage reflectance from 300 to 700 nm, encompassing the avian visual spectrum, in 1-nm intervals (Supporting Information Table S1). Measurements were taken at a 90° angle incident to the feather surface with a QR200-7-UV-VIS bifurcated reflection probe outfitted with a custom probe holder. The reflectance values are measured relative to a Spectralon 99% reflection standard. We focused on five plumage regions: back, belly, greater covert feathers (wing bar and adjacent area), and rectrices (tail feathers). For each patch type we took the average of five measurements per individual. For back and belly measurements we sampled uniformly over the area of the plumage. On the greater covert feather, the wing bar and the area adjacent to the wing bar were measured based on the readily distinguishable boundary between the unmelanized (wing bar) and melanized parts of the covert (Price and Pavelka 1996, Scordato *et al.* 2012). Three species (*Phylloscopus affinis*, *P. xanthoschistos*, *P. sindianus*; Fig. 1) have no discernible wing bar. For these species we measured the distal tip of the greater covert feathers as the 'wing bar' and the proximal region of the feather 4 mm away from the tip as the adjacent area. These areas corresponded to the same location on the greater covert feathers as in the species with visually distinct wing bars. For tail measurements we sampled the area on the outer vane of the outermost left rectrix. Five species have varying extent of white in the outer tail feathers (Fig. 1) and for these we took two separate reflectance measures: white and nonwhite. If the outermost left rectrix had both white and nonwhite areas, we took the white and nonwhite samples from the same feather. However, if the outermost rectrix was all white then we took nonwhite tail measurements from the next tail feather that showed a nonwhite area (usually the third rectrix).

We measured 72 individuals from 12 species. For wing bar, area adjacent to the wing bar, back, and belly plumage areas we measured three males and three females per species. For tail we measured three males and three females for 11 species except for *P. affinis* in which we only measured two females due to tail damage in the third specimen ($N = 71$ individuals for tail). For the five species with white on the outer retrices we measured reflectance of these areas for three males and three females of *Phylloscopus maculipennis*, *P. whistleri*, *P. pulcher*, and *P. xanthoschistos*, but for *P. reguloides* only males were measured because the extent of white on females was too narrow to capture with the spectrometer.

Colour quantification

We conducted all colour analyses using pavo (Maia *et al.* 2013, 2019) in R version 4.2.2 (R Core Team 2022). We calculated the average reflectance of each patch per individual across the five replicates and smoothed the spectra using locally weighted scatterplot smoothing (LOESS) with a span of 0.03, using the *procspec* function. To control for overall brightness, we subtracted the mean reflectance across all 401 values. We then binned to 20-nm intervals and ran a principal component analysis (PCA) using all individuals and all patches across all species. We extracted the PC1 and PC2 scores and subset the data by patch type (Supporting Information Table S2). We ran a two-way analysis of variance (ANOVA) for both PC1 and PC2 scores for each of the six plumage regions across sex and species, using individuals as replicates. We also ran a multivariate analysis of variance (MANOVA) where we included both patch and adjacent area as dependent variables, for each of the three comparisons separately. To better visualize colour variation and distribution of different patch types we averaged the reflectance spectra within each sex and species. We then separately conducted local PCAs on each of the three patch pairings (back–belly, wing bar–adjacent area, white–nonwhite tail) (Figs 2– 4).

Variability of patches

Socially selected signals are expected to be relatively variable across species. To compare differences in variability between putatively signalling patches and the nonsignalling adjacent plumage, we first ran Pitman's (Pitman 1939) test (which is appropriate for paired samples) based on the mean values of the 12 species (five for tail), separately for each sex (Supporting Information Table S3). Second, we compared variances using phylogenetic controls by estimating evolutionary rates (the Brownian motion parameter) using the functions *CompareRates.multTrait* (Adams, 2013) and *ratebytree* (Revell, 2012).

Visual models

To analyse how plumage colour is perceived in an avian visual system we assessed the discriminability of adjacent patches under an avian visual model. First, we estimated photoreceptor catches using a blue tit avian visual model (Hart *et al.* 2000) under a homogeneous flat illuminant across all wavelengths using the *vismodel* function in pavo. From these photoreceptor catches we calculated colour distances between adjacent patches using the *coldist* function in pavo based on the receptor-noise model (Vorobyev and Osorio 1998). These colour distances are measured in units of 'just noticeable differences', with a JND > 1 taken to imply that the patch comparison would be discernible to an avian receiver. While widely used, we note that the JND measure comes from experiments with the red-billed leiothrix, *Leiotrix lutea*, based on responses to coloured lights in a small cage (Maier 1992, Vorobyev *et al.* 1998). Whether this is directly transferrable to field conditions is uncertain, and it may be that

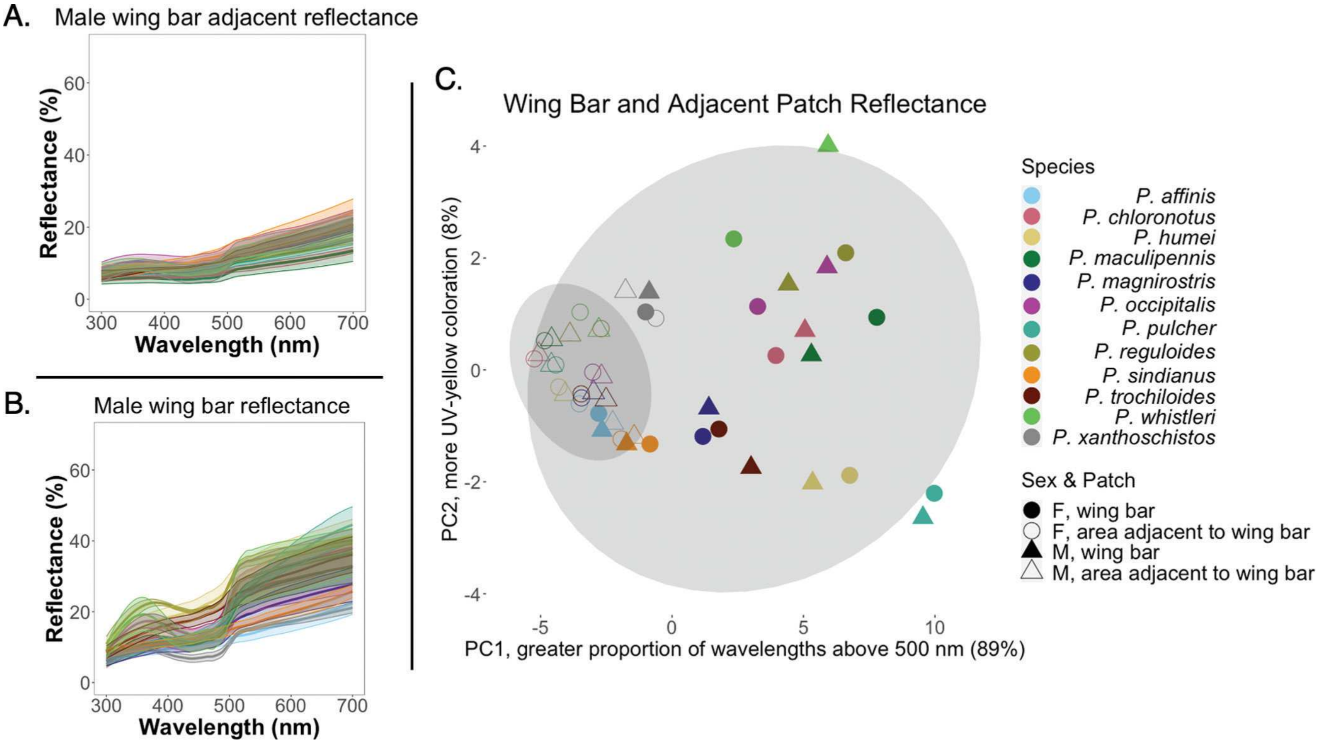

Figure 2. Wing colour variation in *Phylloscopus* warblers. A, average reflectance spectra (solid lines) and their standard deviation (shading) for the area adjacent to wing bars ($N = 3$ individuals per species, only males shown for clarity). B, average reflectance spectra (solid lines) and their standard deviation (shading) for male wing bars ($N = 3$ individuals per species). C, plot of PC2 vs PC1 of the wing bar and adjacent patch reflectances ($N = 48$, being based on the mean values of two traits from 72 individuals). Shape denotes sex (circles for females, triangles for males) and fill denotes patch type (solid shapes are wing bars, open shapes are adjacent areas). The grey ellipses are 95% predictive intervals for each patch type. When comparing the two adjacent wing patches, wing bars are more variable than adjacent feather areas. PC scores for each set of plumage patch comparisons can be found in Supporting Information Table S9.

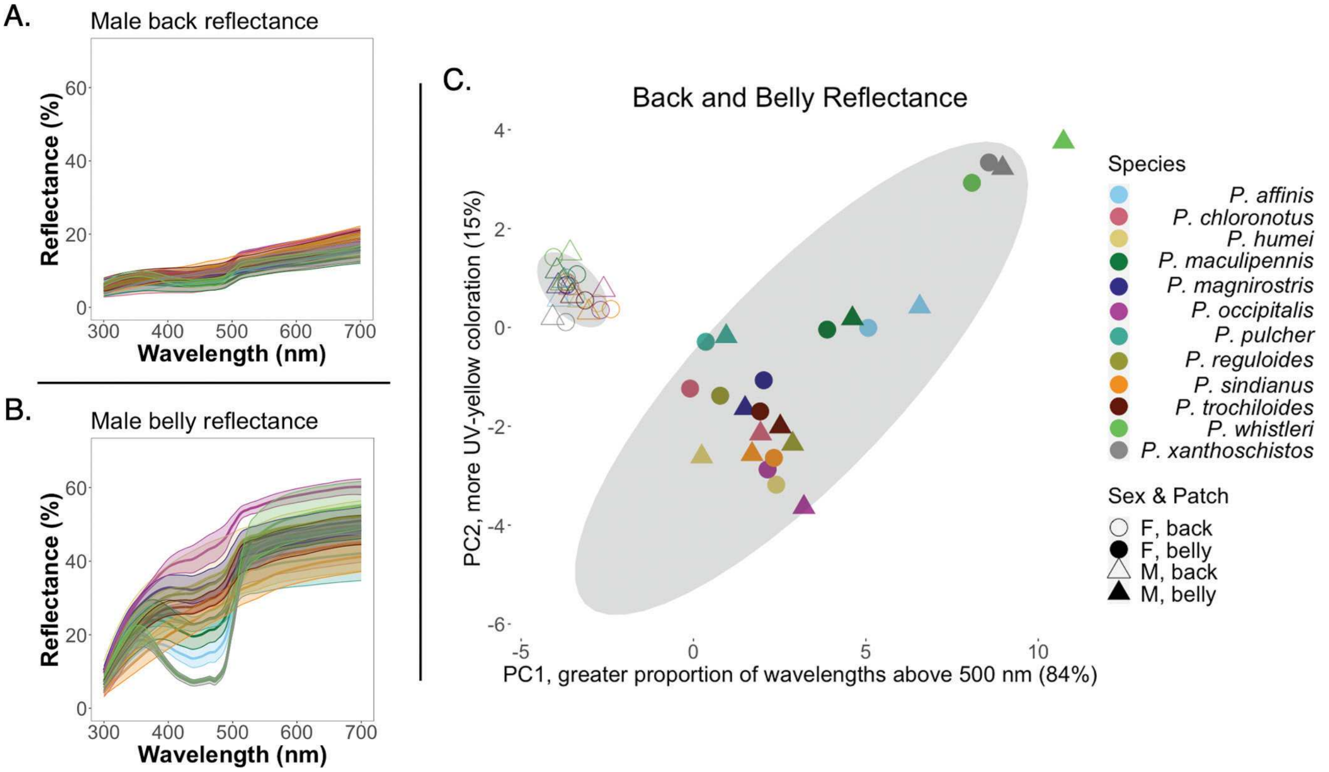

Figure 3. Back and belly colour variation in *Phylloscopus* warblers. Average reflectance spectra for male back reflectance (A), belly reflectance (B), and a PC plot of standardized reflectances for back (solid) and belly (open) comparisons (C). Belly plumage colours are more variable than back plumage. PC scores for each set of plumage patch comparisons can be found in Supporting Information Table S9.

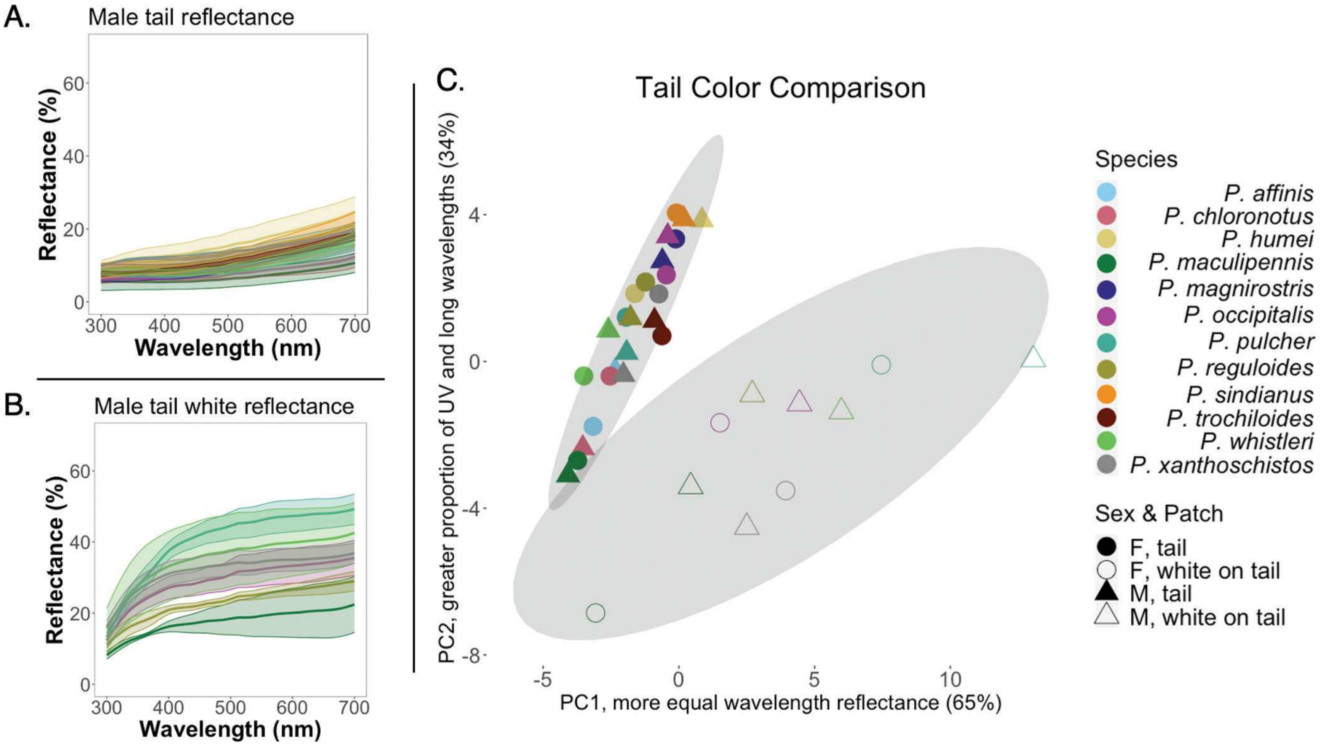

Figure 4. Tail colour variation in *Phylloscopus* warblers. Average reflectance spectra for male tails (A) and white tail areas (B) only for those species with white in the tails. C, PC plot of white and nonwhite tail standardized reflectances. PC scores for each set of plumage patch comparisons can be found in Supporting Information Table S9.

the experimentally assessed JNDs underestimate the difference required to distinguish colour patches. On the other hand, more recent work with chickens suggests close-range discrimination can be achieved with a smaller difference than implied by the *Leiothrix* study (Olsson *et al.* 2015). Hence, we use the JND as a guide only. We used the four-cone catches to calculate chromatic distances between adjacent patches [also termed chromatic contrast (ΔS)] and the double-cone catch to calculate achromatic distances (the Weber fraction for the double cone, which forms the basis for the JND, is typically assumed to be the same as that for the long-wavelength single cone, Olsson *et al.* 2018). While we focus most of our analysis and interpretation on chromatic distances, we include an estimate from the double cone because it is probably the primary means of motion detection, and hence is particularly applicable to display movements.

Light environment

To assess ambient light conditions in the natural environment of these species we took irradiance measurements during the breeding season in Manali Wildlife Sanctuary, Himachal Pradesh, India (32.25°N, 77.17°E, spanning 2000–3600 m, 27 May to 13 June 2022), and at Nain Gahar village, Himachal Pradesh, India (32.73°N, 76.86°E, spanning 3100–3700 m, 15 June to 8 July 2022). Habitats were designated based on the primary associations of the species studied (Fig. 1). We focused on birch (*Betula utilis*), conifer (primarily *Abies pindrow* and *Picea smithiana*), oak (*Quercus semecarpifolia*) and rhododendron (*Rhododendron campanulata*) and understorey. For the habitats dominated by tree species (birch, conifer, oak, rhododendron), we chose locations where the forest was largely composed of these species. For understorey measurements we sampled areas in dense vegetation that corresponded to the habitat preferences of *P. whistleri.* We sampled eight birch sites (all in Nain Gahar), six conifer sites (three in Manali, three in Nain Gahar), four oak sites (all in Manali), four rhododendron sites (all in Manali) and four understorey sites (one in Manali, three in Nain Gahar). Sample sites within a habitat were at least 20 m apart. We sampled habitat light measurements between 5.30 a.m. and 11.35 a.m. in sunny conditions which we define as the sky >75% without cloud cover. To remove the effects of mountain slope on the time when the sun crests over the highest ridge we filtered data to only include times between 7.30 a.m. and 11.35 a.m.. Although ambient light conditions can vary greatly through the day (Foster and Nascimento 1994, Moyen *et al.* 2006), aggressive interactions and displays are largely confined to the morning. To sample irradiance, we used an Ocean Insight Flame spectrometer and P400-5-UV-VIS fibre optic probe that were both calibrated prior to fieldwork by Ocean Insight for absolute irradiance, using a light source of known spectral power. Light in forests is heterogeneous in spectral shape due to the geometry of sun penetration (Endler 1993). To capture this variation, we measured light across two conditions—sun and shade—within each forest type. The species studied readily displayed in both conditions, moving actively between perches during territorial responses (our pers. obs.). Shaded areas were defined as areas without direct sunlight, and we specifically searched for areas blocked by tree canopy. Sun areas were often quite small and identified by looking for sunspots or sun flecks along the ground. We measured irradiance from 300 to 700 nm. For each light condition at each site, we took five measurements with the fibre optic probe lifted at least 1.5 m above the ground and above the measurer's head to avoid any effect of clothing or other objects. In both light conditions, measurements were taken away from large breaks in the canopy or forest edges and away from large obstructing objects such as tree trunks.

Light environment analysis

We converted spectral data from watts to photon flux using the *irrad2flux* function in pavo. For each light condition, we averaged the measurements taken at the same sample site and smoothed the spectra using locally weighted scatterplot smoothing (LOESS) with a span of 0.03 again using the *procspec* function in pavo. We then extracted a set of colourimetric variables from the data, including mean relative brightness over the whole spectrum ('B2' in pavo; this is better referred to as luminance, as brightness refers to how an object is perceived, rather than its reflection properties per se). Luminance differences may affect the evolution of colour. For example, some colours appear brighter than others, and luminance in the signalling environment may affect the kind of displays that are used. To test for differences between habitat luminance we conducted a two-way ANOVA for average relative brightness (B2) on habitat × light (sun/shade) condition.

To assess whether habitats differed in their spectral shape, we removed effects of brightness by subtracting the mean reflectance across all 401 values and then binned the spectra to 20-nm intervals. Like the methods for plumage colour, we ran a PCA on all samples from all locations (Supporting Information Table S4). We then conducted a two-way ANOVA for both PC1 and PC2 on habitat × light condition.

Plumage variation under different light regimes

If differences in species plumage colour are the result of adaptation to specific light environments, we predict that when moving between light conditions (sun or shade), change in patch appearance (measured by chromatic distance) should be smallest in a species' primary breeding habitat compared to nonassociated habitats. To test this, we ran visual models using the same parameters as described in the previous section but changed the illuminant from a homogeneous flat spectrum to one of the irradiance conditions measured in the field: birch sun, birch shade, oak sun, oak shade, conifer shade, conifer sun, rhododendron shade, rhododendron sun, understorey sun, understorey shade. For each habitat and sun condition we averaged the corresponding irradiance samples across sites to obtain an average spectrum for each of these habitats and light conditions. For every patch, we measured the perceptual distance between the illuminants using the *coldist* function. We repeated this for all six patch types per species under every pair of possible light conditions.

In the genus *Phylloscopus*, lighter coloured patches are often found adjacent to darker ones. Because the colour of an adjacent patch affects the perception of the focal patch, we measured how the contrast between focal and adjacent patch varies when viewed under different illuminants. Here, we focused on the habitats where spectral shapes between sun and shade differed the most: conifer and rhododendron. Using averaged irradiance samples for conifer sun, conifer shade, rhododendron sun, and rhododendron shade, we asked how chromatic distances of adjacent patch pairs change across these four light conditions, which represent the full range of variability across all habitats. We ran four visual models with the same avian visual system parameters but changed the illuminant to one of four irradiance comparisons: conifer shade, conifer sun, rhododendron shade, and rhododendron sun. As before, we calculated colour distances between adjacent patches using the *coldist* function in pavo for each visual model. We filtered the data to only include species patches with chromatic distances of 1.5 and below, assuming distances greater than 1.5 are unlikely to be significantly affected by changes in illuminant. Using a linear regression analysis, we compared chromatic distances between sun and shaded conditions for the two habitat types.

RESULTS

Plumage

We quantified the colour of six regions of the plumage for 12 species of *Phylloscopus*: back, belly, greater covert feathers (wing bar and adjacent area), and rectrices (white and nonwhite tail feathers) and summarized reflectance curves using PCA. The first two principal components in the global analysis (all individuals together) account for 96% of the variance (PC1: 85%, PC2: 11%). Loadings on PC1 correspond to the proportion of short versus long wavelengths in the reflectance curves. Species with higher values of PC1 have a greater proportion of reflectance above 500 nm, which corresponds to a sharp jump in the spectral curve for patches that have carotenoid-based coloration (yellow and orange) compared with patches that are greener and browner (Supporting Information Fig. S1). Loadings on PC2 correspond to an increase in wavelength reflectance at opposite extremes of the spectrum. A plumage patch with high values of PC2 has relatively high reflectance in both the UV and long wavelengths, a signature of carotenoid pigment-based colour (MacDougall and Montgomerie 2003).

Species differences

Two-way ANOVAs on sex × species (using individuals as replicates) showed that species differ significantly ($P < .001$) in colour for all patches (Supporting Information Table S5, post-hoc Tukey tests in Table S6). Males and females differ slightly in patch colour for the back, based on PC1 ($F_{1,48} = 5.99$, $P = .018$). The sex × species interaction term was marginally significant along PC2 for both belly ($F_{11,48} = 2.05$, $P = .044$) and tail patches ($F_{11,48} = 2.02$, $P = .048$). MANOVA on patch pairs (i.e. PC1 and PC2 combined) paralleled the results for the two-way ANOVAs (Table S5). In the three restricted PCAs of the adjacent patch pairings, where we first averaged across individuals within each sex by species (back–belly, wing bar–adjacent area, white–nonwhite tail), the loadings on PC1 and PC2 for back–belly and wing bar–adjacent area showed the same general pattern as the global analysis (Fig. S2). In the white–nonwhite tail analysis, PC1 loadings corresponded to more equal wavelength reflectance (65% of the variance) while PC2 loadings matched that of prior analyses, describing a greater proportion of UV and longer wavelength reflectance.

Variances

Pitman tests comparing the variances of the mean PC scores from the pairwise computations confirm that wing bars are significantly more variable in colour across species than the adjacent areas on the greater covert feathers. Belly plumage is significantly more variable than the back. However, white areas of the tail are not significantly more variable than nonwhite areas of the tail (Supporting Information Table S3). We compared evolutionary rates between species using the global PC scores. Brownian motion rate parameters for PC1 were 36× higher for belly than back (belly: 1.45, back: 0.04, likelihood ratio test $P < .001$) and 10× higher for wing bar than adjacent patch (wing bar: 0.61, adjacent patch: 0.06, $P < .001$) (too few species carry tail patches for this analysis). Similar results apply to PC2 (48× higher for belly than back, $P < .0001$, 7.5× higher for wing bar than adjacent patch, $P = .001$). We conclude that the carotenoid-based belly and wing bar are especially likely to be involved in conspecific signalling, given they evolve at much faster rates (i.e. are more variable across species) than adjacent nonsignalling locations.

Discriminability

To assess the discriminability between adjacent patches we modelled all patch types under an ideal illuminant (homogeneous illuminant of 1 across wavelengths). Chromatic distances between the back and belly differ the most between species, from JNDs < 1 to ~7 (Fig. 5). The three species that do not have discernible wing bars (*P. affinis*, *P. xanthoschistos*, *P. sindianus*; Fig. 1) all have chromatic distances of JND < 1 between the distal and proximal areas of the greater covert feathers, which matches human visual assessment. All species with discernible wing bars have chromatic distances greater than a discriminability threshold of JND > 1 except for *P. reguloides* (both sexes) and *P. trochiloides* females. The chromatic distance between the white and nonwhite areas of the tail have JNDs > 1 (Fig. 5), expected as the comparison is white against brownish-green areas.

In Fig. 3 we also show achromatic distances, which have JNDs < 1 for the three species without discernible wing bars. Achromatic distances are greatest for back and belly comparisons and these comparisons are the least variable between species (Fig. 5), because all species possess darker back plumage and lighter belly plumage. In sum, all patches as perceived by us are probably also discriminable along a brightness axis to an avian receiver, and in many species along a chromatic axis as well.

Light environment

Chromatic axis

We measured sun and shade irradiance across five different habitat types (Fig. 6). The loadings of PC1 (96% of the variance) on all habitats and light conditions correspond to a step function around 430 nm such that habitats with negative PC1 scores have a greater proportion of UV and short wavelengths and those with positive PC1 scores have a greater proportion of longer wavelengths (Supporting Information Fig. S3). The loadings of PC2 (3% of the variance) correspond to a difference between middle and extreme wavelength reflectance: habitats with negative

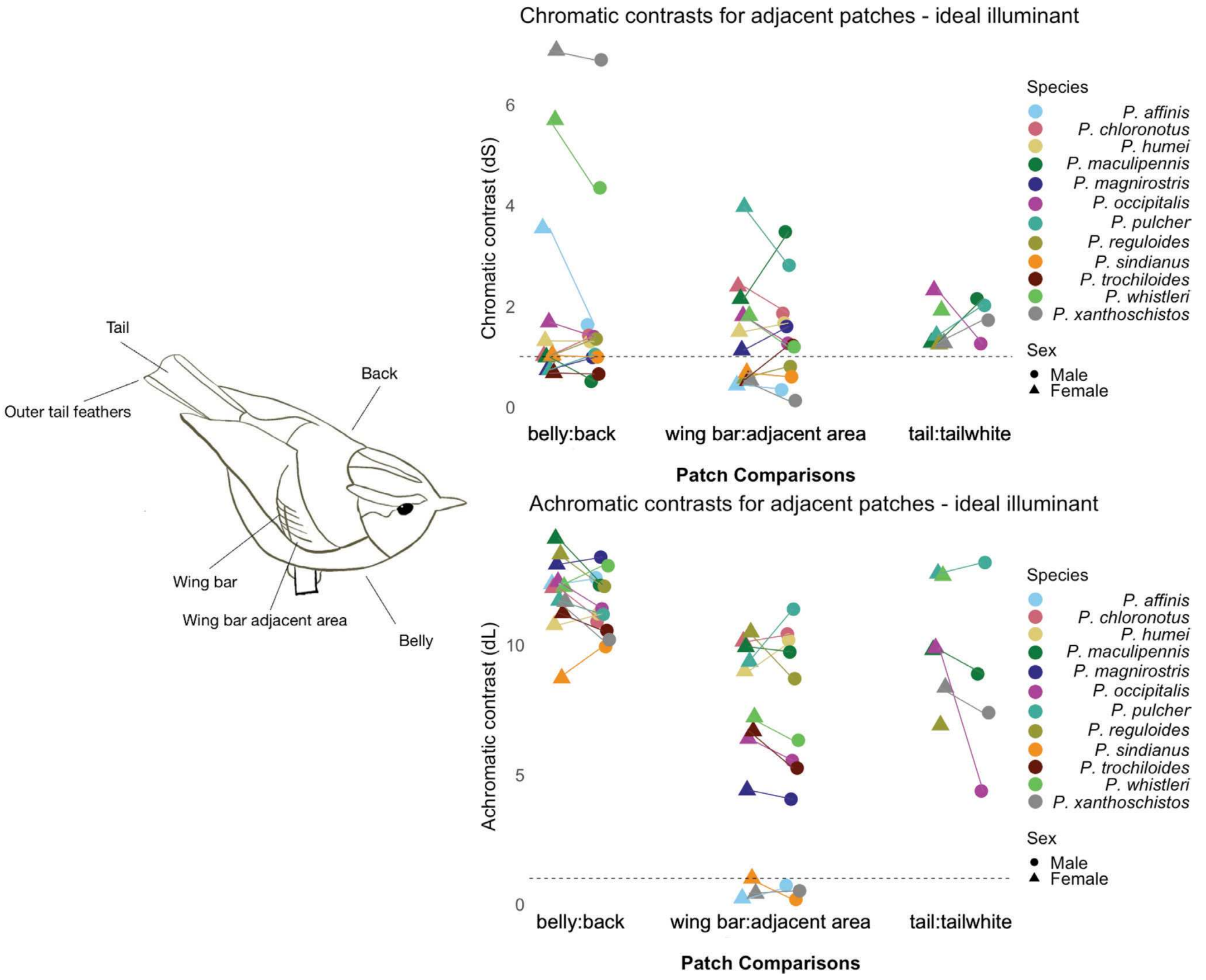

Figure 5. Adjacent patch discriminability in an avian visual model. Left, location of adjacent plumage patches. Top right, chromatic distances for the three adjacent patch comparisons in an avian visual model under an ideal illuminant (equal energy white). JND values are available in Supporting Information Table S10. The black dashed line denotes a JND of 1 under the assumptions of Vorobyev *et al.* (1998). Points that lie above the black line indicate that these adjacent patches should be chromatically distinct to a nearby avian viewer. Lines connect males (circles) and females (triangles) of each species. Bottom right, achromatic distances for the three adjacent patch comparisons in an avian visual model. Same as for the top plot, where the black dashed line represents a JND of 1. All patches have an achromatic distance of JND > 1. Note that *P. xanthoschistos*, *P. sindianus*, and *P. affinis* do not have discernible wing bars. Several species do not have discernible tail patches either, but they are not included in this figure.

PC2 scores have more wavelength reflectance between 400 and 500 nm while those with positive PC2 scores have a greater proportion of short and long wavelengths. PC1 differs significantly between habitats (two-way ANOVA, $F_{4,35} = 4.99$, $P = .002$), and between sun and shade ($F_{1,35} = 92.12$, $P < .00001$), with a marginal interaction ($F_{4,35} = 3.02$, $P = .03$, Table S7). Sun has a greater proportion of long wavelengths than shade. In sunlight, conifer habitats differ significantly in PC1 from rhododendron, birch, and oak (Table S7). Habitats or light conditions did not vary significantly in PC2 (Table S7).

Luminance

Based on the 'B2' metric in pavo (mean relative brightness), in a two-way ANOVA, unsurprisingly sun is brighter than shade ($F_{1,35} = 95$, $P < .001$, Fig. 7). Habitats vary significantly ($F_{4,35} = 3.6$, $P < .02$) and with a habitat × light interaction ($F_{4,35} = 2.9$, $P = .03$) (Supporting Information Table S8). Post-hoc pairwise Tukey tests (Table S8) indicate that the interaction results because sunspots in conifer are darker than sunspots in rhododendron ($P < .0005$) and oak ($P < .04$), whereas shaded habitats are similar in luminance (Table S8). Sun and shaded areas differ significantly within rhododendron ($P < .0001$), birch ($P < .0001$), and oak ($P = .003$) in luminance (Table S8), implying these habitats have two quite distinct light regimes. In contrast, sun and shade conditions did not differ significantly in luminance for understorey or conifer habitats.

Effects of light environment on plumage

Next, we considered how plumage colour changes when species move between habitats. As assessed by the avian visual system,

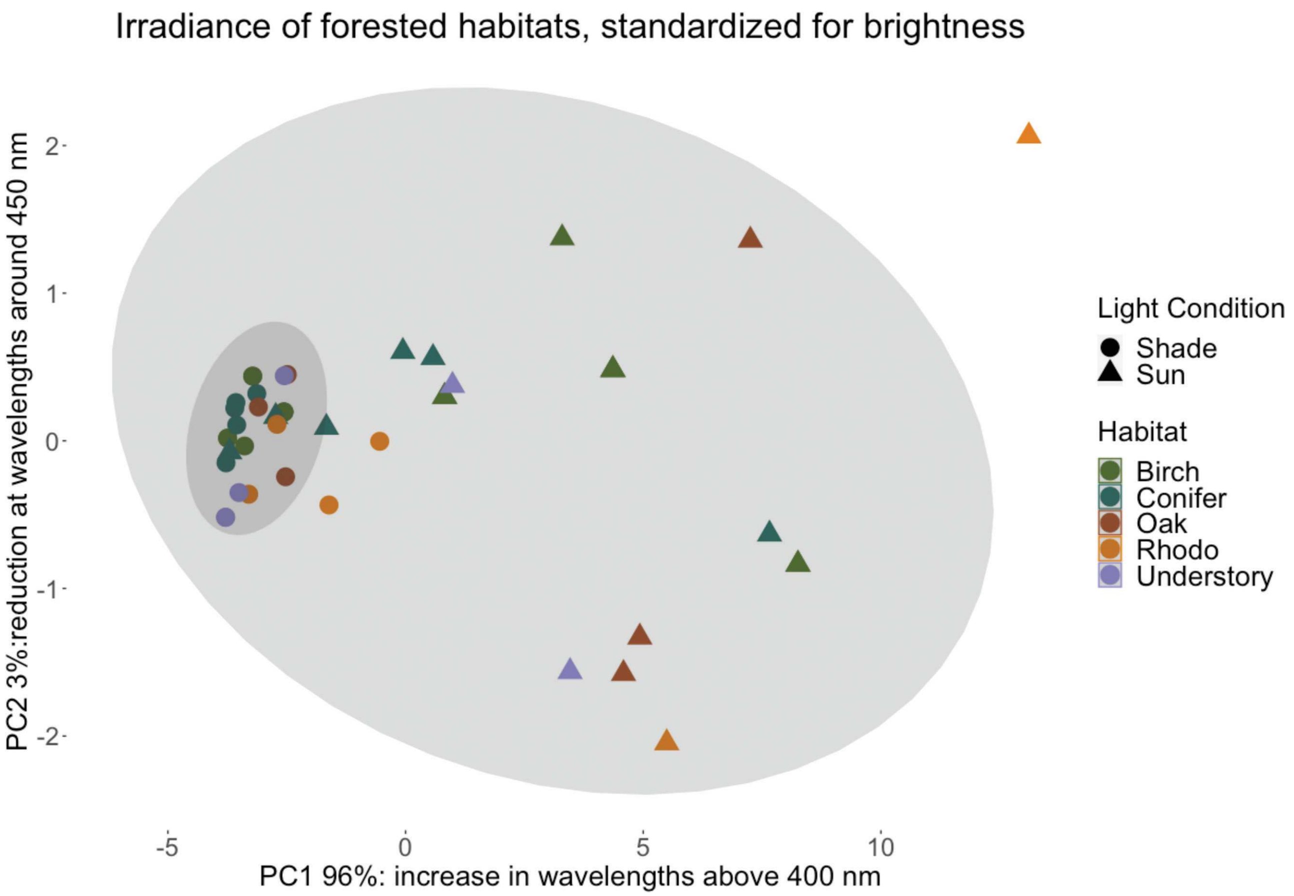

Figure 6. PCA of forested habitat spectral shape colour variation. Shape denotes light condition, where circles represent shaded areas and triangles represent sunny areas. Colours correspond to the habitat type determined by dominant tree type. In the PC analyses, all spectra are first standardized for brightness. The grey ellipses are 95% predictive intervals for each light condition.

the individual patches appear similar in colour across all habitats when in the sun. However, in the shade, we found that, moving from birch to rhododendron, oak, or conifer results in a larger change in colour distance, but the change applies more or less equally to all patches (Supporting Information Figs S4, S5). In other words, while the appearance of a plumage patch can shift when moved between shady environments, no species or patch type is more affected.

We next focus on the contrast between the patch and its adjacent nonsignalling plumage. Given rhododendron and conifer habitats encompass all the significant variation associated with spectral shape, brightness, and differences between sun and shade, we used the spectra from these habitats to evaluate how adjacent patch contrasts might change under different natural illuminants. Chromatic discriminability of adjacent patches does not vary significantly across light condition in either conifer or rhododendron (Fig. 8). Chromatic distances in sun and shade were very tightly correlated ($r > .99$), indicating that the light environment has very little influence on the perception of colour patches even between light conditions that are distinct from each other.

DISCUSSION

We tested the role of light spectra on colour variation among similar species in a system where plumage variation along the achromatic axis (patch quantity and wing bar brightness) has been related to a light–dark environmental axis; darker species (less patterned) occupy more open, brighter habitats while brighter species (more patterned) occupy darker, forested habitats (Marchetti 1993). Variation in habitat spectral shape and brightness has some effect on colour distance, as modelled though the avian visual system. Notably, shifts between a few habitat types in the shade (but not the sun) impact spectral shape (for example, we find a 3 JND difference between birch shade and conifer shade). However, changes in colour distance are similar across all patch types and species [i.e. all *Phylloscopus* species show this 3 JND difference between birch shade and conifer shade (Supporting Information Figs S4, S5), whether or not the species occupies one of other habitats, or neither]. Further, when we consider colour contrast of adjacent patches, we see no differences between habitats (Fig. 8). We conclude that species differences in colour cannot be explained by the light environment. We first ask why the irradiance hypothesis fails and then consider alternative explanations for plumage colour variation.

One reason why irradiance makes little difference to plumage reflectance spectra is that, with a few exceptions, the effect of habitat is small. Notably, variation is greater between sun and shade than across habitat types. A second reason refers specifically to patch contrasts. In the human visual system, colour contrasts remain largely invariant over the different light environments

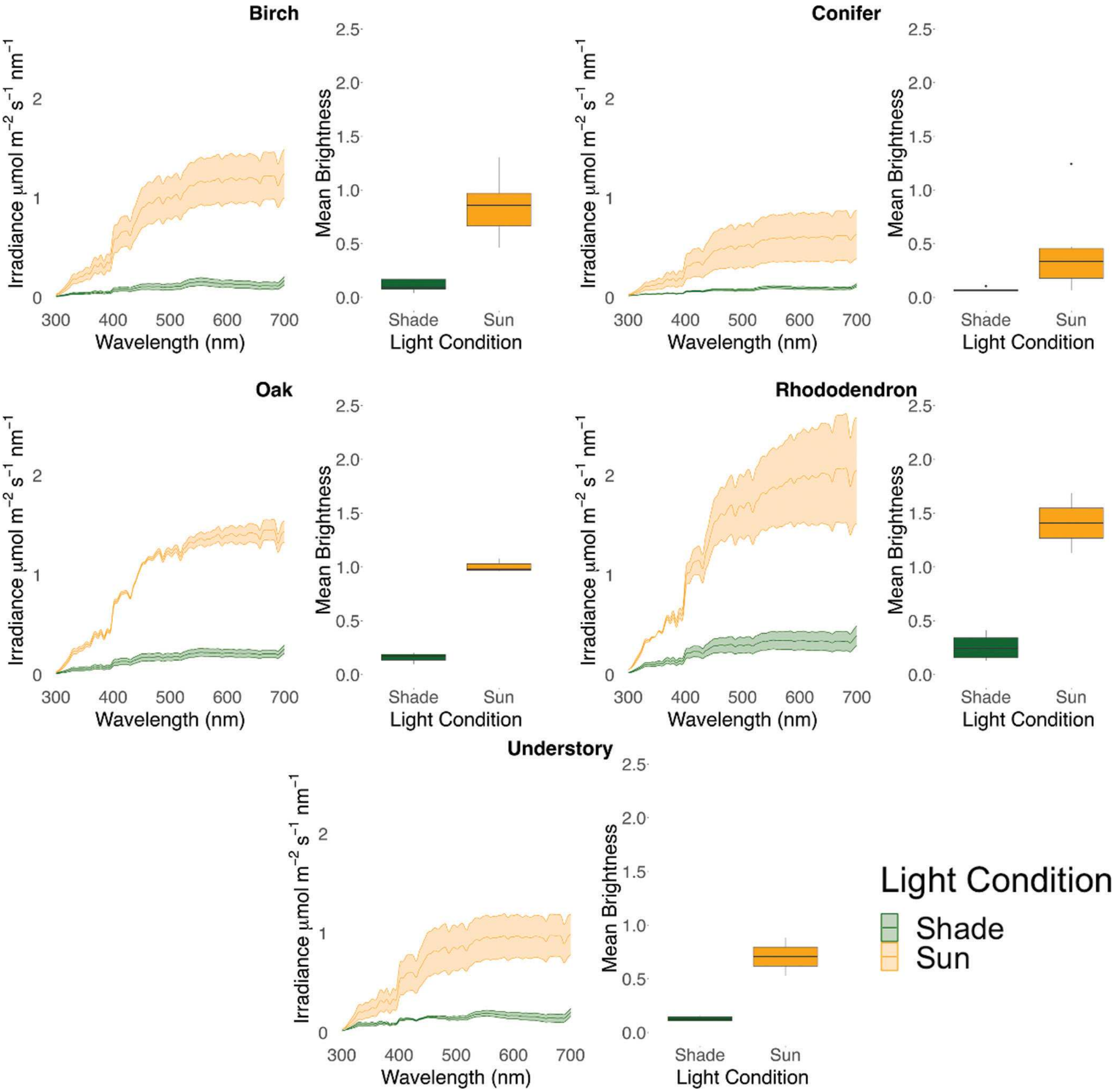

Figure 7. Irradiance spectra (left) and associated boxplots (right) for shade (green) and sun (orange) light conditions for five habitat types. Each habitat is measured between 7.30 a.m. and 11:35 a.m. (birch shade $N = 8$, sun $N = 8$; conifer shade $N = 5$, sun $N = 6$; oak shade $N = 3$, sun = 3; rhododendron shade $N = 4$, sun $N = 3$; understorey shade $N = 4$, sun $N = 2$). Irradiance spectra means are represented by solid lines and shading around the line corresponds to the standard error. Box plots show the distribution of the mean relative irradiance over the spectral range with the line representing the median brightness, the coloured areas above and below the line showing the third and first quartiles respectively, the top and bottom whiskers extending to the largest and smallest data value within the inner fence, and points corresponding to data falling outside the inner fence. In an ANOVA for brightness, habitats ($F_{4,35} = 3.6$, $P < .02$), sun/shade condition ($F_{1,35} = 95$, $P < .001$), and their interaction ($F_{4,35} = 2.9$, $P = .03$) are all statistically significant. Post-hoc pairwise Tukey tests (Supporting Information Table S8) indicate that rhododendron, birch, and oak differ significantly in mean brightness between sun and shaded light conditions. Sun and shade conditions are not significantly different for understorey or conifer habitats.

humans experience (Foster and Nascimento 1994). This phenomenon, termed relational colour constancy, differs from true colour constancy in which assessment of the colour of the patch per se does not change across illuminants, and requires some means of assessing the illuminant (Foster 2011). It appears that the avian visual system generates relational colour constancy, in much the same way the human visual system does. For humans, Foster and Nascimento (1994) showed that across a range of daylight spectra, the ratio of cone catches from one location (e.g. the wing bar in our case) to another (e.g. the plumage adjacent to the wing bar) stays approximately constant for each cone, so the ratio between two cones also stays constant, and it is this

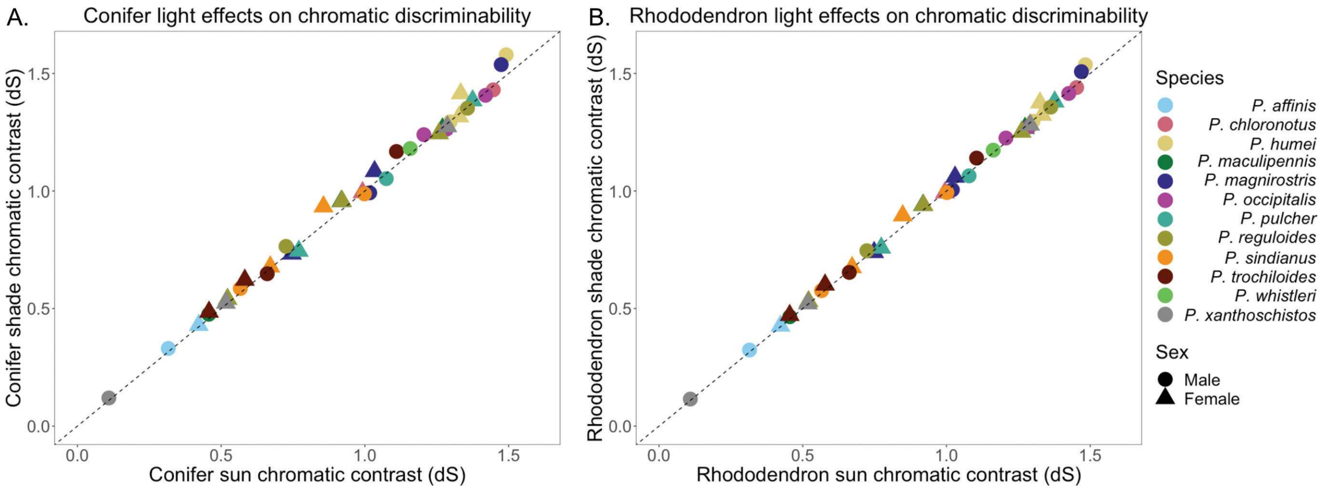

Figure 8. Correlation of chromatic contrasts in sun and shade for conifer (left) and rhododendron (right), as illustrated in Fig. 3. Data have been filtered to include those with a JND < 1.5. Chromatic discriminability does not vary significantly across light condition. The very tight correlations with little scatter ($r > .99$ in both plots) indicate little influence of light environment (sun/shade) on perception.

ratio that affects chromatic discrimination. We expect relational colour constancy to apply even more strongly to birds because their cone absorbance spectra are of narrower bandwidth (e.g. Price *et al.* 2019) being enhanced by their oil droplets (Vorobyev *et al.* 1998). Under relational colour constancy, the appearance of both patches may change as one moves between environments (i.e. the plumage itself could change colour and not remain constant), but the JND distance between the two patches will not. Relational colour constancy has been confirmed for the chicken (*Gallus gallus*) and other animals (Olsson *et al.* 2016, Olsson and Kelber 2017).

While we found no correlation of colour with irradiance across habitats, some comparative studies have identified weak correlates of colour with light gradients, notably darker habitats have a higher proportion of species with red-shifted hues (McNaught and Owens 2002, Gomez and Théry 2004, 2007). One explanation could be that blue-shifted colours appear brighter in the canopy than the understorey (Endler 1993). Alternatives include habitat differences that are not related to the light environment and effects of background. For example, Delhey *et al.* (2023) emphasize the importance of camouflage, and in an intraspecific study Simpson and McGraw (2018) found that red individuals were more often found in darker habitats, but suggested this was because red is associated with dominance which gives access to the preferred denser habitats, rather any direct effect of the light environment.

Camouflage may also play a role (Endler and Mappes 2017). In the genus *Phylloscopus* the upperparts of all species are greenish and similar. This coloration is generally thought to result in crypsis against leaves (Brooke 2010). All species have pale underparts and dark (melanized) upperparts; the achromatic distances between back and belly are strong and relatively similar across species (Fig. 5). The achromatic difference between back and belly has been attributed to counter-shading, whereby an individual becomes camouflaged by masking the shadows cast on its underparts (Thayer 1896). If back and belly coloration were driven by camouflage pressures, we would expect that both should be similarly variable across species. Instead, we find the belly plumage is exceptionally variable across species but the back much less so (Fig. 3). This suggests that belly coloration may be under different selection pressures than the rather invariable back plumage, such as use in intraspecific signalling, as inferred to be the case for finches (Cardoso and Mota 2022). Ventral plumage such as the belly has been shown to be more variable than dorsal plumage in other species (Friedman and Remeš 2024).

Habitats may vary along axes other than irradiance. Our study focused on the total light environment (irradiance) because *Phylloscopus* species are interacting at short range during the relevant signalling contexts and are assumed to be assessing patches against other parts of the plumage. However, the radiance, or colour of the background may influence the perception of plumage patches due to the contrast of the bird against the background (Gomez and Théry 2007). Empirically, the background has been shown to affect perception of colour contrast between patches despite the expectation of relational colour constancy (Lind 2016). Comparative work on *Anolis* lizards further demonstrates that the interacting effects of habitat light intensity and background influence the perception of colour signals, with detectability of red signals reduced in low light conditions (Fleishman *et al.* 2020, 2022). Features of the habitat may also affect the evolution of visual systems (sensory bias; Ryan and Keddy Hector 1992, Ryan and Cummings 2013). Sensory biases may also arise from attention to a specific feature; the preference for orange spots in male guppy (*Poecilia reticulata*) coloration has been related to sensory biases arising from a preference for a particular food source—orange fruit (Rodd *et al.* 2002). In our case, the buff-barred warbler, *P. pulcher*, has noticeably orange wing bars (extreme rightmost points in the PC plot in Fig. 2). *Phylloscopus pulcher* is a rhododendron specialist, and rhododendron has orange under-leaves. Birds foraging for insects resting on the underside of rhododendron leaves will be constantly evaluating prey against an orange background, which may create a sensory bias leading birds to prefer more orange coloration.

The different colour patches in *Phylloscopus* probably serve differing functions, shaped by their placement. A striking feature is that for those species with a tail patch, the patch is always white, whereas the other patches (for all species) are always yellowish, containing at least some carotenoid. The tail patches are concealed (Fig. 1) except during flight or display, and therefore act as conspicuous flashes when the tail is spread. Hence the tail is intimately tied to motion, which is likely to be detected achromatically, and white should be most conspicuous against a dark background. The presence of flash markings (patches on the plumage that can be concealed and exposed) has been correlated with flocking behaviour in shorebirds (Brooke 1998). Alternative hypotheses for the evolution of white tail patches (Randler 2016), such as their use in prey flushing (Mumme 2002), seem unlikely in these warblers. Ghosh-Harihar and Price (2014) found that the species with the highest frequency of flycatching (*P. whistleri*) only caught 8% of its prey in flight, and found no correlation of white patch with those species that were or were not observed flycatching. In contrast to the tail, the yellowish wing bar is constantly exposed on the greater covert feathers. Given the role of wing bar size in conspecific aggression in *Phylloscopus* (Marchetti, 1993) and the use of carotenoid coloration in aggression more generally (Kenyon and Martin 2022, 2023), we suggest that the wing bar colour functions in aggressive interactions. Thus, the colour of these two patch types may be driven by different selection pressures and should be considered as modular units. The extent to which, if any, they interact to stimulate a receiver during a composite visual display remains to be tested.

CONCLUSION

In terrestrial forested environments, variation in ambient spectral conditions experienced by a species appears to be larger than differences between habitats and is much less than differences along the aquatic depth gradient. While consistent differences along a vertical gradient (canopy to understorey) may create some fixed differences in perception and consequent evolution of colour (Endler 1993, Théry 2001, Gomez and Théry 2004), our results support the proposition that sensory drive, at least when restricted to influences of the ambient light environment, is much more strongly a phenomenon of the water (Cummings 2007, Cummings and Endler 2018).

SUPPLEMENTARY DATA

Supplementary data are available at *Biological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

The authors do not have any conflict of interest to declare.

DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided, which can be accessed online at: https://datadryad.org/stash/share/RcX7mJ9hI5bUFI9uQHXqG3UJd2jkjJ5Xb4fnd6JG4Qc

REFERENCES

Adams DC. Comparing evolutionary rates for different phenotypic traits on a phylogeny using likelihood. *Systematic Biology* 2013;**62**:181–92. https://doi.org/10.1093/sysbio/sys083

Alström P, Rheindt FE, Zhang R *et al.* Complete species-level phylogeny of the leaf warbler (Aves: Phylloscopidae) radiation. *Molecular Phylogenetics and Evolution* 2018;**126**:141–52. https://doi.org/10.1016/j.ympev.2018.03.031

Arak A, Enquist M. Hidden preferences and the evolution of signals. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 1993;**340**:207–13. https://doi.org/10.1098/rstb.1993.0059

Beco R, Silveira LF, Derryberry EP *et al.* Ecology and behavior predict an evolutionary trade-off between song complexity and elaborate plumages in antwrens (Aves, Thamnophilidae). *Evolution* 2021;**75**:2388–410. https://doi.org/10.1111/evo.14325

Bliard L, Paquet M, Robert A *et al.* Examining the link between relaxed predation and bird coloration on islands. *Biology Letters* 2020;**16**:20200002. https://doi.org/10.1098/rsbl.2020.0002

Boughman JW. Divergent sexual selection enhances reproductive isolation in sticklebacks. *Nature* 2001;**411**:944–8. https://doi.org/10.1038/35082064

Brooke M de L. Ecological factors influencing the occurrence of 'flash marks' in wading birds. *Functional Ecology* 1998;**12**:339–46. https://doi.org/10.1046/j.1365-2435.1998.00204.x

Brooke M de L. Unexplained recurrent features of the plumage of birds. *Ibis* 2010;**152**:845–7. https://doi.org/10.1111/j.1474-919x.2010.01055.x

Cardoso GC, Mota PG. Same colors for different functions: implications for the evolution of carotenoid-based ornamentation. *The American Naturalist* 2022;**200**:E237–47. https://doi.org/10.1086/721371

Carleton KL, Parry JWL, Bowmaker JK *et al.* Colour vision and speciation in Lake Victoria cichlids of the genus *Pundamilia*. *Molecular Ecology* 2005;**14**:4341–53. https://doi.org/10.1111/j.1365-294X.2005.02735.x

Cummings ME. Sensory trade-offs predict signal divergence in Surfperch. *Evolution* 2007;**61**:530–45. https://doi.org/10.1111/j.1558-5646.2007.00047.x

Cummings ME, Endler JA; Handling editor: Rebecca C. Fuller. 25 years of sensory drive: the evidence and its watery bias. *Current Zoology* 2018;**64**:471–84. https://doi.org/10.1093/cz/zoy043

Cummings ME, Partridge JC. Visual pigments and optical habitats of surfperch (Embiotocidae) in the California kelp forest. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 2001;**187**:875–89. https://doi.org/10.1007/s00359-001-0258-6

Cuthill IC, Sanghera NS, Penacchio O *et al*. Optimizing countershading camouflage. *Proceedings of the National Academy of Sciences of the United States of America* 2016;**113**:13093–7. https://doi.org/10.1073/pnas.1611589113

Dale J, Dey CJ, Delhey K *et al*. The effects of life history and sexual selection on male and female plumage colouration. *Nature* 2015;**527**:367–70. https://doi.org/10.1038/nature15509

Delhey K, Valcu M, Muck C *et al*. Evolutionary predictors of the specific colors of birds. *Proceedings of the National Academy of Sciences of the United States of America* 2023;**120**:e2217692120. https://doi.org/10.1073/pnas.2217692120

Dunn PO, Armenta JK, Whittingham LA. Natural and sexual selection act on different axes of variation in avian plumage color. *Science Advances* 2015;**1**:e1400155. https://doi.org/10.1126/sciadv.1400155

Endler JA. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Research* 1991;**31**:587–608. https://doi.org/10.1016/0042-6989(91)90109-i

Endler JA. Signals, signal conditions, and the direction of evolution. *The American Naturalist* 1992;**139**:S125–53. https://doi.org/10.1086/285308

Endler JA. The color of light in forests and its implications. *Ecological Monographs* 1993;**63**:1–27. https://doi.org/10.2307/2937121

Endler JA, Basolo AL. Sensory ecology, receiver biases and sexual selection. *Trends in Ecology & Evolution* 1998;**13**:415–20. https://doi.org/10.1016/s0169-5347(98)01471-2

Endler JA, Mappes J. The current and future state of animal coloration research. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 2017;**372**:20160352. https://doi.org/10.1098/rstb.2016.0352

Fleishman LJ, Wadman CS, Maximov KJ. The interacting effects of total light intensity and chromatic contrast on visual signal visibility in an *Anolis* lizard. *Animal Behaviour* 2020;**167**:263–73. https://doi.org/10.1016/j.anbehav.2020.07.008

Fleishman LJ, Perez-Martinez CA, Leal M. Can sensory drive explain the evolution of visual signal diversity in terrestrial species? a test with *Anolis* lizards. *The American Naturalist* 2022;**200**:236–49. https://doi.org/10.1086/720267

Foster DH. Color constancy. *Vision Research* 2011;**51**:674–700. https://doi.org/10.1016/j.visres.2010.09.006

Foster DH, Nascimento SM. Relational colour constancy from invariant cone-excitation ratios. *Proceedings Biological Sciences* 1994;**257**:115–21. https://doi.org/10.1098/rspb.1994.0103

Friedman NR, Remeš V. Dorsal and ventral plumage coloration evolve as distinct modules with different environmental correlations. *The American Naturalist* 2024;**203**:528–34. https://doi.org/10.1086/728766

Fuller RC. Lighting environment predicts the relative abundance of male colour morphs in bluefin killifish (*Lucania goodei*) populations. *Proceedings Biological Sciences* 2002;**269**:1457–65. https://doi.org/10.1098/rspb.2002.2042

Fuller RC, Carleton KL, Fadool JM *et al*. Genetic and environmental variation in the visual properties of bluefin killifish, *Lucania goodei*. *Journal of Evolutionary Biology* 2005;**18**:516–23. https://doi.org/10.1111/j.1420-9101.2005.00886.x

Ghosh-Harihar M, Price TD. A test for community saturation along the Himalayan bird diversity gradient, based on within-species geographical variation. *The Journal of Animal Ecology* 2014;**83**:628–38. https://doi.org/10.1111/1365-2656.12157

Gomez D, Théry M. Influence of ambient light on the evolution of colour signals: comparative analysis of a Neotropical rainforest bird community. *Ecology Letters* 2004;**7**:279–84. https://doi.org/10.1111/j.1461-0248.2004.00584.x

Gomez D, Théry M. Simultaneous crypsis and conspicuousness in color patterns: comparative analysis of a neotropical rainforest bird community. *The American Naturalist* 2007;**169**:S42–61. https://doi.org/10.1086/510138

Hart NS, Partridge JC, Cuthill IC *et al*. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (*Parus caeruleus*) and the blackbird (*Turdus merula*). *Journal of Comparative Physiology A* 2000;**186**:375–87. https://doi.org/10.1007/s003590050437

Helbach J, Frey J, Messier C *et al*. Light heterogeneity affects understory plant species richness in temperate forests supporting the heterogeneity–diversity hypothesis. *Ecology and Evolution* 2022;**12**:e8534. https://doi.org/10.1002/ece3.8534

Jones JA, Tisdale AC, Bakermans MH *et al*. Multiple plumage ornaments as signals of intrasexual communication in Golden-winged warblers. *Ethology* 2017;**123**:145–56. https://doi.org/10.1111/eth.12581

Kenyon HL, Martin PR. Aggressive signaling among competing species of birds. *PeerJ* 2022;**10**:e13431. https://doi.org/10.7717/peerj.13431

Kenyon HL, Martin PR. Color as an interspecific badge of status: a comparative test. *The American Naturalist* 2023;**202**:433–47. https://doi.org/10.1086/725916

Lande R. Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America* 1981;**78**:3721–5. https://doi.org/10.1073/pnas.78.6.3721

Ligon RA, Diaz CD, Morano JL *et al*. Evolution of correlated complexity in the radically different courtship signals of birds-of-paradise. *PLoS Biology* 2018;**16**:e2006962. https://doi.org/10.1371/journal.pbio.2006962

Lind O. Colour vision and background adaptation in a passerine bird, the zebra finch (*Taeniopygia guttata*). *Royal Society Open Science* 2016;**3**:160383. https://doi.org/10.1098/rsos.160383

Maan ME, Hofker KD, van Alphen JJM *et al*. Sensory drive in cichlid speciation. *The American Naturalist* 2006;**167**:947–54. https://doi.org/10.1086/503532

MacDougall AK, Montgomerie R. Assortative mating by carotenoid-based plumage colour: a quality indicator in American goldfinches, *Carduelis tristis*. *Naturwissenschaften* 2003;**90**:464–7. https://doi.org/10.1007/s00114-003-0459-7

Maia R, Eliason CM, Bitton PP *et al*. pavo: an R package for the analysis, visualization and organization of spectral data. *Methods in Ecology and Evolution* 2013;**4**:906–13. https://doi.org/10.1111/2041-210x.12069

Maia R, Gruson H, Endler JA *et al*. pavo 2: New tools for the spectral and spatial analysis of colour in R. *Methods in Ecology and Evolution* 2019;**10**:1097–107. https://doi.org/10.1111/2041-210x.13174

Maier EJ. Spectral sensitivities including the ultraviolet of the passeriform bird *Leiothrix lutea*. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 1992;**170**:709–14. https://doi.org/10.1007/BF00198981

Marchetti K. Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* 1993;**362**:149–52. https://doi.org/10.1038/362149a0

Marcondes RS, Brumfield RT. Fifty shades of brown: macroevolution of plumage brightness in the Furnariida, a large clade of drab Neotropical passerines. *Evolution* 2019;**73**:704–19. https://doi.org/10.1111/evo.13707

Mason NA, Riddell EA, Romero FG *et al*. Plumage balances camouflage and thermoregulation in Horned Larks (*Eremophila alpestris*). *The American Naturalist* 2023;**201**:E23–40. https://doi.org/10.1086/722560

Matsuo T, Martínez-Ramos M, Bongers F *et al*. Forest structure drives changes in light heterogeneity during tropical secondary forest succession. *Journal of Ecology* 2021;**109**:2871–84. https://doi.org/10.1111/1365-2745.13680

McCoy DE, Prum RO. Convergent evolution of super black plumage near bright color in 15 bird families. *The Journal of Experimental Biology* 2019;**222**:jeb208140. https://doi.org/10.1242/jeb.208140

McNaught MK, Owens IPF. Interspecific variation in plumage colour among birds: species recognition or light environment? *Journal of Evolutionary Biology* 2002;**15**:505–14. https://doi.org/10.1046/j.1420-9101.2002.00431.x

Mendelson TC, Martin MD, Flaxman SM. Mutation-order divergence by sexual selection: diversification of sexual signals in similar environments as a first step in speciation. *Ecology Letters* 2014;**17**:1053–66. https://doi.org/10.1111/ele.12313

Miles MC, Fuxjager MJ. Synergistic selection regimens drive the evolution of display complexity in birds of paradise. *The Journal of Animal Ecology* 2018;**87**:1149–59. https://doi.org/10.1111/1365-2656.12824

Moyen F, Gomez D, Doutrelant C *et al.* Interacting effects of signalling behaviour, ambient light and plumage colour in a temperate bird, the Blue Tit *Parus caeruleus*. *Revue d'Écologie (La Terre et La Vie)* 2006;**61**:367–82. https://doi.org/10.3406/revec.2006.1331

Mumme RL. Scare tactics in a neotropical warbler: white tail feathers enhance flush–pursuit foraging performance in the Slate-throated Redstart (*Myioborus miniatus*). *The Auk* 2002;**119**:1024–35. https://doi.org/10.1642/0004-8038(2002)119[1024:stianw]2.0.co;2

Olsson P, Kelber A. Relative colour cues improve colour constancy in birds. *Journal of Experimental Biology* 2017;**220**:1797–802. https://doi.org/10.1242/jeb.155424

Olsson P, Lind O, Kelber A. Bird colour vision: behavioural thresholds reveal receptor noise. *The Journal of Experimental Biology* 2015;**218**:184–93. https://doi.org/10.1242/jeb.111187

Olsson P, Wilby D, Kelber A. Quantitative studies of animal colour constancy: using the chicken as model. *Proceedings Biological Sciences* 2016;**283**:20160411. https://doi.org/10.1098/rspb.2016.0411

Olsson P, Lind O, Kelber A. Chromatic and achromatic vision: parameter choice and limitations for reliable model predictions. *Behavioral Ecology* 2018;**29**:273–82. https://doi.org/10.1093/beheco/arx133

Pitman EJG. A note on normal correlation. *Biometrika* 1939;**31**:9–12. https://doi.org/10.2307/2334971

Price T. Morphology and ecology of breeding warblers along an altitudinal gradient in Kashmir, India. *Journal of Animal Ecology* 1991;**60**:643–64. https://doi.org/10.2307/5303

Price TD. Sensory drive, color, and color vision. *The American Naturalist* 2017;**190**:157–70. https://doi.org/10.1086/692535

Price T, Pavelka M. Evolution of a colour pattern: history, development, and selection. *Journal of Evolutionary Biology* 1996;**9**:451–70. https://doi.org/10.1046/j.1420-9101.1996.9040451.x

Price T, Zee J, Jamdar K *et al.* Bird species diversity along the Himalaya: a comparison of Himachal Pradesh with Kashmir. *Journal of Bombay Natural History Society* 2003;**100**:394–410.

Price TD, Stoddard MC, Shevell SK *et al.* Understanding how neural responses contribute to the diversity of avian colour vision. *Animal Behaviour* 2019;**155**:297–305. https://doi.org/10.1016/j.anbehav.2019.05.009

Randler C. Tail movements in birds – current evidence and new concepts. *Ornithological Science* 2016;**15**:1–14. https://doi.org/10.2326/osj.15.1

R Core Team. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing, 2022. https://www.R-project.org/.

Revell LJ. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 2012;**3**:217–23. https://doi.org/10.1111/j.2041-210x.2011.00169.x

Rodd FH, Hughes KA, Grether GF *et al.* A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proceedings Biological Sciences* 2002;**269**:475–81. https://doi.org/10.1098/rspb.2001.1891

Rogalla S, Shawkey MD, D'Alba L. Thermal effects of plumage coloration. *Ibis* 2022;**164**:933–48. https://doi.org/10.1111/ibi.13100

Ryan MJ, Cummings ME. Perceptual biases and mate choice. *Annual Review of Ecology, Evolution, and Systematics* 2013;**44**:437–59. https://doi.org/10.1146/annurev-ecolsys-110512-135901

Ryan MJ, Keddy Hector A. Directional patterns of female mate choice and the role of sensory biases. *American Naturalist* 1992;**139**:S4–S35.

Schluter D, Price T. Honesty, perception and population divergence in sexually selected traits. *Proceedings Biological Sciences* 1993;**253**:117–22. https://doi.org/10.1098/rspb.1993.0089

Scordato ESC, Bontrager AL, Price TD. Cross-generational effects of climate change on expression of a sexually selected trait. *Current Biology: CB* 2012;**22**:78–82. https://doi.org/10.1016/j.cub.2011.11.044

Scott BF, Shultz AJ, Burns KJ. The impact of habitat and migration on plumage colour in Cardinalidae. *Biological Journal of the Linnean Society* 2024;**141**:264–77. https://doi.org/10.1093/biolinnean/blad066

Seddon N, Botero CA, Tobias JA *et al.* Sexual selection accelerates signal evolution during speciation in birds. *Proceedings of the Royal Society B: Biological Sciences* 2013;**280**:20131065. https://doi.org/10.1098/rspb.2013.1065

Seehausen O, Terai Y, Magalhaes IS *et al.* Speciation through sensory drive in cichlid fish. *Nature* 2008;**455**:620–6. https://doi.org/10.1038/nature07285

Shultz AJ, Burns KJ. Plumage evolution in relation to light environment in a novel clade of Neotropical tanagers. *Molecular Phylogenetics and Evolution* 2013;**66**:112–25. https://doi.org/10.1016/j.ympev.2012.09.011

Shultz AJ, Burns KJ. The role of sexual and natural selection in shaping patterns of sexual dichromatism in the largest family of songbirds (Aves: Thraupidae). *Evolution* 2017;**71**:1061–74. https://doi.org/10.1111/evo.13196

Simpson RK, McGraw KJ. Multiple signaling in a variable environment: expression of song and color traits as a function of ambient sound and light. *Biotropica* 2018;**50**:531–40. https://doi.org/10.1111/btp.12528

Thayer AH. The law which underlies protective coloration. *The Auk* 1896;**13**:124–9. https://doi.org/10.2307/4068693

Théry M. Forest light and its influence on habitat selection. In: Linsenmair KE, Davis AJ, Fiala B, Speight MR, eds. *Tropical Forest Canopies: Ecology and Management: Proceedings of ESF Conference, Oxford University, 12–16 December 1998*. Dordrecht: Springer Netherlands, 2001, 251–61.

Veen T, Brock C, Rennison D *et al.* Plasticity contributes to a fine-scale depth gradient in sticklebacks' visual system. *Molecular Ecology* 2017;**26**:4339–50. https://doi.org/10.1111/mec.14193

Vorobyev M, Osorio D. Receptor noise as a determinant of colour thresholds. *Proceedings Biological Sciences* 1998;**265**:351–8. https://doi.org/10.1098/rspb.1998.0302

Vorobyev M, Osorio D, Bennett AT *et al.* Tetrachromacy, oil droplets and bird plumage colours. *Journal of Comparative Physiology A: Sensory Neural and Behavioral Physiology* 1998;**183**:621–33. https://doi.org/10.1007/s003590050286

West-Eberhard MJ. Sexual selection, social competition, and speciation. *The Quarterly Review of Biology* 1983;**58**:155–83. https://doi.org/10.1086/413215