



Original Article

The effects of ecology and behavior on the evolution of coloration in Coraciiformes

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What drives the evolution of plumage color in birds? Bird color is likely to be under both natural and sexual selection where natural selection may favor evolution toward crypsis or camouflage whereas sexual selection may favor evolution toward conspicuousness. The responses to selection are predicted to relate to species' ecology, behavior, and life history. Key hypotheses have focused on habitat and light environment, breeding strategy, territoriality, and hunting behavior. We tested these potential causes of color variation in the Coraciiformes, a colorful clade of non-passerine birds, using phylogenetic comparative methods and data on chromatic and achromatic properties of plumage coloration measured from museum specimens. We found that correlates of color evolution in Coraciiformes vary across body regions and depend on the focal color property (chromatic or achromatic properties of plumage coloration). While the light environment showed widespread effects on coloration in multiple body regions for both color properties, selection pressures related to behavioral characteristics had more spatially localized effects (e.g. territoriality on achromatic properties of wing feathers and hunting strategy on chromatic properties of belly feathers). Our results reveal both general patterns that may hold across other bird clades and more nuanced effects of selection that are likely to be mediated through the visual ecology of the signaler and receiver and the behavioral characteristics of Coraciiform species.

Key words: behavior, color evolution, Coraciiformes, ecology, macroevolution.

INTRODUCTION

Birds are one of the most colorful groups of animals on the planet (Hill and McGraw 2006; Stoddard and Prum 2011; Cuthill et al. 2017). The range of avian vision and the avian color gamut spans the entire human-visible light spectrum and extends into the ultraviolet (UV) spectrum (Bennett and Cuthill 1994; Hunt et al. 1998). This variation in coloration has many functions in the life of birds, from attracting a mate (conspicuousness) to camouflage from predators (crypsis). Conspicuousness has been broadly attributed to sexual and social selection, while concealment (camouflage and crypsis) is often attributed to natural selection for predator avoidance or for successfully catching prey (Ruiz-Rodriguez et al. 2013; Troscianko et al. 2016). The evolution of bird plumage coloration is therefore multifaceted, with many environmental, ecological, behavioral, and life history traits potentially interacting to drive evolutionary divergence in color (Dale et al. 2015; Dunn et al. 2015). The detectability of a plumage patch (or body part) is the combination of chromatic [hue (the dominant wavelength of light) and saturation (the color intensity)] and achromatic (relative brightness)

properties of the signal itself, the visual system of the receiver, and the light environment in which the signal is transmitted (Endler 1992; Bennett and Cuthill 1994; Stoddard and Prum 2008, 2011; Cuthill et al. 2017). Variation in selection pressures may lead to different responses in chromatic and achromatic color properties, particularly across different parts of the birds body (e.g. McNaught and Owens 2002; Gomez and Théry 2004; Andersson and Prager 2006).

How and why each of these components evolve has been tackled previously, but our understanding of how they evolve in response to different selection pressures on different body parts remains unresolved (McNaught and Owens 2002; Gomez and Théry 2004; Shultz and Burns 2013; Dunn et al. 2015; Maia et al. 2016; Marcondes and Brumfield 2019; Delhey 2020). Various ecological, behavioral, and life history traits have been proposed to influence color evolution (Dale et al. 2015; Dunn et al. 2015). First, relative conspicuousness or crypsis may be contingent on the light environment (the light environment hypothesis; Endler 1992, 1993; Marchetti 1993; Endler and Thery 1996; Espmark et al. 2000). Under this hypothesis, signal detectability is affected by aspects of the signaling environment, such as light intensity, canopy thickness, time of day, and the amount of cloud cover in the sky (Endler

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1993). Second, several studies argue that body size can restrict color evolution (Endler 1992; Hagman and Forsman 2003; Galván et al. 2013; Igic et al. 2018; Winebarger et al. 2018; Cooney et al. 2022). The sensory and ecological constraints hypothesis predicts that body size determines detectability of the animal in the habitat and mediates its predation risk. Specifically, being large is expected to reduce predation risk and therefore facilitate increased signal intensity, whereas being small is expected to increase predation risk and therefore constrain signaling capacity (regardless of its chromatic variance) (Hagman and Forsman 2003; Dale et al. 2015; Hossie et al. 2015). Second, hunting strategy is predicted to influence color evolution. For example, if hunting success is increased with more cryptic coloration that reduces detectability by prey (Götmark 1987; Bretagnolle 1993; Tate et al. 2016). Third, the establishment or maintenance of a territory has been suggested to affect color evolution and its distribution on the body (Røskoft and Rohwer 1987). Among other behavioral traits, presence or absence of cooperative breeding could mediate intersexual and intrasexual contact leading to the evolution of conspicuous coloration in both males and females for signaling purposes (Rubenstein and Lovette 2009).

The opposing effects of selection for crypsis or conspicuousness on coloration may also be reflected in color variation across the birds' body (Doucet et al. 2007; Gomez and Théry 2007; Shultz and Burns 2017; Marcondes and Brumfield 2019). Because of variation in the extent to which body regions are exposed to predators, prey, or conspecific competitors, different body parts are likely to

experience different levels of selection for crypsis relative to conspicuity. For example, countershading is a common way for animals to achieve concealment within the environment that involves gradual shading of the entire body from darker to lighter across dorsal to ventral body parts (Edmunds and Dewhurst 1994; Rowland et al. 2007; Allen et al. 2012). In contrast, front-facing body regions that can be directed at the potential signal receiver are commonly used in intraspecific communication (Andersson and Amundsen 1997; Keyser and Hill 2000; Stein and Uy 2006; Pryke and Griffith 2007). Overall, ventral body parts are thought to be under stronger selection for conspicuity than dorsal body parts which are easily seen by predators, while ventral body parts are often concealed from the predators view, making evolution of their coloration less constrained, at least in birds (Shultz and Burns 2017; Marcondes and Brumfield 2019). Together, this suggests that understanding the evolution of avian coloration requires consideration of effects of its proximate drivers on each body part separately.

To explore key factors influencing the evolution of plumage coloration, we focused on the non-passerine order Coraciiformes (bee-eaters, ground rollers, rollers, todies, motmots, and kingfishers). Coraciiform species (Figure 1) have diverse plumage coloration including pigmentary and structural colors, live in a range of different environments, show variable levels of territoriality, variability in the presence or absence of cooperative breeding (but with near uniform social monogamy), and different types of hunting strategy (Fry et al. 1992; Stavenga et al. 2011;



Figure 1

A collage showing some of the plumage color diversity in the Coraciiformes. (a) Forest kingfisher (*Todiramphus macleayii*), Alcedinidae; (b) Common kingfisher (*Alcedo atthis*), Alcedinidae; (c) White-fronted bee-eater (*Merops bullockoides*), Meropidae; (d) Red-bearded bee-eater (*Nyctyornis amictus*), Meropidae; (e) European roller (*Coracias garrulus*), Coraciidae; (f) Lilac-breasted roller (*Coracias caudatus*), Coraciidae; (g) Broad-billed today (*Todus subulatus*), Todidae; (h) Narrow-billed today (*Todus angustirostris*), Todidae. All photos © Daniel J. Field, University of Cambridge. Used with permission.

Eliason et al. 2019). This diversity makes them an ideal study system for addressing the significance of life history traits on the evolution of coloration, as well as disentangling the interaction between light environment and plumage color and how it affects conspicuousness and concealment. We measured plumage coloration from digital images of museum specimens and quantified several proxies for factors that could play a key role in the evolution of coloration including sex, body size, hunting strategy, habitat light environment, territoriality, and social mating system. This information allows us to 1) disentangle different possible biotic and abiotic factors affecting the evolution of Coraciiform coloration, and 2) test how chromatic and achromatic properties of plumage coloration have evolved in response to these variables and whether they have evolved for the same or different purposes.

MATERIALS AND METHODS

Specimen selection

To collect data on plumage coloration, we used study skins of 135 species of Coraciiformes (families Meropidae, Brachypteraciidae, Coraciidae, Todidae, Momotidae, Alcedinidae) from the bird collections of the Natural History Museum at Tring, UK. We aimed to sample three male and three female study skins per species. For most patches, we had 135 species sampled, except for tail (134) and tail underside (122) due to these patches being obscured in some specimens (Supplement 1: Table S1). The number of species in subsequent analysis depends on the availability of museum specimens and data from the literature on predictor variables traits. We included a total of 117 species for males for every patch other than tail (116 species) and tail underside (113 species), and 114 species for females for every patch but tail underside (110). Across all analysis this ranges from ~75% to ~80% of the entire order when compared with the 146 species in the phylogeny of Jetz et al. (2012) (Supplement 1: Table S1).

Plumage color

Calibrated digital images of study skins were taken using methods described in Cooney et al. (2019) and were used to quantify both chromatic (hue and saturation) and achromatic (brightness) components of color. Briefly, a Nikon D7000 digital single-lens reflex camera with two filters (permitting human visible and UV wavelengths) was used for imaging of study skins and each bird specimen was photographed six times: from three different angles (dorsal, lateral, and ventral) and with each filter. For full details regarding the technical specificity of camera, lens filters, and illumination, see Cooney et al. (2019).

Digital images were then linearized and converted to TIFF files using DCRAW (Coffin 2016). Each linearized photo was normalized by comparison of pixel values of five gray standards with known reflectance, as suggested by Troscianko and Stevens (2015). On each image, a series of polygons were drawn in IMAGEJ (Rueden et al. 2017) using custom scripts to demarcate 11 body regions for color measurement. The selected body regions were: crown, nape, mantle, rump, tail, wing coverts, wing primaries and secondaries, throat, breast, belly, and tail underside. By measuring the color of these 11 regions, thorough coverage of whole-plumage color variability was achieved (Maia et al. 2016). For each of these polygons, RGB values were extracted for both the human visible and UV range.

To convert mean RGB values to avian color space values we used a method developed by Troscianko and Stevens (2015) to generate

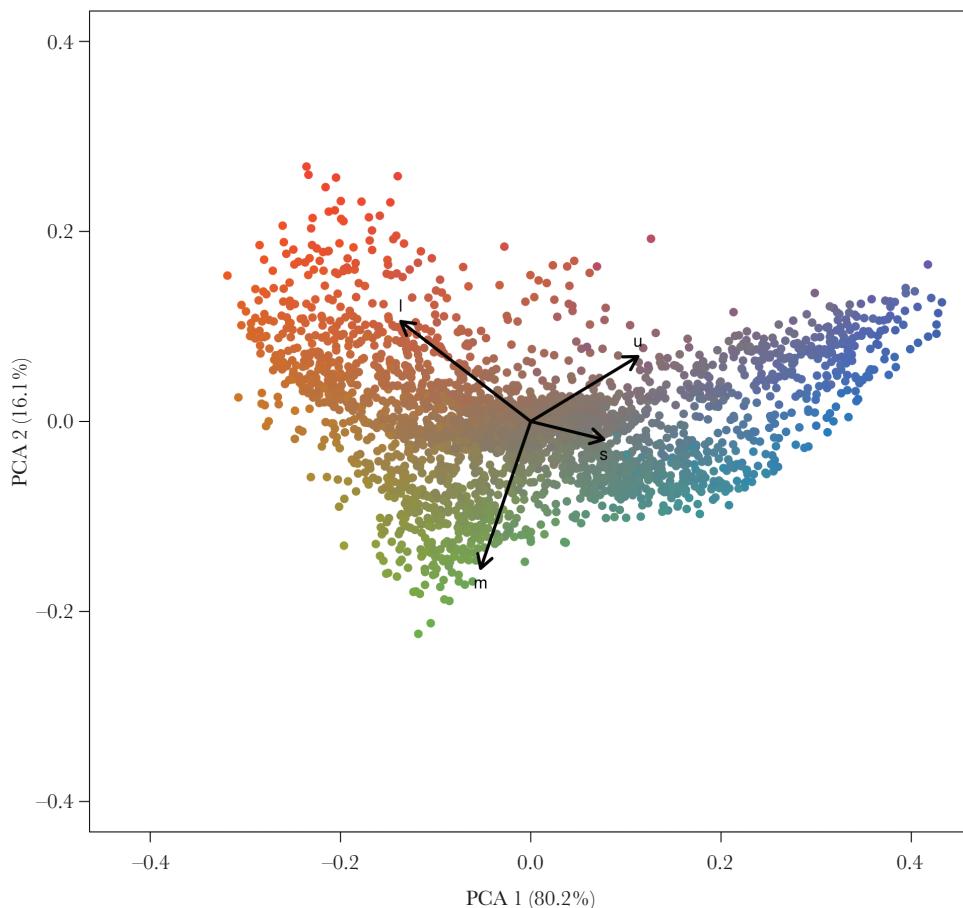
mapping functions that convert RGB color values into cone-catch values adjusted to avian color vision (see Cooney et al. 2019 for full details). We based our analysis on UVS avian visual system since genomic sequencing of the UV/violet SWS1 cone opsin gene indicated presence of amino acid residues signifying UV sensitivity in Coraciiformes (Ödeen and Håstad 2013). Mapping functions were used to convert RGB values for each patch on each specimen into raw cone-catch values. We then calculated average patch values (separately for each sex) as a species-level measure for each body patch. These values were then projected into avian tetrahedral color space, using methods from Stoddard and Prum (2008) implemented in the R package pavo (Maia et al. 2019). This method generated relative cone stimulation values (ultraviolet cone—u, short-wavelength cone—s, medium-wavelength cone—m, long-wavelength cone—l) that were used in subsequent analyses.

In addition to chromatic variation, we also quantified achromatic color variation as the stimulation values of double cones, with higher values indicating a brighter patch (Maia et al. 2016). The full dataset is provided in Supplement 1: Table S2.

Predictor variables

We compiled data on sex, light environment, body size, territoriality, hunting strategy, and cooperative breeding (Supplement 1: Table S3).

- (i) Sex of each specimen was recorded from specimen labels during the collection of calibrated digital images.
- (ii) Body size data were taken from the EltonTraits database (Wilman et al. 2014).
- (iii) We quantified light environment using habitat preference as a proxy. Data on habitat preferences were collected from Fry et al. (1992). First, we assigned each species to one of three habitat types: forest, woodland, and open. Categories represent major light environment types that differ according to the dominant canopy geometry (Endler 1992, Figure 3). The “forest shade” light environment occurs when the light is filtered through the thick forest canopy, and this can be further divided into canopy and understorey light conditions. These two differ in the distance from the tree top and thus the resulting filtered wavelengths. The tree canopy is rich in blue and UV light (peak wavelength ~470 nm) while the understorey is predominately rich in green light (peak wavelength ~550 nm), generating a light gradient from the canopy to the ground (Endler 1993). The forest shade category includes forest understorey, dense undergrowth and shrubby habitats, but excludes the tree canopy which we instead class as “woodland shade.” “Woodland shade” is dominated by bluish or blue-gray light with peak wavelength ~470 nm and is similar to light conditions in tree canopies (see above). These conditions are produced when light coming from the sky is filtered through a discontinuous canopy with large gaps. The “woodland shade” light environment has a spatially uniform distribution of bluish light and is found in habitats including woodlands, sparsely aggregated shrubs and, as mentioned, upper forest canopy and forest edge habitats. Finally, “open” light environments lack any canopy coverage and refer to light conditions found in habitats including riversides, open plains, and grasslands. In “open” light environments, all wavelengths come directly from the sky without filtration through the canopy, and light intensity is more evenly distributed all wavelengths, albeit with a distinct peak in blue part of the spectrum (below ~470 nm) (Théry

**Figure 2**

Principal components (PC) of cone-catch values (u , s , m , and l) for all body patches across all species. Each point in the plot represents one of 11 body patches for one species, with point color providing an indication of patch color in the visible spectrum. PC1 explains 80.2% of the variation of color scores. Higher PC1 value indicates a tendency toward blue and UV color, while lower PC1 scores indicate a tendency toward red and green color. PC2 explains 16.1% of variation in color. Higher PC2 values are ascribed to red hues, while lower PC2 scores are indicative of green and blue hues.

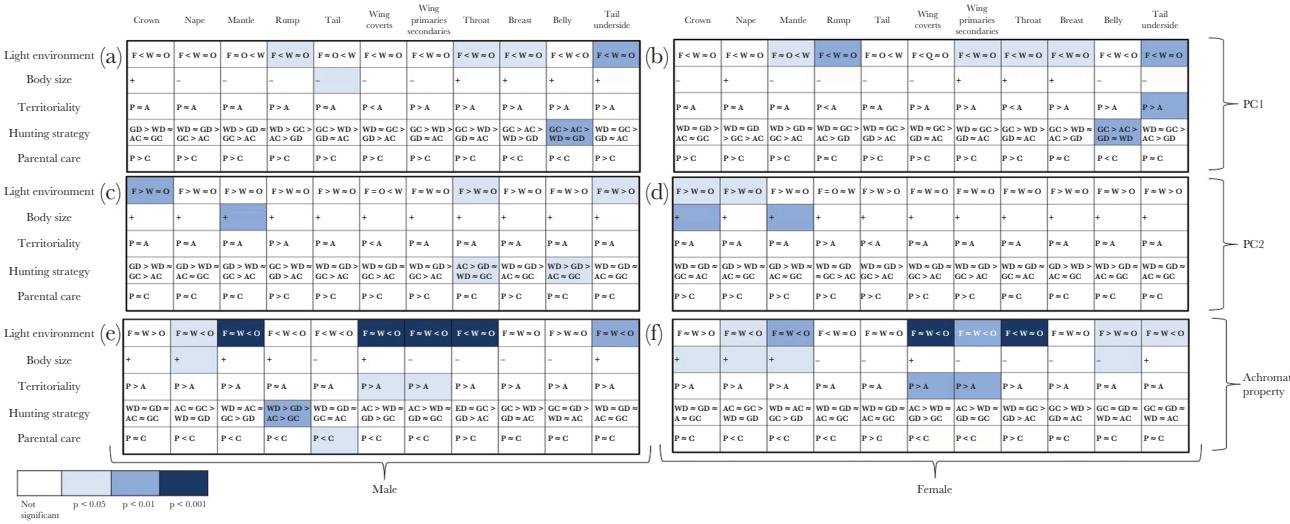
2006). Species were assigned to a single light environment category based on their habitat preferences, with forest-dwelling species divided into either “forest shade” or “woodland shade” category depending on whether birds predominantly live in the understorey or upper levels of the forest, respectively (Endler 1992, 1993; Marchetti 1993; Gomez and Théry 2004).

(iv) Data on hunting strategies were collected from the *Birds of the World* and a monogram on Coraciiformes (Fry et al. 1992; Billerman et al. 2022). We assigned each species in our dataset to one of the following hunting strategies: aerial catcher, ground dweller, ground catcher, and water diver. The hunting strategy provides a proxy for which body part is most exposed to potential prey during hunting. For example, fish catching-behavior that involves underwater diving, has been shown to be related to the evolution of belly coloration in seabirds (Götmark 1987; Bretagnolle 1993). We assigned species to one the following hunting strategies: water diver (which submerge under the water), ground dweller (digging in the soil for worms, following ant trails, lifting leaves for insects), aerial catcher (perching on a branch and flying above and ahead to catch prey in the air), and ground catchers (species that perch on a tree and fly down to the ground to catch food low in the understorey or on the ground).

- (v) Territoriality was assigned for each species using descriptions in Fry et al. (1992). Territoriality was coded as the presence or absence of both intra- and/or interspecific aggressive behaviors. For example, *Tanysiptera danae*, the Brown-headed Paradise Kingfisher, shows intraspecific territoriality (strongly territorial, three or four birds chasing each other from branch to branch), whereas *Dacelo gaudichaud*, the Rufous-bellied Kingfisher shows both intra- and interspecific territoriality (they are strongly territorial, chasing their own species and being aggressive towards some others).
- (vi) Cooperative breeding was coded for each species in our dataset based on a larger dataset of the modes of parental care of birds (Cockburn 2006). We coded for the presence and absence of pair breeding and cooperative breeding. Each species was assigned to one of these two categories.

Analysis

Relative cone-catch values (u , s , m , and l) represent the relative stimulation of four avian color cones and together describe avian tetrahedral colourspace, a sensory equivalent of morphospace where the distance between two colors is comparable to their similarity (Stoddard and Prum 2008). We estimated both

**Figure 3**

Multipredictor model results summary. Panels a and b represent results for PC1, panels c and d represent results for PC2 and panels e and f represent results for brightness. Panels on left-hand side represent results for males and panels on right-hand side represent results for females. Predictor variables are represented as rows with their names indicated further left. Body patches are represented as a column with each one represented on top of the column. White squares are non-significant results, light blue squares represent $P < 0.05$ level of significance, darker blue represent $P < 0.01$ level of significance and dark blue represent $P < 0.001$ level of significance. Within each box, the effect of each variable is indicated. The plus and minus sign for body size (continuous variable) indicate the direction of the effect. For categorical variables, the letters represent abbreviations of categories of each variable with the approximate relations indicated between them (light environment: F—forest, W—woodland, O—open; hunting strategy: GD—ground dwelling, WD—water diving, GC—ground catching, AC—aerial catching; territoriality: A—absent, P—present; parental care: P—pair, C—cooperative).

chromatic properties of color (hue and saturation) via cone-catch values and reduced the dimensionality of the colourspace using Principal Component Analysis (PCA; Jolliffe 2002) applied to the entire database, covering color values for all measured color patches. Our measurement of color does not allow us to separate hue and saturation. Instead, the principal components that we use (PC1 and PC2) capture both elements of chromatic variation.

To assess sex differences in coloration, we compared color variables between sexes using phylogenetic reduced major axis regression (phyloRMA) as implemented in the function phyl.RMA (“lambda” method) in the phytools R-package (Revell 2012), with values for males as x -variable and values for females as y -variable.

To test hypotheses regarding the predictors of color variation we used Phylogenetic Generalized Least Squares (PGLS) regression (Grafen and Hamilton 1989) as implemented in the R package caper (Orme et al. 2013). Using multipredictor models, we tested the influence of the predictor variables (light environment, body size, hunting strategy, territoriality, and parental care) separately for PC1, PC2, and achromatic variation and for each body patch. We analyzed data for each sex separately. To provide a phylogenetic framework for our analyses, we used molecular phylogenies for Coraciiformes available from birdtree.org (Jetz et al. 2012). We downloaded 1000 random trees and extracted the maximum clade credibility tree in R using maxCladeCred function from phangorn package (Schliep 2011).

Finally, we tested for the predictability of color between different patches and sexes with Bayesian phylogenetic mixed models in the R package MCMCglmm (Hadfield 2010). We ran models with PC1, PC2, and the achromatic property of plumage color as dependent variables with sex, patch and their interaction as predictors. We used a flat prior and ran for each model for 220 000

iterations, sampled every 20 iterations with the first 20 000 iterations taken as a burnin and removed.

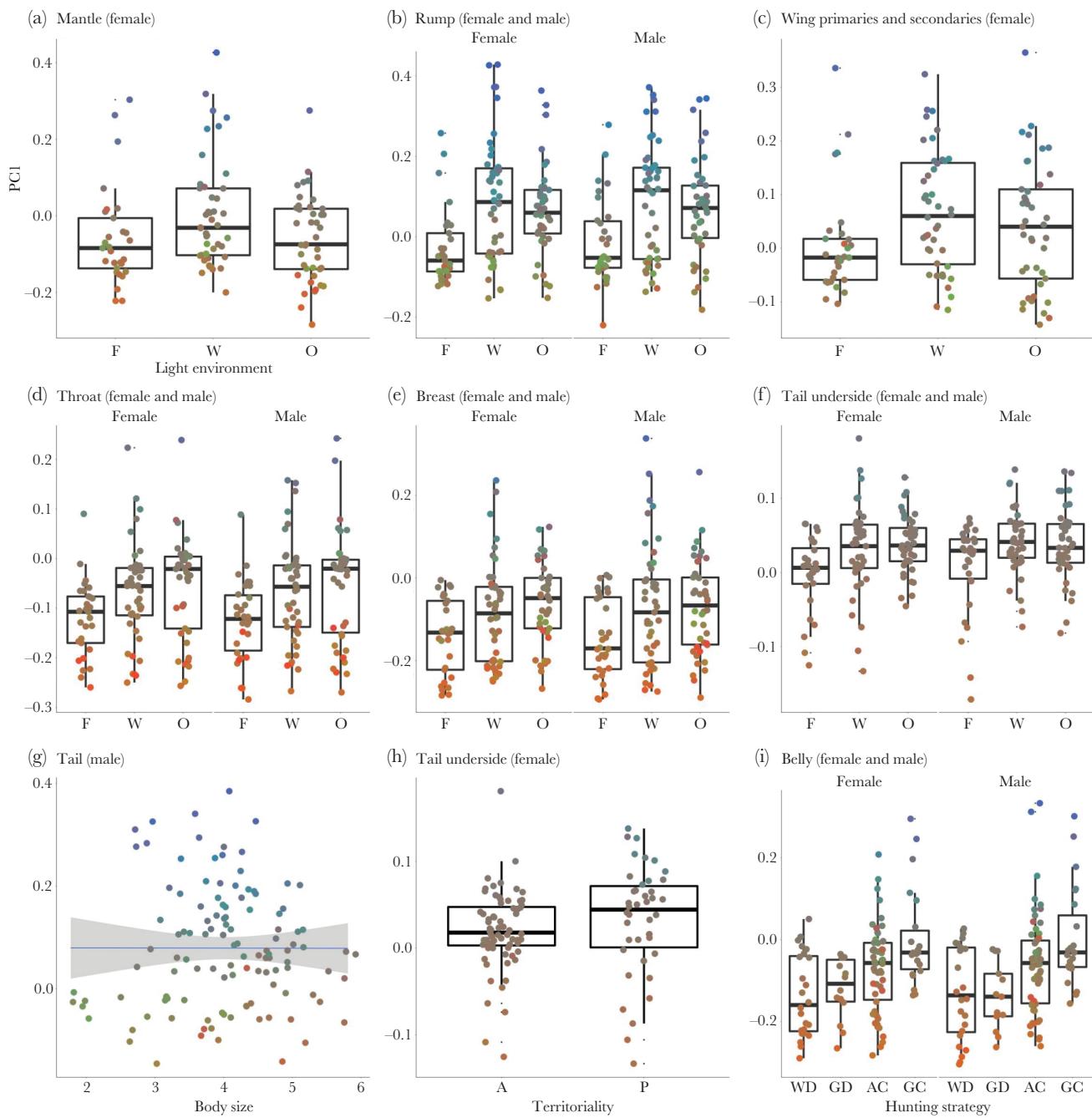
RESULTS

Coraciiform color space

The first two principal components explained 96.27% of the variance in raw cone-catch values (u , s , m , and l) (PC1 80.21% and PC2 16.07%) and were used in further analysis to describe chromatic variation (Supplement 1: Table S2). Lower values on PC1 indicated greater stimulation of m and l cones (green and red coloration), while higher values of PC1 indicated greater stimulation of s and u cones (blue and UV coloration). Lower PC2 values indicated stimulation of the m cone (green coloration) while higher PC2 values indicated simulation of the l cone (red coloration) (Figure 2). The relationship between raw cone-catch values and PC scores is shown in Supplement 2: Figures S10–S12.

Sex

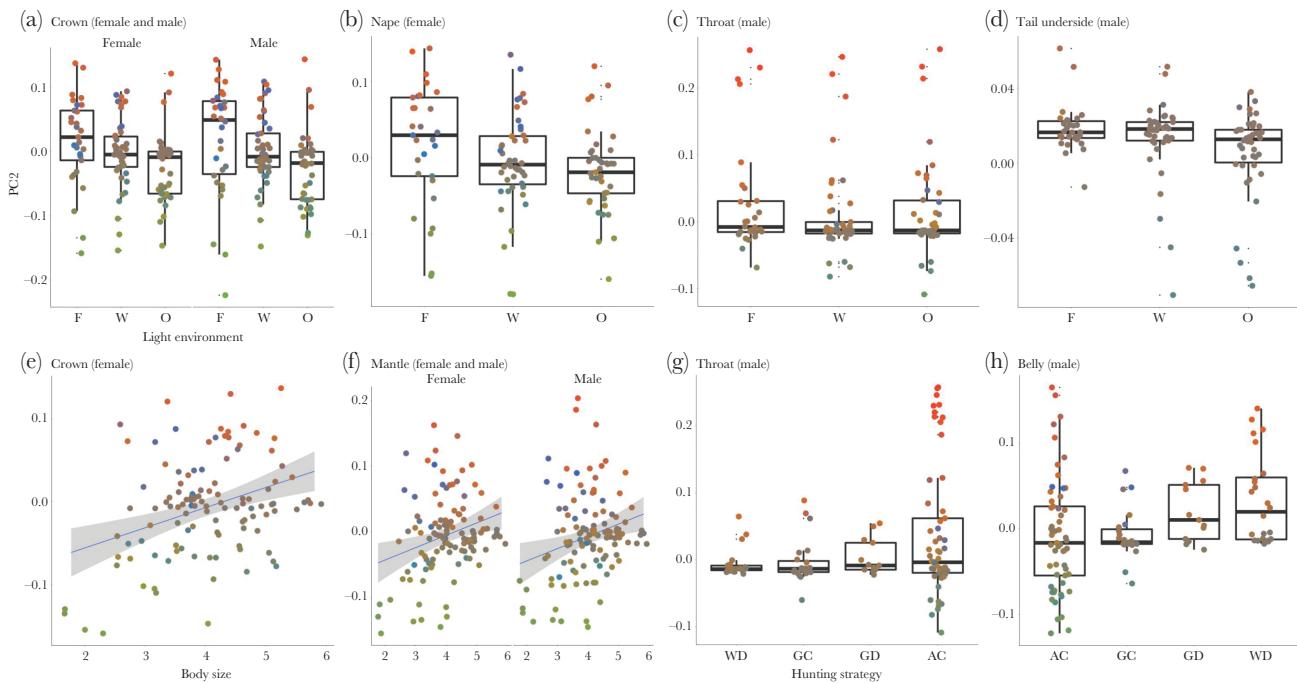
Color variation (PC1, PC2, and achromatic) between the sexes was analyzed with phyloRMA regression (Supplement 1: Table S4), with slopes and intercepts that differ significantly from one and zero, respectively, indicating differences in coloration between the sexes (plots shown in Supplement 2: Figures S7–S9). In total, significant differences in plumage coloration between the sexes were detected in four body patches for achromatic variation, one body patch for PC1, and seven body patches for PC2. Regression of female against male PC1 values showed slopes significantly different from one for crown (Supplement 1: Table S4.1). For crown, slope values of <1 suggest that male plumage has more blue-UV reflectance than female plumage but that this difference decreases as PC1 values increases. Analysis of the relationship between

**Figure 4**

Predictors of PC1. Only body patches for which at least one independent variable indicated significant result are shown. Within each panel, each point represents a species, and the color of each point represents the approximate reflectance of that body patch in visible spectrum. In the title of each panel, a patch and for which sex a significance has been detected is indicated. Panels a–f represent variation in PC1 across different light environment categories. (x axis on each panel for light environment variable has abbreviations for light environment categories that represent following: F—forest, W—woodland, and O—open.) Panel g shows the relationship between PC1 and body size. Panel h shows the relationship between PC1 and territoriality. (x axis on each panel for territoriality variable has abbreviations for territoriality categories that represent following: A—absent, and P—present.) Panel i shows the relationship between PC1 and hunting strategy. (x axis on each panel for hunting strategy variable has abbreviations for hunting strategy categories that represent following: GD—ground dweller, WD—water diver, AC—aerial catcher, and GC—ground catcher.)

male and female PC2 values revealed significant between-sex variation for crown, nape, wing coverts, wing primaries and secondaries, throat, breast, and belly (Supplement 1: Table S4.12–S4.13, S4.17–S4.21). Slope values significantly <1 and negative intercepts for crown, nape, wing coverts, and belly indicated that males are

generally redder in these patches than females, but that the difference reduces as PC2 values increase. A slope value significantly <1 and a positive intercept for wing primaries and secondaries and throat indicated that males become redder than females as PC2 value increases. Comparison of achromatic variation between the

**Figure 5**

Predictors of PC2. Only body patches for which at least one independent variable indicated significant result are shown. Within each panel, each point represents a species, and the color of each point represents the approximate reflectance of that body patch in visible spectrum. In the title of each panel, a patch and for which sex a significance has been detected is indicated. Panels a–d represent variation of PC2 values across different light environment categories. (x axis on each panel for light environment variable has abbreviations for light environment categories that represent following: F—forest, W—woodland, and O—open.) Panels e and f show relation of PC2 with body size. Panels g and h represent association of PC2 values with different hunting strategies. (x axis on each panel for hunting strategy variable has abbreviations for hunting strategy categories that represent following: GD—ground dweller, WD—water diver, AC—aerial catcher, and GC—ground catcher.)

sexes revealed a slope significantly <1 and a positive intercept in wing coverts, wing primaries and secondaries, and tail. For these patches, this suggests that as species become brighter, males tend to be relatively more bright than females (Supplement 1: Table S4.27–S4.29). For the nape patch, however, a slope <1 and a negative intercept indicate that males tend to be brighter than females, but that this difference reduces as achromatic intensity increases (Supplement 1: Table S4.24). Overall, this suggests that there are significant differences between the sexes in color variation for some body patches.

Multipredictor model results summary

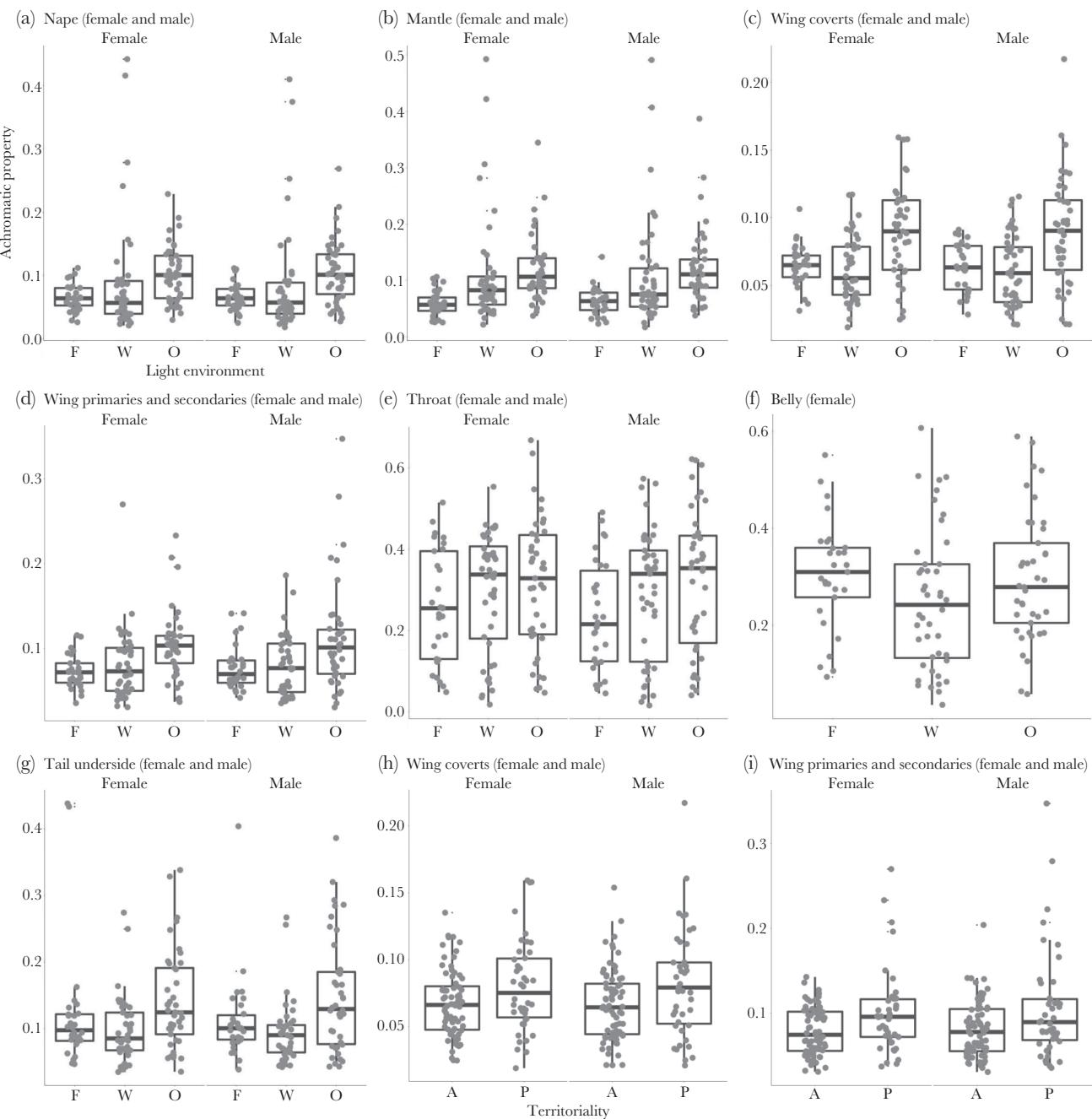
We present an overview of our results here and in Figure 3, followed by key results in relation to each predictor variable in turn below and in Figures 4–7. We report full details (P values, parameter estimates and R^2 values) in Supplement 1: Table S5 and Supplement 2: Figures S1–S6.

In total, light environment showed a significant association with color variables in 10 body patches for PC1 (4 in males and 6 in females) (Figure 3a,b), 5 body patches for PC2 (3 in males and 2 in females) (Figure 3c,d), and 13 body patches for achromatic property (6 in males and 7 in females) (Figure 3e,f). In nine instances, color variables were correlated with body size, including one patch for PC1, three patches with PC2 (one in males and two in females) (Figure 3a,c–d) and five patches with achromatic property (one in males and four in females) (Figure 3e,f). Territoriality correlated with PC1 in one body patch (only in females) (Figure 3b) and with

achromatic variation in four body patches (two in males and two in females) (Figure 3e,f). Hunting strategy had a significant effect in two body patches with PC1 (one in males and two in females) (Figure 3a,b), two patches with PC2 (both in males) (Figure 3c), and one patch with achromatic variation (only in males) (Figure 3e). Cooperative breeding is associated with achromatic variation in one body patch (in males) only (Figure 3e). Explanatory power (R^2) for PC1 analysis in males is ranging from 0.013 (mantle) to 0.1 (belly), in females from 0.004 (wing coverts) to 0.108 (tail underside). R^2 for PC2 analysis in males is ranging from −0.032 (wing primaries/secondaries) to 0.094 (throat) and in females from −0.023 (wing primaries/secondaries) to 0.082 (crown). R^2 for achromatic property analysis in males is ranging from 0.002 (breast) to 0.258 (wing coverts) and in females from 0.002 (breast) to 0.223 (wing coverts). Overall, R^2 was greater for models describing achromatic variation in color across species than for either principal component (PC1 and PC2) describing chromatic variation (Supplement 1: Table S5).

Light environment

We found lower values on PC1 among forest species and higher PC1 values for woodland and open environment species for several patches, namely the mantle and wing primaries/secondaries in females, and the rump, throat, breast, and tail underside in both females and males. This suggests a tendency toward reds and greens in forest light environments and UV-blues in open and woodland shade light environments (Figure 4a–f).

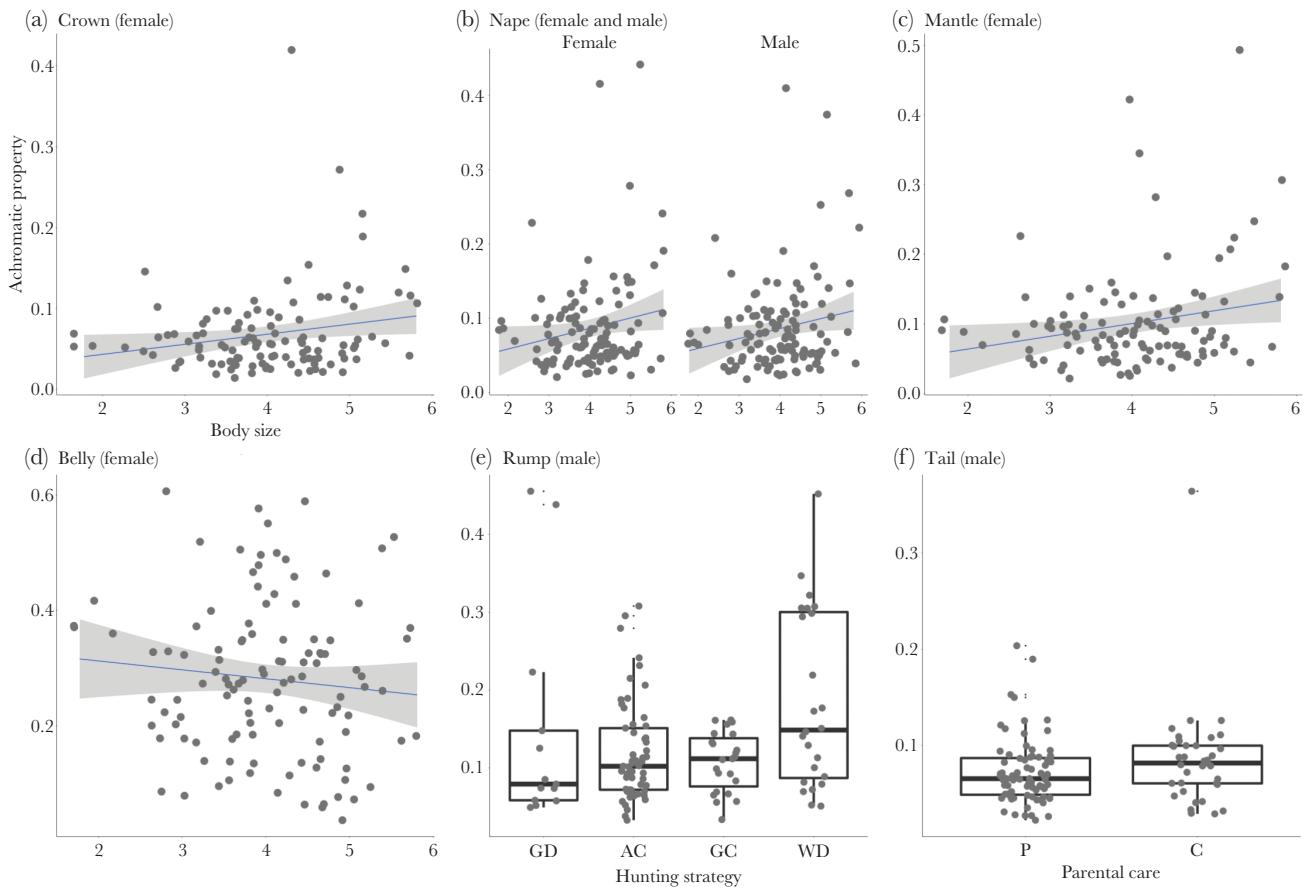
**Figure 6**

Light environment and territoriality as predictors of achromatic property. Only body patches for which at least one independent variable indicated significant result are shown. Within each panel, each point represents a species. In the title of each panel, a patch and for sex a significance has been detected is indicated. Panels a-g represent variation in brightness across different light environment categories. (x axis on each panel for light environment variable has abbreviations for light environment categories that represent following: F—forest, W—woodland, and O—open.) Panels h and i show relationship between brightness and territoriality. (x axis on each panel for territoriality variable has abbreviations for territoriality categories that represent following: A—absent, and P—present.)

We found that the crown (males and females), nape (females), and throat (males) have higher PC2 scores for forest species, while open and woodland shade species show lower and comparable values indicating a tendency toward reddish plumage color in forest species and greens and UV-blues in woodland and open environment species. For PC2 tail underside scores, forest and woodland

environment species have higher and similar values when compared with open species (Figure 5a-d).

Values for achromatic (brightness) variation are higher in open light environments (for both males and females) for the nape, mantle, wing coverts, wing primaries/secondaries and tail underside (Figure 6a-d, g). For male and female throat patches, species

**Figure 7**

Body size, hunting strategy, and parental care as predictors of achromatic property. Only body patches for which at least one independent variable indicated significant result are shown. Within each panel, each point represents a species. In the title of each panel, a patch and for which sex a significance has been detected is indicated. Panels a–d show relation of brightness with body size. Panel e shows relationship between brightness and hunting strategy. (x axis on each panel for hunting strategy variable has abbreviations for hunting strategy categories that represent following: GD—ground dweller, AC—aerial catcher, GC—ground catcher and WD—water diver.) Panel i shows relationship between brightness and parental care. (x axis on each panel for parental care variable has abbreviations for parental care categories that represent following: C—cooperative breeding, and P—pair breeding.)

living in forest light environments have lower average achromatic scores compared with woodland and open light environment species (Figure 6e), while for female belly patches, species living in forest light environments have higher average achromatic scores (Figure 6f).

Body size

For PC1, tail of larger bodied males is weakly associated with the blue part of the color spectrum (Figure 4g). Larger bodied species are also associated with higher PC2 values for the crown (females) and mantle (males and females) indicating a shift toward the red part of the color spectrum (Figure 5e,f). We also found that larger size was correlated with brighter plumage for the crown and mantle in females, and nape in both males and females (Figure 7a–c). For the belly patch (in females), larger body size is associated with reduced achromatic values (Figure 7d).

Territoriality

Territorial species have higher PC1 values for tail underside in females, indicating a tendency toward increased UV-blue coloration compared with non-territorial species (Figure 4h). Territorial

species also have higher achromatic values on wing coverts and wing primaries/secondaries in both males and females when compared with non-territorial species (Figure 6h,i).

Hunting strategy

We found significant associations between PC1 values and hunting strategy for the belly in both males and females (Figure 4i). For the belly patch, ground dwelling and water diving species have the lowest (and similar) values, aerial catching species have higher values and ground catching species have the highest values. This reflects ground dwelling and water diving species having a tendency toward duller brownish plumage, aerial catching species a tendency toward UV-blues, while ground catching species tending toward green coloration.

For the belly patch (only in males) mean values on PC2 across hunting strategies are lowest and similar for aerial catching species and ground catching species, and increases for ground dwelling species, and have the highest mean values among water diving species (Figure 5h). This indicates a tendency toward green for aerial and ground catching species, while ground dwelling and water diving species tend more toward brown and duller colors in general. For

the throat patch (only in males), we found opposing trend than for the belly patch with aerial catching species having the highest values and ground dwelling, ground catching and water diving species having lower values for PC2 (Figure 5g).

Males of water diving species have the highest average achromatic values for rumps, followed by ground catching species and aerial catching species, while ground dwelling species have the lowest mean values (Figure 7e).

Cooperative breeding

In cooperative breeders, males have higher average achromatic values for tails than pair breeding species (Figure 7f). The same effect was not detected for females, where both cooperative breeders and pair breeders exhibit no difference in achromatic values in the tail.

Bayesian phylogenetic mixed models

Analyses with MCMCglmm confirm that color varies greatly among patches but not, on average, between the sexes (Supplement 1: Table S6 and Supplement 2: Figure S13).

DISCUSSION

Our results show that among multiple ecological and behavioral indices, light environment is the dominant correlate of plumage color in the order Coraciiformes. Importantly, however, there is nuanced variation dependent on the specific property of color variation (chromatic or achromatic) and the location of the color on the bird's body. In particular, we found consistent effects of light environment on both chromatic and achromatic properties of plumage color across multiple body regions. Other variables capturing variation in Coraciiform life history indicated more idiosyncratic effects on coloration and only for subsets of body patches. We also find some divergence in coloration between the sexes, particularly in patches associated with signaling (e.g. ventral body regions), with males having more UV-blue for certain body patches but more red reflectance for other body patches. Achromatic variation between the sexes is also significant for certain body patches and, together, this could be indicative of the influence of sexual selection. Overall, these results may indicate both the generality of light environment as a consistent predictor of coloration but also more nuanced roles for other selection pressures.

Whether colors appear conspicuous or cryptic will depend on the environment they are found in. Conspicuousness is achieved by utilizing colors that overlap in peak wavelength with the predominant wavelengths of the light environment and that do not overlap with the color of the background (Endler 1992). In contrast, cryptic plumage colors should not overlap with the predominant light wavelength and should match the background color (Endler 1992). The prevailing wavelengths of light in woodland are blue (peak wavelength ~ 470 nm, Endler 1992, Figure 3), which overlaps with our observed tendency toward increased UV-blue reflectance among woodland species (Figure 4a–f), consistent with selection for conspicuousness and a possible role of UV as a signal (Gomez and Théry 2004). Species that live in open light environments also showed a tendency toward UV-blue reflectance, which is predicted to have a signaling function in these localities. However, when compared with the effect of the same color in woodlands, it is likely to be less optimal for achieving conspicuousness. Forest shade produces light environments that peak at ~ 550 nm (green) with small spots of direct sunlight rich in longer wavelengths appearing

yellow-orange, against a green background (Endler 1990, Figure 3; Théry 2006). Therefore, our observed red and green plumage patches in forest shade could locally achieve both conspicuity and crypsis. Our result differed slightly for PC2 with a trend toward more green plumage in woodland and open environments when compared with PC1 (Figure 5a–d). In woodlands, green would indicate a mismatch with the predominant light in the environment (blue), and therefore lesser potential for conspicuity. In open light environments, green is amongst a set of possible colors that could theoretically achieve conspicuity (alongside blue, gray, yellow-green, and red plumage colors), but less so than in a green-dominated light environment (e.g. forest shade with no gaps) (Endler 1990, 1992). Forest species have similar results for particular plumage patches with PC2 as with PC1, that is redder plumage patches. Taken together, our results suggest that selection for signaling purposes plays an important role in shaping chromatic color variation in Coraciiformes, with a tendency toward the evolution of colors that are likely to be highly conspicuous within particular light environments (e.g. UV-blue in woodland).

Our results in relation to light environment also highlight potentially different explanations for the chromatic and achromatic properties of plumage coloration (Endler 1992, 1993; Marcondes and Brumfield 2019). Several studies indicate a general trend for matching achromatic attributes of plumage color to the environment to facilitate crypsis (McNaught and Owens 2002; Gomez and Théry 2004; Shultz and Burns 2013; Dunn et al. 2015; Maia et al. 2016). In contrast, Marchetti (1993) inferred conspicuity because of increased achromatic brightness in closed light environments in *Phylloscopus* warblers. Our results show increased brightness of plumage in lighter (i.e. open) environments relative to darker (forest and woodland) environments in most cases. Thus, in Coraciiformes this suggests selection for crypsis rather than conspicuity in terms of achromatic color properties, at least for the nape, mantle, wing coverts, wing primaries and secondaries, and tail underside (Figure 6a–d, g). Our results therefore suggest that variation in chromatic properties of plumage coloration is associated with increasing conspicuity, whereas variation in achromatic property of plumage coloration is associated with reducing conspicuity. This could indicate at a compromise between intraspecific signaling and avoidance of detection by predators (Endler 1992). This is similar to the private channel hypothesis which suggests that due to visual system variation across the animal kingdom, certain animals can use particular colors for signaling purposes while also avoiding detection from predators or prey (Endler 1992; Håstad et al. 2005; Stevens and Cuthill 2007).

In contrast to light environment, we found localized and variable effects of life history and behavior. We recognize that our analytical approach might suffer from multiple comparisons issue due to large number of analyses and while the results for light environment are consistent and widespread across our analyses, we are more cautious in individually interpreting other, often patch and predictor specific, results. Nonetheless, some results are tentatively interesting. For example, hunting strategy was associated with chromatic variation for the ventral body parts (throat and belly) and with achromatic variation (but only in the rump). This is consistent with previous research suggesting that successful hunting in birds is associated with ventral body parts that are camouflaged against their natural background (Johnson and Brush 1972; Preston 1980; Götmark 1987; Bretagnolle 1993). Our results suggest that the belly would be camouflaged to some extent against the likely

background, potentially aiding hunting success in this group that contains many aerial hunters. We also found that territorial species have higher achromatic values for wings (coverts, primaries, and secondaries) than non-territorial species, in both males and females (Figure 6h,i). Wing color is important for establishing and maintaining territories in warblers (Marchetti 1993; Marchetti and Price 1997) and our results are consistent with the prediction that territorial species are showier (lighter/brighter) than non-territorial species (Pek 1972; Røskart and Rohwer 1987; Marchetti and Price 1997). We also found that body size affects both achromatic and chromatic properties of plumage coloration on some patches, but the results make generalization difficult. Body size is related to animals' detectability within the environment, with bigger animals theoretically achieving greater signal to background noise ratio for the receiver because of the greater signal intensity. The increase of achromatic values in the crown and nape with body size could improve their signaling capacity (Endler 1992) (Figure 7a–c). However, the reduced achromatic values for the belly patch could be related to the hunting strategy and need for lesser visibility from the prey (Figure 7d) (Götmark 1987; Bretagnolle 1993). We found a link to cooperative breeding only to tail coloration in males (Figure 7f).

Taken together, our results suggest that color evolution in Coraciiformes is dominated by light environment and the contrasting need for both crypsis and conspicuousness. Properties of plumage coloration, that is chromatic and achromatic variance, showed differential response to light environment, with achromatic properties indicating camouflage with adjacent environment and chromatic properties conspicuousness. However, while selection imposed by the light environment may drive evolution of coloration on most body regions, some regions do not follow this pattern and are more strongly affected by other factors. These include the belly patch that varies with hunting strategy, and the wings that vary with territorial defence. Our results are in line with the interpretation that the evolution of avian coloration is shaped by a set of interacting general ecological selection pressures and clade specific, idiosyncratic, life history traits.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

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DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Babarović et al. (2023).

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