The effects of ecology and behaviour on the evolution of colouration in Coraciiformes

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Data Availability Statement

Analyses reported in this article can be reproduced using the data provided by Babarovic et al., 2023.

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Abstract

What drives the evolution of plumage colour in birds? Bird colour is likely to be under both natural and sexual selection where natural selection may favour evolution towards crypsis or camouflage whereas sexual selection may favour evolution towards conspicuousness. The responses to selection are predicted to relate to species' ecology, behaviour, and life history. Key hypotheses have focused on habitat and light environment, breeding strategy, territoriality, and hunting behaviour. We tested these potential causes of colour variation in the Coraciiformes, a colourful clade of non-passerine birds, using phylogenetic comparative methods and data on chromatic and achromatic properties of plumage colouration measured from museum specimens. We found that correlates of colour evolution in Coraciiformes vary across body regions and depend on the focal colour property (chromatic or achromatic properties of plumage colouration). While the light environment showed widespread effects on colouration in multiple body regions for both colour properties, selection pressures related to behavioural 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 signaller and receiver and the behavioural characteristics of Coraciiform species.

Introduction:

Birds are one of the most colourful groups of animals on the planet (Cuthill et al., 2017; Hill & McGraw, 2006; Stoddard & Prum, 2011). The range of avian vision and the avian colour gamut spans the entire human-visible light spectrum and extends into the ultraviolet (UV) spectrum (Bennett & Cuthill, 1994; Hunt et al., 1998). This variation in colouration has many functions in the life of birds, from attracting

47 a mate (conspicuousness) to camouflage from predators (crypsis). Conspicuousness has been broadly
48 attributed to sexual and social selection, while concealment (camouflage and crypsis) is often
49 attributed to natural selection for predator avoidance or for successfully catching prey (Ruiz-Rodríguez
50 et al., 2013; Troscianko et al., 2016). The evolution of bird plumage colouration is therefore
51 multifaceted, with many environmental, ecological, behavioural and life history traits potentially
52 interacting to drive evolutionary divergence in colour (Dale et al., 2015; Dunn et al., 2015). The
53 detectability of a plumage patch (or body part) is the combination of chromatic [hue (the dominant
54 wavelength of light) and saturation (the colour intensity)] and achromatic (relative brightness)
55 properties of the signal itself, the visual system of the receiver, and the light environment in which the
56 signal is transmitted (Bennett & Cuthill, 1994; Cuthill et al., 2017; Stoddard & Prum, 2011, Endler, 1992,
57 Stoddard & Prum, 2008). Variation in selection pressures may lead to different responses in chromatic
58 and achromatic colour properties, particularly across different parts of the birds body (e.g. McNaught
59 & Owens, 2002, Gomez & Théry, 2004, Andersson & Prager, 2006).

60 How and why each of these components evolve has been tackled previously, but our understanding
61 of how they evolve in response to different selection pressures on different body parts remains
62 unresolved (Delhey, 2020; Dunn et al., 2015; Gomez & Théry, 2004; Maia et al., 2016; Marcondes &
63 Brumfield, 2019; McNaught & Owens, 2002; Shultz & Burns, 2013). Various ecological, behavioural
64 and life history traits have been proposed to influence colour evolution (Dale et al., 2015; Dunn et al.,
65 2015). First, relative conspicuousness or crypsis may be contingent on the light environment (the light
66 environment hypothesis; Endler, 1992, 1993; Endler & Thery, 1996; Espmark et al., 2000; Marchetti,
67 1993). Under this hypothesis, signal detectability is affected by aspects of the signalling environment,
68 such as light intensity, canopy thickness, time of day, and the amount of cloud cover in the sky (Endler,
69 1993). Second, several studies argue that body size can restrict colour evolution (Cooney et al., 2022;
70 Endler, 1992; Galván et al., 2013; Hagman & Forsman, 2003; Igic et al., 2018; Winebarger et al., 2018).
71 The sensory and ecological constraints hypothesis predicts that body size determines detectability of
72 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 signalling capacity (regardless of its chromatic variance) (Dale et al., 2015; Hagman & Forsman, 2003; Hossie et al., 2015). Second, hunting strategy is predicted to influence colour evolution. For example, if hunting success is increased with more cryptic colouration that reduces detectability by prey (Bretagnolle, 1993; Götmark, 1987; Tate et al., 2016). Third, the establishment or maintenance of a territory has been suggested to affect colour evolution and its distribution on the body (Røskaft & Rohwer, 1987). Among other behavioural traits, presence or absence of cooperative breeding could mediate intersexual and intrasexual contact leading to the evolution of conspicuous colouration in both males and females for signalling purposes (Rubenstein & Lovette, 2009).

The opposing effects of selection for crypsis or conspicuousness on colouration may also be reflected in colour variation across the birds' body (Doucet et al., 2007; Gomez & Théry, 2007; Marcondes & Brumfield, 2019; Shultz & Burns, 2017). 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 conspicuousness. 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 (Allen et al., 2012; Edmunds & Dewhirst, 1994; Rowland et al., 2007). In contrast, front-facing body regions that can be directed at the potential signal receiver are commonly used in intraspecific communication (Andersson & Amundsen, 1997; Keyser & Hill, 2000; Pryke & Griffith, 2007; Stein & Uy, 2006). Overall, ventral body parts are thought to be under stronger selection for conspicuousness 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 colouration less constrained, at least in birds (Marcondes & Brumfield, 2019; Shultz & Burns, 2017). Together, this suggests that understanding the evolution of avian colouration requires consideration of effects of its proximate drivers on each body part separately.

To explore key factors influencing the evolution of plumage colouration, we focused on the non-passerine order Coraciiformes (bee-eaters, ground rollers, rollers, todies, motmots and kingfishers). Coraciiform species (Fig. 1) have diverse plumage colouration including pigmentary and structural colours, 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 (Eliason et al., 2019; Fry et al., 1992; Stavenga et al., 2011). This diversity makes them an ideal study system for addressing the significance of life history traits on the evolution of colouration, as well as disentangling the interaction between light environment and plumage colour and how it affects conspicuousness and concealment. We measured plumage colouration from digital images of museum specimens and quantified several proxies for factors that could play a key role in the evolution of colouration including sex, body size, hunting strategy, habitat light environment, territoriality, and social mating system. This information allows us to (i) disentangle different possible biotic and abiotic factors affecting the evolution of Coraciiform colouration, and (ii) test how chromatic and achromatic properties of plumage colouration 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 colouration, 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

124 females for every patch but tail underside (110). Across all analysis this ranges from ~75% to ~80% of
125 the entire order when compared to the 146 species in the phylogeny of Jetz et al., 2012 (Table S1.).

126 **Plumage Colour:**

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

134 Digital images were then linearized and converted to .TIFF files using DCRAW (Coffin, 2016). Each
135 linearized photo was normalized by comparison of pixel values of five grey standards with known
136 reflectance, as suggested by Troscianko & Stevens (2015). On each image, a series of polygons were
137 drawn in IMAGEJ (Rueden et al., 2017) using custom scripts to demark 11 body regions for colour
138 measurement. The selected body regions were: crown, nape, mantle, rump, tail, wing coverts, wing
139 primaries and secondaries, throat, breast, belly, and tail underside. By measuring the colour of these
140 11 regions, thorough coverage of whole-plumage colour variability was achieved (Maia et al., 2016).
141 For each of these polygons, RGB values were extracted for both the human-visible and UV range.

142 To convert mean RGB values to avian colourspace values we used a method developed by Troscianko
143 and Stevens (2015) to generate mapping functions that convert RGB colour values into cone-catch
144 values adjusted to avian colour vision (see Cooney et al. 2019 for full details). We based our analysis
145 on UVS avian visual system since genomic sequencing of the UV/violet SWS1 cone opsin gene
146 indicated presence of amino acid residues signifying UV sensitivity in Coraciiformes (Ödeen & Håstad,
147 2013). Mapping functions were used to convert RGB values for each patch on each specimen into raw
148 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 colourspace, using methods from Stoddard & 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 colour 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, Fig. 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 understory, dense undergrowth and shruby habitats, but excludes the tree canopy which we instead

class as “woodland shade”. “Woodland shade” is dominated by bluish or blue-grey 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, 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; Gomez & Théry, 2004; Marchetti, 1993).

(iv) Data on hunting strategies were collected from the *Birds of the World* and a monogram on Coraciiformes (Billerman et al., 2022; Fry et al., 1992). 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-behaviour that involves underwater diving, has been shown to be related to the evolution of belly colouration in seabirds (Bretagnolle, 1993; Götmark, 1987). 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).

198 (v) Territoriality was assigned for each species using descriptions in Fry et al. (1992). Territoriality was
199 coded as the presence or absence of both intraspecific and/or interspecific aggressive behaviours. For
200 example, *Tanysiptera danae*, the Brown-headed Paradise Kingfisher, shows intraspecific territoriality
201 ("strongly territorial, three or four birds chasing each other from branch to branch"), whereas *Dacelo*
202 *gaudichaud*, the Rufous-bellied Kingfisher shows both intra and interspecific territoriality ("they are
203 strongly territorial, chasing their own species and being aggressive towards some others").

204 (vi) Cooperative breeding was coded for each species in our dataset based on a larger dataset of the
205 modes of parental care of birds (Cockburn, 2006). We coded for the presence and absence of pair
206 breeding and cooperative breeding. Each species was assigned to one of these two categories.

207 **Analysis**

208 Relative cone-catch values (u, s, m, l) represent the relative stimulation of four avian colour cones and
209 together describe avian tetrahedral colourspace, a sensory equivalent of morphospace where the
210 distance between two colours is comparable to their similarity (Stoddard & Prum, 2008). We
211 estimated both chromatic properties of colour (hue and saturation) via cone catch values and reduced
212 the dimensionality of the colourspace using Principal Component Analysis (PCA; Jolliffe, 2002) applied
213 to the entire database, covering colour values for all measured colour patches. Our measurement of
214 colour does not allow us to separate hue and saturation. Instead, the principal components that we
215 use (PC1 and PC2) capture both elements of chromatic variation.

216 To asses sex differences in colouration, we compared colour variables between sexes using
217 phylogenetic reduced major axis regression (phyloRMA) as implemented in the function phyl.RMA
218 ("lambda" method) in the phytools R-package (Revell, 2012), with values for males as x-variable and
219 values for females as y-variable.

220 To test hypotheses regarding the predictors of colour variation we used Phylogenetic Generalized
221 Least Squares (PGLS) regression (Grafen & Hamilton, 1989) as implemented in the R package caper

(Orme et al., 2018). 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 analysed 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 colour 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 colour as dependent variables with sex, patch and their interaction as predictors. We used a flat prior and ran for each model for 220000 iterations, sampled every 20 iterations with the first 20 000 iterations taken as a burnin and removed.

Results

Coraciiform colour space

The first two principal components explained 96.27% of the variance in raw cone-catch values (u, s, m, 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 colouration), while higher values of PC1 indicated greater stimulation of s and u cones (blue and UV coluration). Lower PC2 values indicated stimulation of the m cone (green colouration) while higher PC2 values indicated simulation of the l cone (red colouration) (Fig. 2.). The relationship between raw cone catch values and PC scores are shown in Supplement 2: Fig. S10-S12.

Sex

Colour variation (PC1, PC2, achromatic) between the sexes was analysed with phyloRMA regression (Supplement 1: Table S4), with slopes and intercepts that differ significantly from one and zero

246 respectively indicating differences in colouration between the sexes (plots shown in Supplement 2:
247 Fig. S7-S9). In total, significant differences in plumage colouration between the sexes were detected
248 in four body patches for achromatic variation, one body patch for PC1, and seven body patches for
249 PC2. Regression of female against male PC1 values showed slopes significantly different from one for
250 crown (Supplement 1: Table S4.1). For crown, slope values of <1 suggest that male plumage has more
251 blue-UV reflectance than female plumage but that this difference decreases as PC1 values increases.
252 Analysis of the relationship between male and female PC2 values revealed significant between-sex
253 variation for crown, nape, wing coverts, wing primaries and secondaries, throat, breast, and belly
254 (Supplement 1: Table S4.12-S4.13, S4.17-S4.21). Slope values significantly <1 and negative intercepts
255 for crown, nape, wing coverts, and belly indicated that males are generally redder in these patches
256 than females, but that the difference reduces as PC2 values increase. A slope value significantly <1
257 and a positive intercept for wing primaries and secondaries and throat indicated that males become
258 redder than females as PC2 value increases. Comparison of achromatic variation between the sexes
259 revealed a slope significantly <1 and a positive intercept in wing coverts, wing primaries and
260 secondaries, and tail. For these patches, this suggests that as species become brighter, males tend to
261 be relatively more bright than females (Supplement 1: Table S4.27-S4.29). For the nape patch,
262 however, a slope <1 and a negative intercept indicate that males tend to be brighter than females, but
263 that this difference reduces as achromatic intensity increases (Supplement 1: Table S4.24). Overall,
264 this suggests that there are significant differences between the sexes in colour variation for some body
265 patches.

266 Multipredictor model results summary

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

In total, light environment showed a significant association with colour variables in ten body patches for PC1 (four in males and six in females) (Fig. 3, a-b), five body patches for PC2 (three in males and two in females) (Fig. 3, c-d), and thirteen body patches for achromatic property (six in males and seven in females) (Fig. 3, e-f). In nine instances, colour variables were correlated with body size, including one patch for PC1, three patches with PC2 (one in males and two in females) (Fig. 3, a, c-d) and five patches with achromatic property (one in males and four in females) (Fig. 3, e-f). Territoriality correlated with PC1 in one body patch (only in females) (Fig. 3, b) and with achromatic variation in four body patches (two in males and two in females) (Fig. 3, e-f). Hunting strategy had a significant effect in two body patches with PC1 (one in males and two in females) (Fig. 3, a-b), two patches with PC2 (both in males) (Fig. 3, c), and one patch with achromatic variation (only in males) (Fig. 3, e). Cooperative breeding is associated with achromatic variation in one body patch (in males) only (Fig. 3, e). 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 colour 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 towards reds and greens in forest light environments and UV-blues in open and woodland shade light environments (Fig. 4, a-f)

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 towards reddish plumage colour 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 to open species. (Fig. 5, a-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 (Fig. 6, a-d, g). For male and female throat patches, species living in forest light environments have lower average achromatic scores compared to woodland and open light environment species (Fig. 6, e), while for female belly patches, species living in forest light environments have higher average achromatic scores (Fig. 6, f).

Body size

For PC1, tail of larger bodied males is weakly associated with the blue part of the colour spectrum (Fig. 4, g). Larger bodied species are also associated with higher PC2 values for the crown (females) and mantle (males and females) indicating a shift towards the red part of the colour spectrum (Fig. 5, e-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 (Fig. 7, a-c). For the belly patch (in females), larger body size is associated with reduced achromatic values (Fig. 7, d).

Territoriality

Territorial species have higher PC1 values for tail underside in females, indicating a tendency towards increased UV-blue colouration compared to non-territorial species (Fig. 4, h). Territorial species also have higher achromatic values on wing coverts and wing primaries/secondaries in both males and females when compared to non-territorial species (Fig. 6, h-i).

Hunting strategy

We found significant associations between PC1 values and hunting strategy for the belly in both males and females (Fig. 4, i). 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 towards duller brownish plumage, aerial catching species a tendency towards UV-blues, while ground catching species tending towards green colouration.

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 (Fig. 5, h). This indicates a tendency towards green for aerial and ground catching species, while ground dwelling and water diving species tend more towards brown and duller colours 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 (Fig. 5, g).

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 (Fig. 7, e).

Cooperative breeding

In cooperative breeders, males have higher average achromatic values for tails than pair breeding species (Fig. 7, f). 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 colour varies greatly among patches but not, on average, between the sexes (Supplement 1: Table S6 and Supplement 2: Fig. S13.).

Discussion

Our results show that among multiple ecological and behavioural indices, light environment is the dominant correlate of plumage colour in the order Coraciiformes. Importantly, however, there is nuanced variation dependent on the specific property of colour variation (chromatic or achromatic) and the location of the colour on the bird's body. In particular, we found consistent effects of light environment on both chromatic and achromatic properties of plumage colour across multiple body regions. Other variables capturing variation in Coraciiform life history indicated more idiosyncratic effects on colouration and only for subsets of body patches. We also find some divergence in colouration between the sexes, particularly in patches associated with signalling (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 colouration but also more nuanced roles for other selection pressures.

Whether colours appear conspicuous or cryptic will depend on the environment they are found in. Conspicuousness is achieved by utilising colours that overlap in peak wavelength with the predominant wavelengths of the light environment and that do not overlap with the colour of the background (Endler, 1992). In contrast, cryptic plumage colours should not overlap with the predominant light wavelength and should match the background colour (Endler, 1992). The prevailing wavelengths of light in woodland are blue (peak wavelength ~470 nm, Endler, 1992, Fig. 3.), which overlaps with our observed tendency towards increased UV-blue reflectance among woodland species (Fig. 4, a-f), consistent with selection for conspicuousness and a possible role of UV as a signal (Gomez & Théry, 2004). Species that live in open light environments also showed a tendency towards UV-blue reflectance, which is predicted to have a signalling function in these localities. However, when compared to the effect of the same colour 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

368 background (Endler, 1990, Fig. 3.; Théry, 2006). Therefore, our observed red and green plumage
369 patches in forest shade could locally achieve both conspicuousness and crypsis. Our result differed
370 slightly for PC2 with a trend toward more green plumage in woodland and open environments when
371 compared to PC1 (Fig. 5, a-d). In woodlands, green would indicate a mismatch with the predominant
372 light in the environment (blue), and therefore lesser potential for conspicuousness. In open light
373 environments, green is amongst a set of possible colours that could theoretically achieve
374 conspicuousness (alongside blue, grey, yellow-green and red plumage colours), but less so than in a
375 green-dominated light environment (e.g. forest shade with no gaps) (Endler, 1990, 1992). Forest
376 species have similar results for particular plumage patches with PC2 as with PC1, i.e. redder plumage
377 patches. Taken together, our results suggest that selection for signalling purposes plays an important
378 role in shaping chromatic colour variation in Coraciiformes, with a tendency towards the evolution of
379 colours that are likely to be highly conspicuous within particular light environments (e.g. UV-blue in
380 woodland).

381 Our results in relation to light environment also highlight potentially different explanations for the
382 chromatic and achromatic properties of plumage colouration (Endler, 1992, 1993; Marcondes &
383 Brumfield, 2019). Several studies indicate a general trend for matching achromatic attributes of
384 plumage colour to the environment to facilitate crypsis (Dunn et al., 2015; Gomez & Théry, 2004; Maia
385 et al., 2016; McNaught & Owens, 2002; Shultz & Burns, 2013). In contrast, Marchetti (1993) inferred
386 conspicuousness because of increased achromatic brightness in closed light environments in
387 *Phylloscopus* warblers. Our results show increased brightness of plumage in lighter (i.e. open)
388 environments relative to darker (forest and woodland) environments in most cases. Thus, in
389 Coraciiformes this suggests selection for crypsis rather than conspicuousness in terms of achromatic
390 colour properties, at least for the nape, mantle, wing coverts, wing primaries and secondaries and tail
391 underside (Fig. 6, a - d, g). Our results therefore suggest that variation in chromatic properties of
392 plumage colouration is associated with increasing conspicuousness, whereas variation in achromatic
393 property of plumage colouration is associated with reducing conspicuousness. This could indicate at a

394 compromise between intraspecific signalling and avoidance of detection by predators (Endler, 1992).
395 This is similar to the private channel hypothesis which suggests that due to visual system variation
396 across the animal kingdom, certain animals can use particular colours for signalling purposes while
397 also avoiding detection from predators or prey (Endler, 1992; Håstad et al., 2005; Stevens & Cuthill,
398 2007).

399 In contrast to light environment, we found localised and variable effects of life history and behaviour.
400 We recognize that our analytical approach might suffer from multiple comparisons issue due to large
401 number of analyses and while the results for light environment are consistent and widespread across
402 our analyses, we are more cautious in individually interpreting other, often patch and predictor
403 specific, results. Nonetheless, some results are tentatively interesting. For example, hunting strategy
404 was associated with chromatic variation for the ventral body parts (throat and belly) and with
405 achromatic variation (but only in the rump). This is consistent with previous research suggesting that
406 successful hunting in birds is associated with ventral body parts that are camouflaged against their
407 natural background (Bretagnolle, 1993; Götmark, 1987; Johnson & Brush, 1972; Preston, 1980). Our
408 results suggest that the belly would be camouflaged to some extent against the likely background,
409 potentially aiding hunting success in this group that contains many aerial hunters. We also found that
410 territorial species have higher achromatic values for wings (coverts, primaries, and secondaries) than
411 non-territorial species, in both males and females (Fig. 6, h-i). Wing colour is important for establishing
412 and maintaining territories in warblers (Marchetti, 1993; Marchetti & Price, 1997) and our results are
413 consistent with the prediction that territorial species are showier (lighter/brighter) than non-
414 territorial species (Røskaft & Rohwer, 1987; Peek, 1972; Marchetti & Price, 1997). We also found that
415 body size affects both achromatic and chromatic properties of plumage colouration on some patches,
416 but the results make generalisation difficult. Body size is related to animals' detectability within the
417 environment, with bigger animals theoretically achieving greater signal to background noise ratio for
418 the receiver because of the greater signal intensity. The increase of achromatic values in the crown
419 and nape with body size could improve their signalling capacity (Endler, 1992) (Fig. 7, a-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 (Fig. 7, d) (Bretagnolle, 1993; Götmark, 1987). We found a link to cooperative breeding only to tail colouration in males (Fig. 7, f).

Taken together, our results suggest that colour evolution in Coraciiformes is dominated by light environment and the contrasting need for both crypsis and conspicuousness. Properties of plumage colouration, i.e. 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 colouration 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 colouration is shaped by a set of interacting general ecological selection pressures and clade specific, idiosyncratic, life history traits.

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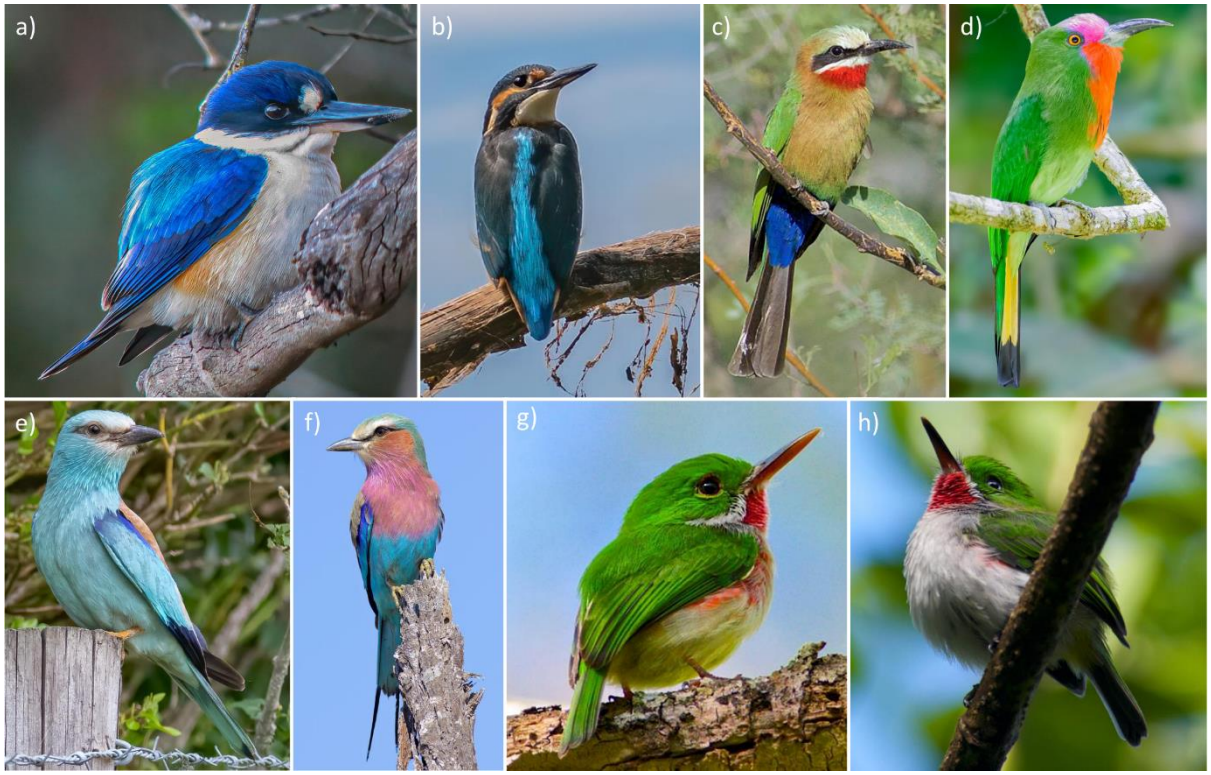
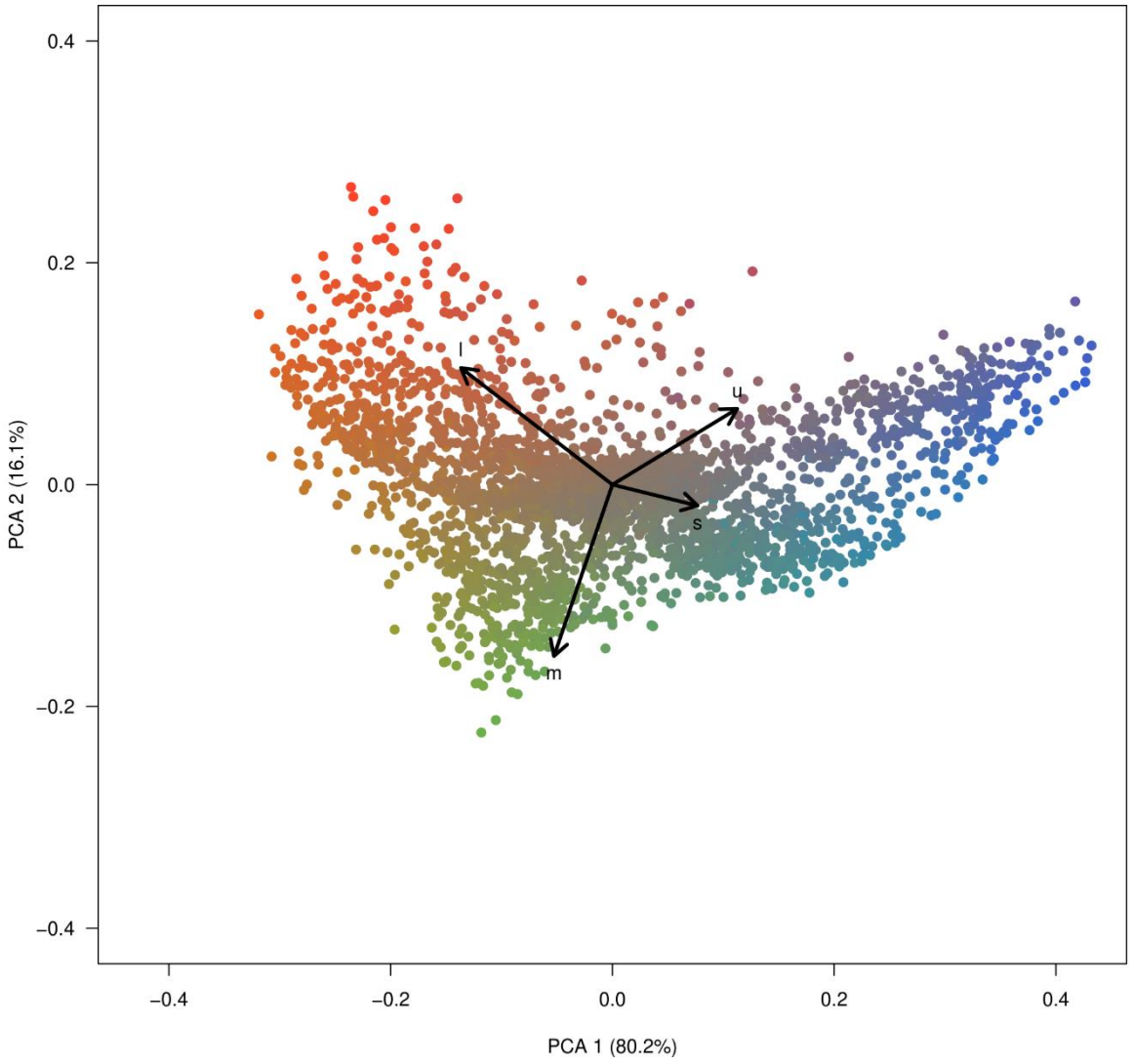
582 **Figures**



583

584 Figure 1. A collage showing some of the plumage colour diversity in the Coraciiformes. a) Forest
585 kingfisher (*Todiramphus macleayii*), Alcedinidae; b) Common kingfisher (*Alcedo atthis*), Alcedinidae; c)
586 White-fronted bee-eater (*Merops bullockoides*), Meropidae; d) Red-bearded bee-eater (*Nyctyornis*
587 *amictus*), Meropidae; e) European roller (*Coracias garrulus*), Coraciidae; f) Lilac-breasted roller
588 (*Coracias caudatus*), Coraciidae; g) Broad-billed tody (*Todus subulatus*), Todidae; h) Narrow-billed tody
589 (*Todus angustirostris*), Todidae. All photos © Daniel J. Field, University of Cambridge. Used with
590 permission.



591

592 Figure 2. Principal components (PC) of cone catch values (u, s, m, l) for all body patches across all
593 species. Each point in the plot represents one of 11 body patches for one species, with point colour
594 providing an indication of patch colour in the visible spectrum. PC1 explains 80.2 % of the variation of
595 colour scores. Higher PC1 value indicates a tendency toward blue and UV colour, while lower PC1
596 scores indicates a tendency toward red and green colour. PC2 explains 16.1% of variation in colour.
597 Higher PC2 values are ascribed to red hues, while lower PC2 scores are indicative of green and blue
598 hues.

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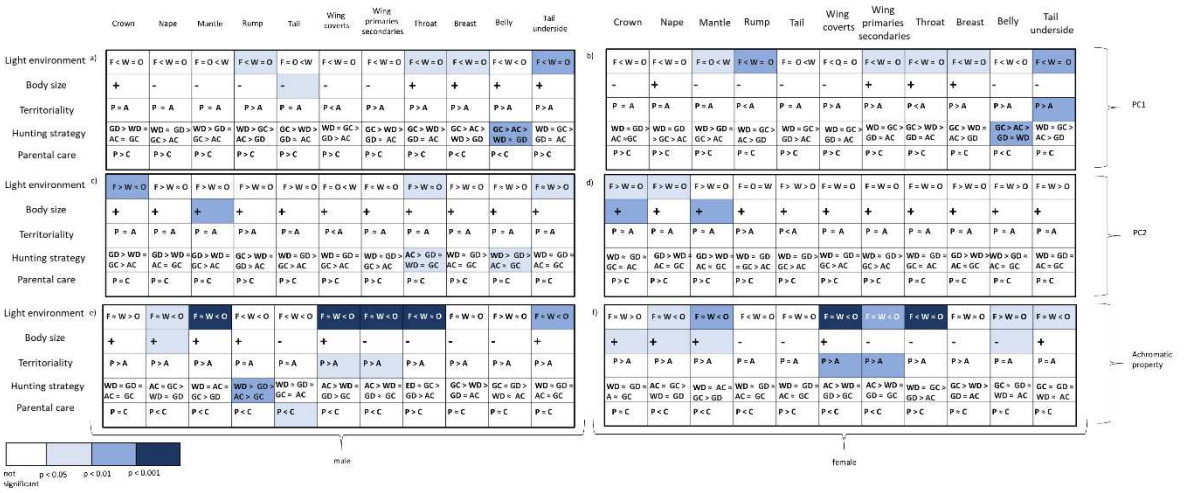

600

601 Figure 3. Multipredictor model results summary. Panels a-b represent results for PC1, panels c-d
602 represent results for PC2 and panels e-f represent results for brightness. Panels on left hand side
603 represent results for males and panels on right hand side represent results for females. Predictor
604 variables are represented as rows with their names indicated further left. Body patches are
605 represented as a column with each one represented on top of the column. White squares are non-
606 significant results, light blue squares represent p<0.05 level of significance, darker blue represent
607 p<0.01 level of significance and dark blue represent p<0.001 level of significance. Within each box, the
608 effect of each variable is indicated. The plus and minus sign for body size (continuous variable) indicate
609 the direction of the effect. For categorical variables, the letters represent abbreviations of categories
610 of each variable with the approximate relations indicated between them (Light environment: F – forest,
611 W – woodland, O – open; Hunting strategy: GD – ground dwelling, WD – water diving, GC – ground
612 catching, AC – aerial catching; Territoriality: A – absent, P – present; Parental care: P – pair, C –
613 cooperative).

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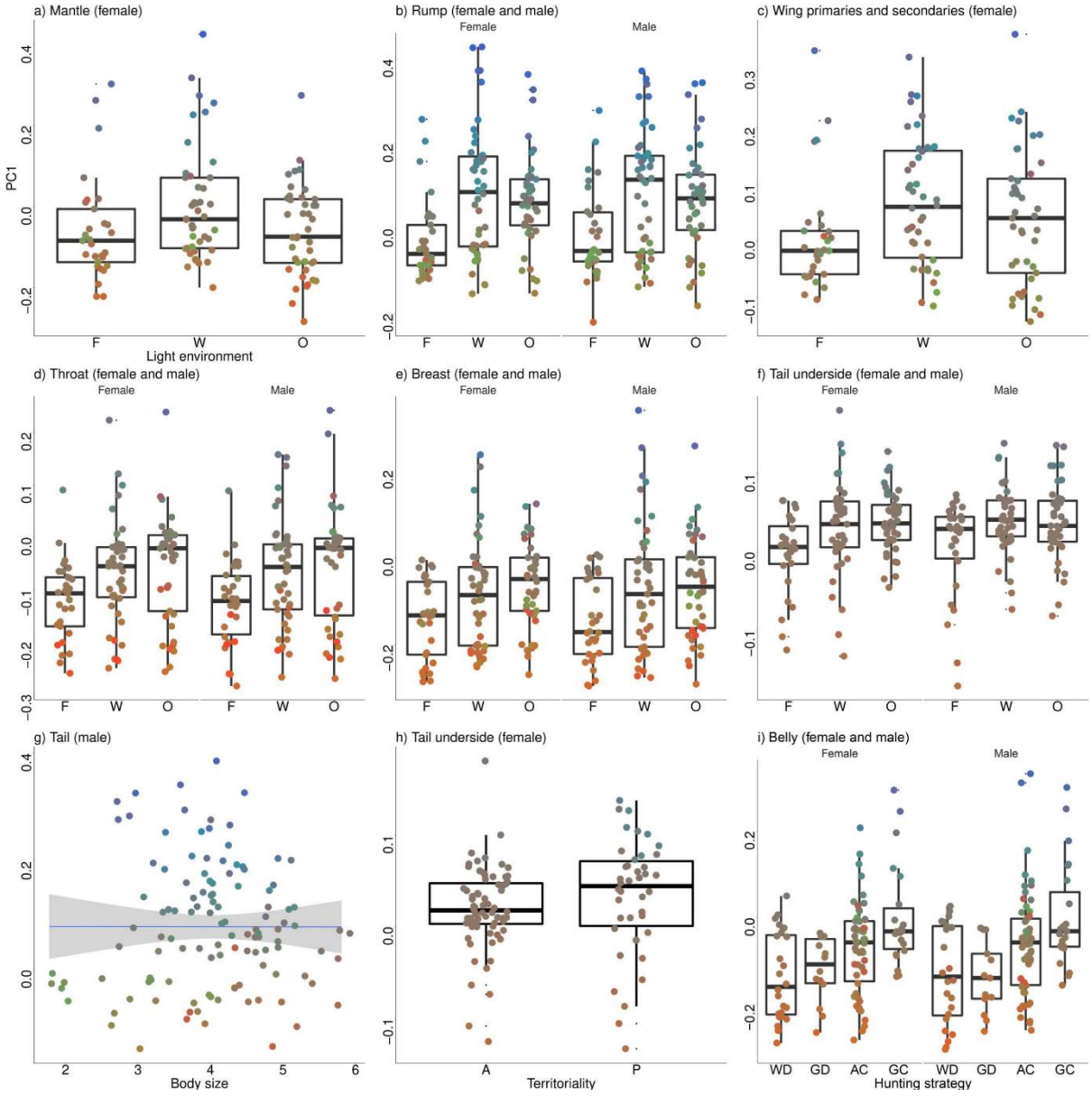


Figure 4. Predictors of PC1. Only body patches for which at least one independent variable indicated significant result are shown. Within each panel, each point represents a species, and the colour of each point represents the approximate reflectance of that body patch in visible spectrum. In the title 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 have 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 have 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 have abbreviations for hunting strategy categories that represent following: GD – ground dweller, WD – water diver, AC – aerial catcher, and GC – ground catcher.)

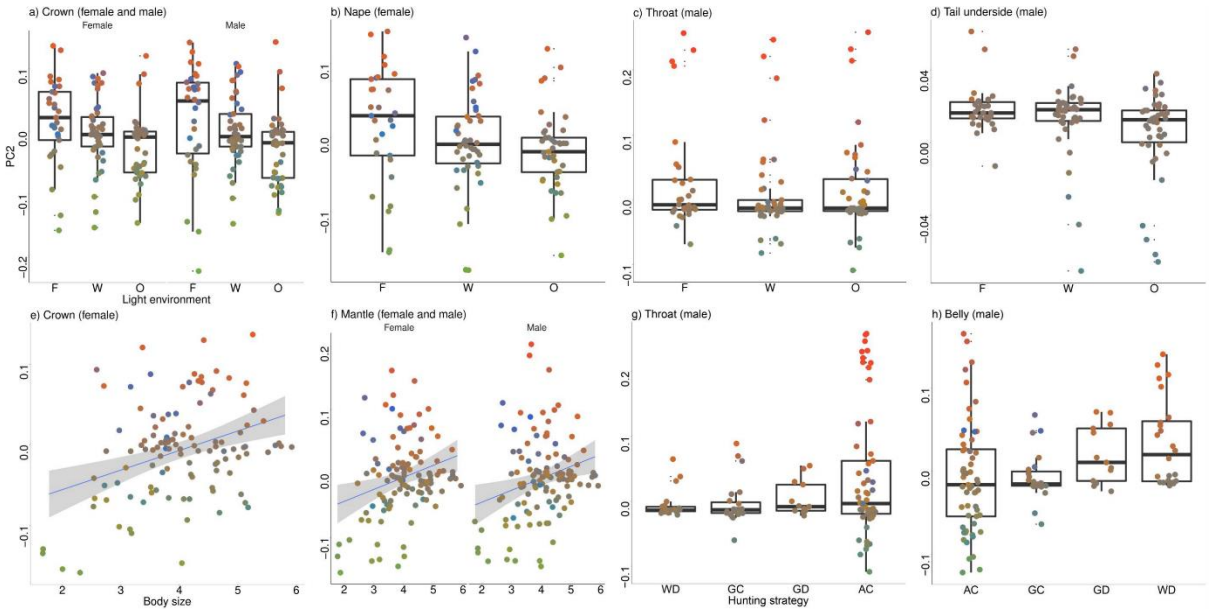
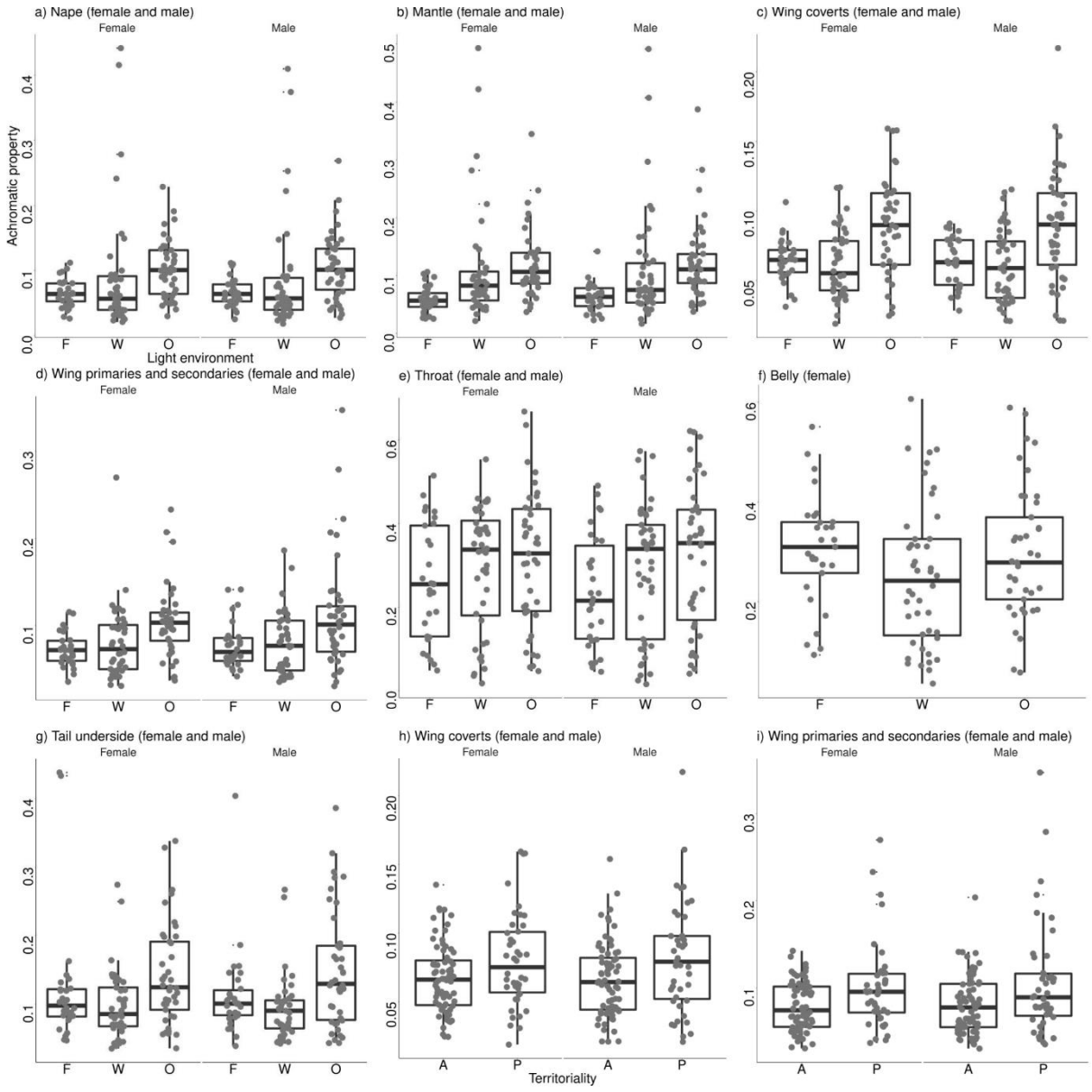


Figure 5. Predictors of PC2. Only body patches for which at least one independent variable indicated significant result are shown. Within each panel, each point represents a species, and the colour of each point represents the approximate reflectance of that body patch in visible spectrum. In the title 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 have abbreviations for light environment categories that represent following: F – forest, W – woodland, and O – open.) Panels e-f show relation of PC2 with body size. Panel g-h represents association of PC2 values with different hunting strategies. (x-axis on each panel for hunting strategy variable have abbreviations for hunting strategy categories that represent following: GD – ground dweller, WD – water diver, AC – aerial catcher, and GC – ground catcher.)

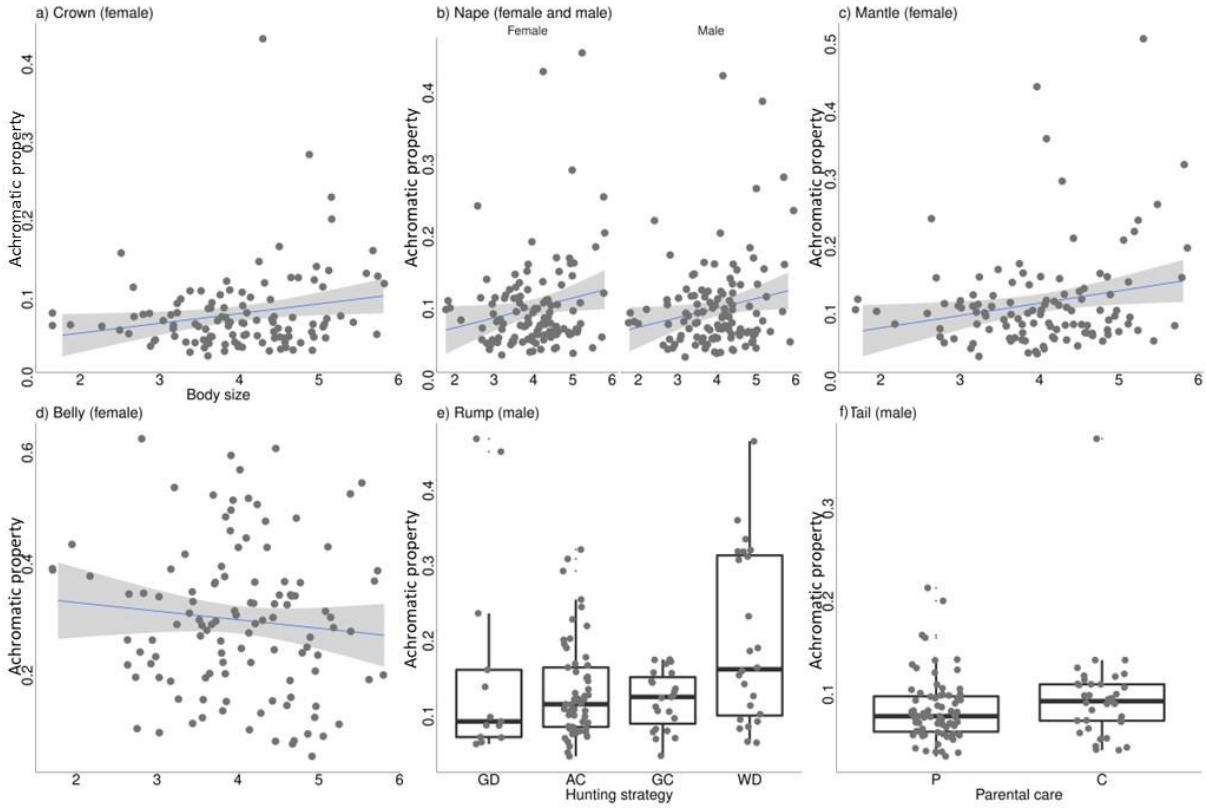


642

643 Figure 6. Light environment and territoriality as predictors of achromatic property. Only body patches
644 for which at least one independent variable indicated significant result are shown. Within each panel,
645 each point represents a species. In the title of each panel, a patch and for which sex a significance has
646 been detected is indicated. Panels a-g represent variation in brightness across different light
647 environment categories. (x-axis on each panel for light environment variable have abbreviations for
648 light environment categories that represent following: F – forest, W – woodland, and O – open.) Panels
649 h-i show relationship between brightness and territoriality. (x-axis on each panel for territoriality

650 variable have abbreviations for territoriality categories that represent following: A – absent, and P -
651 present.)

652



653

654 Figure 7. Body size, hunting strategy, and parental care as predictors of achromatic property. Only
655 body patches for which at least one independent variable indicated significant result are shown.
656 Within each panel, each point represents a species. In the title of each panel, a patch and for which
657 sex a significance has been detected is indicated. Panels a-d show relation of brightness with body size.
658 Panel e shows relationship between brightness and hunting strategy. (x-axis on each panel for hunting
659 strategy variable have abbreviations for hunting strategy categories that represent following: GD –
660 ground dweller, AC – aerial catcher, GC – ground catcher and WD – water diver.) Panel i shows
661 relationship between brightness and parental care. (x-axis on each panel for parental care variable
662 have abbreviations for parental care categories that represent following: C – cooperative breeding,
663 and P – pair breeding.)