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Linking plumage dimorphism and environmental stress

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1 Linking Plumage Dimorphism and Environmental Stress

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3

4 **Linking Plumage Dimorphism and Environmental Stress**

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20 **Abstract:**

21 Besides the importance of pigmentation in species recognition, pigments protect a body against
22 different biotic and abiotic features. Melanin, the dark coloration pigments in skin, hairs, and
23 feathers, is necessary for protecting a body from UV radiation. On the other hand, the lighter a
24 surface is, the more solar radiation is reflected. Based on these arguments, it is possible that
25 pigment distribution would not be the same among all body regions of a unicoloured individual
26 due to the amount of solar exposure. Therefore, three species of the *Egretta* genus (*E. dimorpha*,
27 *E. gularis*, and *E. garzetta*), which all are unicoloured individuals, and two of which are
28 dichromatic (dark grey/black and white), were selected as model studies. We hypothesized that
29 within dark and white unicoloured Egrets, due to foraging and standing postures, body regions
30 that are more exposed to the sun (like back and breast) would be darker and whiter compared to
31 other body regions (vent and tail), respectively. Visual wavelength reflections of five body
32 regions (breast, back, belly, vent, and tail) from 186 museum specimens were measured to
33 indicate the concentration of pigments in each body region. Reflectance among body regions was
34 compared using Kruschke's "BEST" (Bayesian Estimation Supersedes the *t* test) framework to
35 create Bayesian analogues for the paired *t*-test. The results show, regardless of the species, the
36 more exposed body regions to the sun (back followed by breast) are darker among dark
37 individuals and whiter among white individuals in comparison to other body regions. Therefore,
38 our hypothesis that the concentration of pigments is not similar in all body regions of
39 unicoloured individuals was supported.

40 **Keyword:** Melanin, coloration, pigmentation, UV stress, sun exposure

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41 **Introduction**

42 Coloration plays a substantial role in species' ecology and evolution (Poelstra *et al.*, 2014, 2015;
43 Bourgeois *et al.*, 2017; Campagna *et al.*, 2017). Variation in colour, from saturation to hue to
44 patchiness, results from a balance among evolutionary forces such as crypsis, sexual selection,
45 and environmental response, including local adaptation. For crypsis, coloration reduces
46 detectability by background matching (Endler, 1978, 1984). Sexual selection, by contrast,
47 favours patches with maximal contrast (Gomez & Théry, 2007). These two forces may respond
48 to local conditions (Gomez & Théry, 2007; Sun *et al.*, 2013), such that the strength or direction
49 of selection varies with environment. Within a given system, such as birds of the rainforest
50 understory, these forces counterbalance; for example, small, distinctive patches, usually with
51 maximum conspicuousness, aim to attract the opposite sex (sexual selection) (Andersson, 1994),
52 while overall coloration is dark to avoid detection (crypsis selection) (Endler *et al.*, 2005). Even
53 if an individual is patchily coloured, another individual typically sees it as an average of all
54 different colours (Burt, 1986; Gomez & Théry, 2007) even though each patch is distinguishable
55 by itself (Endler & Théry, 2002). In contrast to rainforest understory birds, animals that live in
56 deserts are mostly dark in coloration (Ward *et al.*, 2002). Thermoregulation is one of the reasons.
57 Dark coloration help animals to save energy by using the heat from solar radiation (Walsberg,
58 Campbell & King, 1978). Another explanation is that dark coloration reduces heat stress by
59 absorbing excessive heat from solar radiation in, say, a feather layer and thus keeping skin cooler
60 (Ward *et al.*, 2002).

61 Most research has been done on multicoloured or patchily coloured individuals (i.e., Margalida
62 *et al.* 2008); there are few data on selective forces experienced by unicoloured individuals.

63 Among unicoloured species, evolutionary forces may affect the concentration of pigments in

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64 different body regions in a subtle but predictable manner. It is possible that pigmentation also
65 varies subtly in different regions of the body in response to local adaptation, such as sunlight
66 exposure. This possibility has not been explored.

67 Ultraviolet radiation is part of the sun's radiation with a wavelength between 100 to 400 nm
68 (Schuch *et al.*, 2017). It contains three kinds: UVC with 100–280 nm range, UVB with 280-315
69 nm, and UVA with 315-400 nm range (Schuch *et al.*, 2017). The UVC wavelength and most of
70 the UVB are usually absorbed by the oxygen and ozone in the atmosphere. Therefore, the UV
71 radiation which reaches the earth is mostly UVA and partially UVB (Schuch *et al.*, 2013).

72 Although being exposed to UV has physiological benefits, such as providing vitamin D (Holick
73 2007), a high dosage can be harmful. The excessive amount of UV radiation exposure, chronic or
74 prolonged, is well-known as an environmental genotoxic driver of sunlight (Schuch *et al.*, 2013).
75 Extra UV exposure can generate DNA damage, cell death, mutagenesis, and, eventually,
76 carcinogenesis (Hideg *et al.*, 2013). Thus, the amount of received UV radiation is important for
77 the survivorship of any terrestrial and aquatic species (McKenzie *et al.*, 2011).

78 Different organisms have taken different evolutionary paths for protection against biotic and
79 abiotic conditions. One of the most common protections is pigmentation, specifically melanin
80 (Galván *et al.*, 2018b). Melanin is responsible for pigmentation in many animal and plant species
81 (Galván *et al.*, 2018b). Melanin functions in signaling, as an antioxidant, free radical scavenger,
82 and charge transport facilitator (Herrling *et al.*, 2008), but a key role is photoprotection.

83 Individuals absorb more wavelengths of the sunlight, even those in the ultraviolet (UV)
84 spectrum, with increasing darkness of coloration (Cuthill *et al.*, 2000; Eaton & Lanyon, 2003;
85 Hausmann *et al.*, 2003).

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86 The other approach to protect from UV radiation is absence of pigmentation, in other words,
87 increasing albedo (Mullen & Pohland, 2008). The colour of any object is the reflection of that
88 colour wavelength from the visual sunlight to eye receptors. A white surface means that all the
89 visual wavelengths have been reflected, absorbing nothing. This phenomenon is valid for the UV
90 wavelengths too. For example, in a study on 312 bird species, all-white feathers reflect
91 considerable UV rays (Eaton & Lanyon, 2003). Many other studies on measuring UV reflection
92 of bird feathers have indicated higher reflection of UV from white feathers compared to other
93 colorations (Hausmann *et al.*, 2003; Cuthill *et al.*, 2006).

94 To answer the question about variation in pigmentation among different body parts of
95 unicoloured species, we examined colour variation among different body regions within
96 individuals of three unicoloured bird species: the Little Egret (*Egretta garzetta*), which is entirely
97 white, Dimorphic Egret (*E. dimorpha*), and Western Reef Heron (*E. gularis*), which are
98 dichromatic species with completely white or dark colorations. The way that egrets perch or
99 forage makes their back and breast more exposed to sunlight and UV. Their posture dictates that
100 the belly, vent, and tail are tracts least exposed to the sun (Hancock & Kushlan, 1984; Kushlan &
101 Hancock, 2006). Therefore, as a defence mechanism and as a barrier to absorb UV wavelengths,
102 the tracts with more sunlight exposure (back and breast) will be darker and whiter among dark
103 and white individuals, respectively (Fig. 1).

104 We hypothesized that body regions more exposed to sunlight would be darker for unicoloured
105 individuals with dark coloration. In contrast, a uniformly pale organism may increase albedo in
106 body parts with more sun exposure than less exposed regions to increase sunlight reflection. In
107 short, we predicted higher and lower visual wavelength reflectance in more exposed body
108 regions of white and dark unicoloured individuals, respectively, compared to other body regions.

109 **Methods**

110 **Model organisms:**

111 The Little Egret is always white and is distributed year-round in most of the Old World (Mock,
112 1980). The Dimorphic Egret is either entirely white or completely dark grey to black, and
113 populations of both colour morphs are roughly evenly distributed throughout its range, which
114 extends from eastern Kenya to Madagascar and nearby islands (Zimmerman *et al.*, 1996). The
115 Western Reef Heron is typically dark grey, yet there are a few populations of completely white
116 individuals in west and northeast of Africa; these birds are distributed coastally in the northern
117 half of Africa and around the Red Sea and Persian Gulf (Mock, 1980; Etezadifar & Amini,
118 2010).

119 **Data collection:**

120 All measurements for this study were collected from specimens in the American Museum of
121 Natural History in New York City, NY, USA. Five body regions (back, tail, vent, belly, and
122 breast) of 186 museum specimens (*E. garzetta*: 112 white morphs; *E. gularis*: 23 dark and 11
123 white morphs; *E. dimorpha*: 24 dark and 16 white morphs; in total 139 white unicoloured
124 individuals and 47 unicolour dark individuals). We did not measure head feathers because they
125 include ornamental plumes in the breeding season, which complicates assessment. Each of the
126 body regions of each specimen was measured three times with a Konica-Minolta CR-400
127 Spectrophotometer. The mean of the three measurements was used for subsequent analyses. The
128 spectrophotometer was standardized between each measurement. The wavelength reflection was
129 recorded in Commission International d'Edairage LAB (CIELAB, also known as LAB)
130 measurement system (Schanda, 2007; Hunter Associates Laboratory, 2008). In this method, the
131 colour of the measured area is expressed in three dimensions, L*, a*, and b*. L* ranges from 0
132 (black) to 100 (white) and shows how dark a scanned surface is. Whereas a* and b* range from -

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133 100 to +100 and represent how green/red and blue/yellow, the scanned surface is, respectively.
134 Because the egrets are either white or dark grey, a^* was excluded from analyses, and b^* (the
135 blueness) was used solely for dark-morph individuals as a second criterion for dark pigmentation
136 (Shahrokhi & Patten, 2022).

137 Chemicals used to preserve museum specimens or failure to remove subcutaneous fat discolored
138 feathers of many of our samples; they had turned yellow or brownish. To avoid discoloration
139 bias, we fitted a linear regression to mean yellowness (b^*) and mean whiteness (L^*) for a given
140 feather tract and used resultant residuals as a new response variable (i.e., the tract with
141 discoloration regressed out). For all tracts observed data and bias-corrected data gave similar
142 results (S1). Therefore, hereafter we present the observed data.

143 **Statistical Analyses:**

144 We adopted Kruschke's (2013) "BEST" (Bayesian Estimation Supersedes the t test) framework
145 to create a Bayesian analogue to the paired t -test for comparison among tracts within individuals
146 of a species. The reasons for choosing this method are: first, the distribution of data is flexible
147 (we modeled with a t -distribution but could have used alternatives, such as T); second, output is a
148 distribution of estimates rather than a single point estimate; and, third, pairing controlled for
149 multiple tracts being measured within the same individual specimen. Comparisons of a given
150 feather tract among species were analyzed similarly but with a Bayesian analogue to the two-
151 sample t -test. Both models were built in JAGS and run via R 4.0 using the package 'rjags'
152 (Plummer, 2016). We estimated these parameters via three chains in standard Markov chain
153 Monte Carlo ran for 10,000 iterations with a 1,000 burn-in. Priors were flat, and no thinning was
154 required. Model convergence was checked with standard trace plots. Differences are marked if $>$
155 0.90 of the posterior distribution of the parameter of interest was positive or negative; anything

156 less is too uncertain. Moreover, meaningful differences are those for which magnitude of mean
157 effect size (η)—essentially a Cohen's d —exceeded 0.40, the low end of a moderate effect.

158 **Results**

159 Regardless of species, the back feathers were the darkest tract on dark morphs and
160 whitest tract on white morphs (Fig. 2). Among all pairwise comparisons between every two body
161 tracts, most differences were relative to back feathers differ most. This pattern held between back
162 and any other tracts in all measurements for both morphs (Fig. 3, for *E. gularis*). Since the
163 patterns for the two other species (*E. garzetta* and *E. dimorpha*) were similar; the graphs for those
164 species can be found in the Supplementary Information (S2, and S3).

165 Variation among different body regions was remarkably consistent within white-morph
166 individuals of each of the three species. As predicted, the back was always the whitest part of the
167 body, with the highest difference between back and belly and between back and breast (Table 1).
168 On the ventral side, the breast was noticeably whiter than either the belly or the vent, with the
169 highest difference between breast and belly and the lowest between breast and vent (Table 1).

170 For darkness and blueness measurements, a similar pattern was detected at the intra-individual
171 level among the dark morphs of two species (*E. gularis* and *E. dimorpha*). The back was always
172 the darkest (L values) and bluest (b values) part of the body, with the highest difference between
173 back and belly and the lowest difference between back and breast (Fig. 1; Table 1). Ventrally,
174 the breast was bluer than other body regions, with the highest difference between breast and
175 belly and the lowest between breast and vent (Tables 2).

176 **Discussion**

177 Most previous studies on coloration compare either different species that live in similar
178 environments or individuals within a species whose colour patterns and hues vary (e.g.,

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179 Campagna *et al.*, 2017). Our study is the first to focus on variation among feather tracts within
180 unicoloured individuals across three egret species. For dark individuals, we predicted that the
181 feather tracts that are more exposed to the sun (back and breast) would be darker or more
182 pigmented compared to other tracts (belly, tail, and vent). The feather tracts most exposed to the
183 sun (back and breast) for white morph individuals will be whiter or less pigmented than other
184 tracts (tail, vent, and belly). To test our hypotheses, we measured visual wavelength colour
185 reflection to measure how dark or white each of the body tracts is compared to other body
186 regions. The back feathers were indeed the darkest, which indicates the highest relative
187 eumelanin concentration in this area of the body, among the dark individuals, and indeed whiter
188 than other tracts among the white individuals. The patterns held within each species, which
189 means of neither whiteness nor darkness differed.

190 In other birds, as with egrets, the head feathers of Golden Eagles (*Aquila chrysaetos*) from all
191 around Europe have different melanin concentrations as a response to photodamage (Galván *et*
192 *al.*, 2018a). The variation was not based on isolation, or structure but resulted from local
193 adaptation. Melanin concentration correlated with altitude and UV exposure. As the elevation
194 increases, the UV intensity increases, and as a result feathers contained more melanin. As with
195 Golden Eagles and egrets, more thrushes with dark plumage occur in highlands where the UV
196 intensity is higher (Sandoval & Barrantes, 2019).

197 Other studies, such as Nicolaï *et al.* (2020), Jablonski and Chaplin (2010), Hansson *et al.* (2007),
198 and D'Orazio *et al.* (2006), reported a positive correlation between melanin concentration in skin
199 and hair and UV exposure. All these local adjustments are considered a defence mechanism
200 against photodamage, which means that more exposed body regions to sunlight are darker than

201 other body tracts (Choudhary *et al.*, 2020; Markiewicz & Idowu, 2020). Our results, also, for the
202 dark individuals are consistent with the common defence system.

203 Another hypothesis that could account for darker back feathers would be if dark-morph birds
204 preferentially applied oil from their uropygial gland to those feathers. These oils darken feathers
205 and thus would achieve a photoprotective effect (López-Rull *et al.*, 2010). A preen oil hypothesis
206 could not be generalized to white morphs, though, unless white birds preferentially avoided
207 applying preen oil to their back feathers, an unlikely situation given the role these oils appear to
208 play in maintaining feather integrity (Shawkey *et al.*, 2003) and avoiding ectoparasites (Proctor
209 & Owens, 2000).

210 Most studies on UV have measured reflectance to answer questions about mate choice and avian
211 vision. A protection hypothesis implies that white feathers are not for mate attraction but because
212 they reflect UV radiation. Morph is genetically hardwired, so there is no room for adaptive
213 plasticity—regardless of environment, a white morph cannot become dark or vice versa. It may
214 be that white and dark morphs will segregate via “matching habitat choice” (Edelaar *et al.*,
215 2017), and any habitat matching may increase with environmental harshness, as is UV
216 reflectance (Stella *et al.*, 2018). Future research ought to investigate feather structure, mate
217 choice, and molecular development of white feathers.

218 It may be that solar radiation in general, and not just UV radiation in particular, shapes some of
219 aspects of dichromatism. Birds, like mammals, are endothermic. Regulating core body
220 temperature may pose a challenge in hot environments or seasons (Lovegrove, 2019). The role
221 played by dark or light plumage is debated. It may be that darker feathers absorb solar radiation
222 to prevent transmitting heat to the skin (Wolf & Walsberg, 2000). Conversely, paler feathers
223 reflect more light and thus reduce body temperature (Arai *et al.*, 2017; Fargallo *et al.*, 2018). A

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224 thermoregulation hypothesis would seem to lead to the same predictions as the UV hypothesis.
225 However, it may be more difficult to acquire stable dimorphism on purely thermoregulatory
226 grounds because physiological effects of both the UV hypothesis and thermoregulation
227 hypothesis are expected to be more proximate (relative to a more ultimate response to UV
228 radiation).

229 Besides environmental factors, such as UV exposure, producing melanin is under genetic control
230 too. So far, more than 150 genes have been identified that affect skin and feather colour either
231 directly or indirectly (Brenner & Berking, 2010). When an individual faces UV stress, the stress
232 activates melanogenesis (Ducrest *et al.*, 2008). It activates DNA repair, antioxidant responses,
233 and survival pathways essential for genomic stability and the prevention of harmful
234 transformation or apoptosis (Abdel-Malek *et al.*, 2010). Although some studies, e.g., Golden
235 Eagles (Galván *et al.*, 2018a), have shown no evidence of genetic differences among colour
236 variations, we cannot confirm that the environment solely causes the colour differentiation
237 among egrets' tracts. Therefore, molecular and developmental studies are needed.

238 If the underlying causal mechanisms for the back feathers being darkest on dark morphs
239 (photoprotection) and whitest on white morphs (albedo) hold, then it is plausible that
240 dichromatism in both *E. dimorpha* and *E. gularis* have evolved via disruptive selection. This
241 possibility is in response to the same environmental conditions but different melanin deposition
242 or expression. Disruptive selection is when intermediate phenotypes have reduced fitness while
243 the two phenotypic extremes have a fitness advantage (Rueffler *et al.*, 2006; Planqué *et al.*,
244 2016). Disruptive selection is considered as one of morphological diversification's main drivers
245 (Rueffler *et al.*, 2006). Under this view, it is possible that the intermediate individuals could not
246 resist UV stress and be selected against through time. On the other hand, the unicolour

247 individuals could manage to resist the UV exposure by local adaptation: dark morphs resist UV
248 stress and protect the body from excess UV exposure by increased melanin concentration in the
249 back and breast feathers, while in white morphs those regions are whiter. Our results are
250 consistent with predictions of a model of disruptive selection, yet more morphological,
251 molecular, and mate choice studies need to be done to support this hypothesis.

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257 **Data Availability**

258 The measurements can be found through the doi: [10.17632/jf4ffbny9.1](https://doi.org/10.17632/jf4ffbny9.1).

259 **References:**

- 260 Abdel-Malek, Z.A., Kadekaro, A.L. & Swope, V.B. (2010). Stepping up melanocytes to the challenge of UV
261 exposure. *Pigment Cell Melanoma Res.* **23**, 171–186.
- 262 Andersson, M. & Iwasa, Y. (1996). Sexual Selection. *Trends Ecol. Evol.* **11**, 53–58.
- 263 Bourgeois, Y.X.C., Delahaie, B., Gautier, M., Lhuillier, E., Malé, P.J.G., Bertrand, J.A.M., Cornuault, J.,
264 Wakamatsu, K., Bouchez, O., Mould, C., Bruxaux, J., Holota, H., Milá, B. & Thébaud, C. (2017). A novel
265 locus on chromosome 1 underlies the evolution of a melanic plumage polymorphism in a wild songbird. *R.*
266 *Soc. Open Sci.* **4**, 1–14.
- 267 Brenner, M. & Berking, C. (2010). Grundlagen der hautpigmentierung. *Der Hautarzt* **61**, 554–560.
- 268 Burt, E.H. (1986). An Analysis of Physical, Physiological, and Optical Aspects of Avian Coloration with Emphasis
269 on Wood-Warblers. *Ornithol. Monogr.* **38**, iii–126.

13 Linking Plumage Dimorphism and Environmental Stress

- 270 Campagna, L., Repenning, M., Silveira, L.F., Fontana, C.S., Tubaro, P.L. & Lovette, I.J. (2017). Repeated divergent
271 selection on pigmentation genes in a rapid finch radiation. *Sci. Adv.* **3**, 1–12.
- 272 Choudhary, R., Sharma, A., Kumar, S., Upadhyay, R.C., Singh, S.V. & Mohanty, A. (2020). Role of alpha-
273 melanocyte stimulating hormone (α -MSH) in modulating the molecular mechanism adopted by melanocytes
274 of *Bos indicus* under UVR stress. *Mol. Cell. Biochem.* **465**, 141–153.
- 275 Cuthill, I.C. (2006). Perception and Measurements. In *Bird Coloration. Volume I: Mechanisms And Measurements:*
276 3–40. Hill, G.E. & McGraw, Kevin, J. (Eds.). Harvard University Press.
- 277 Cuthill, I.C., Partridge, J.C., Bennett, A.T.D., Church, S.C., Hart, N.S. & Hunt, S. (2000). Ultraviolet Vision in
278 Birds. *Adv. Study Behav.* **29**, 159–214.
- 279 D’Orazio, J.A., Nobuhisa, T., Cui, R., Arya, M., Spry, M., Wakamatsu, K., Igras, V., Kunisada, T., Granter, S.R.,
280 Nishimura, E.K., Ito, S. & Fisher, D.E. (2006). Topical drug rescue strategy and skin protection based on the
281 role of Mc1r in UV-induced tanning. *Nature* **443**, 340–344.
- 282 Ducrest, A.L., Keller, L. & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural
283 syndromes. *Trends Ecol. Evol.* **23**, 502–510.
- 284 Eaton, M.D. & Lanyon, S.M. (2003). The ubiquity of avian ultraviolet plumage reflectance. *Proc. R. Soc. B Biol.*
285 *Sci.* **270**, 1721–1726.
- 286 Edelaar, P., Jovani, R. & Gomez-Mestre, I. (2017). Should I change or should I go? Phenotypic plasticity and
287 matching habitat choice in the adaptation to environmental heterogeneity. *Am. Nat.* **190**, 506–520.
- 288 Endler, J.A. (1978). A Predator’s View of Animal Color Patterns. *Evol. Biol.* **11**, 319–364.
- 289 Endler, J.A. (1984). Progressive background in moths, and a quantitative measure of crypsis. *Biol. J. Linn. Soc.* **22**,
290 187–231.
- 291 Endler, J.A. & Thery, M. (1996). Interacting Effects of Lek Placement, Display Behavior, Ambient Light, and Color
292 Patterns in Three Neotropical Forest-Dwelling Birds. *Am. Nat.* **148**, 421–452.
- 293 Endler, J.A., Westcott, D.A., Madden, J.R. & Robson, T. (2005). Animal visual systems and the evolution of color

14 Linking Plumage Dimorphism and Environmental Stress

- 294 patterns: Sensory processing illuminates signal evolution. *Evolution (N. Y.)* **59**, 1795–1818.
- 295 Etezadifar, F. & Amini, H. (2010). Current Status of the Breeding Population of the Western Reef Heron *Egretta*
296 *gularis* along the Northern Coasts of the Persian Gulf and Oman Sea , and its Wintering Population in the
297 South of Iran. *Heron* **5**, 71–80.
- 298 Galván, I., Jorge, A., Pacheco, C., Spencer, D., Halley, D.J., Itty, C., Kornan, J., Nielsen, J.T., Ollila, T., Sein, G.,
299 Stój, M. & Negro, J.J. (2018a). Solar and terrestrial radiations explain continental-scale variation in bird
300 pigmentation. *Oecologia* **188**, 683–693.
- 301 Galván, I., Rodríguez-Martínez, S. & Carrascal, L.M. (2018b). Dark pigmentation limits thermal niche position in
302 birds. *Funct. Ecol.* **32**, 1531–1540.
- 303 Gomez, D. & Théry, M. (2007). Simultaneous crypsis and conspicuousness in color patterns: Comparative analysis
304 of a neotropical rainforest bird community. *Am. Nat.* **169**, S42–S61.
- 305 Hancock, J. & Kushlan, J.A. (1984). *The Herons Handbook*. London: Croom and Helm.
- 306 Hansson, L.A., Hylander, S. & Sommaruga, R. (2007). Escape from UV threats in zooplankton: A cocktail of
307 behavior and protective pigmentation. *Ecology* **88**, 1932–1939.
- 308 Hausmann, F., Arnold, K.E., Marshall, N.J. & Owens, I.P.F. (2003). Ultraviolet signals in birds are special. *Proc. R.*
309 *Soc. B Biol. Sci.* **270**, 61–67.
- 310 Hideg, É., Jansen, M.A.K. & Strid, Å. (2013). UV-B exposure, ROS, and stress: Inseparable companions or loosely
311 linked associates? *Trends Plant Sci.* **18**, 107–115.
- 312 Hunter Associates Laboratory, I. (2008). CIE L* a* b* Color Scale. *Vol. 8*.
- 313 Jablonski, N.G. & Chaplin, G. (2010). Human skin pigmentation as an adaptation to UV radiation. *Proc. Natl. Acad.*
314 *Sci. U. S. A.* **107**, 8962–8968.
- 315 Kruschke, J.K. (2013). Bayesian estimation supersedes the t test. *J. Exp. Psychol. Gen.* **142**, 573–603.
- 316 Kushlan, J.A. & Hancock, J. (2005). 14. The Herons: Ardeidea (Bird Families of the World). In *Bird Families of the*
317 *World*: xv–433. New York: Oxford University Press.

15 Linking Plumage Dimorphism and Environmental Stress

- 318 Margalida, A., Negro, J.J. & Galván, I. (2008). Melanin-based color variation in the Bearded Vulture suggests a
319 thermoregulatory function. *Comp. Biochem. Physiol. - A Mol. Integr. Physiol.* **149**, 87–91.
- 320 Markiewicz, E. & Idowu, O.C. (2020). Melanogenic difference consideration in ethnic skin type: A balance
321 approach between skin brightening applications and beneficial sun exposure. *Clin. Cosmet. Investig.*
322 *Dermatol.* **13**, 215–232.
- 323 McKenzie, R.L., Aucamp, P.J., Bais, A.F., Björn, L.O., Ilyas, M. & Madronich, S. (2011). Ozone depletion and
324 climate change: Impacts on UV radiation. *Photochem. Photobiol. Sci.* **10**, 182–198.
- 325 Mock, D.W. (1980). White-dark polymorphism in herons. *Proc. First World Wildl. Found. Symp.* **1**, 145–161.
- 326 Mullen, P. & Pohland, G. (2008). Studies on UV reflection in feathers of some 1000 bird species: Are UV peaks in
327 feathers correlated with violet-sensitive and ultraviolet-sensitive cones? *Ibis (Lond. 1859)*. **150**, 59–68.
- 328 Nicolai, M.P.J., Shawkey, M.D., Porchetta, S., Claus, R. & D’Alba, L. (2020). Exposure to UV radiance predicts
329 repeated evolution of concealed black skin in birds. *Nat. Commun.* **11**, 1–8.
- 330 Planqué, R., Powell, S., Franks, N.R. & van den Berg, J.B. (2016). Disruptive selection as a driver of evolutionary
331 branching and caste evolution in social insects. *J. Evol. Biol.* **29**, 2111–2128.
- 332 Plummer, M. (2016). rjags: Bayesian graphical models using MCMC. *R Packag. version 3-13*.
- 333 Poelstra, J.W., Vijay, N., Bossu, C.M., Lantz, H., Ryll, B., Müller, I., Baglione, V., Unneberg, P., Wikelski, M.,
334 Grabherr, M.G., Wolf, J.B.W., Muller, I., Baglione, V., Unneberg, P., Wikelski, M., Grabherr, M.G., Wolf,
335 J.B.W., Müller, I., Baglione, V., Unneberg, P., Wikelski, M., Grabherr, M.G. & Wolf, J.B.W. (2014). The
336 genomic landscape underlying phenotypic integrity in the face of gene flow in crows. *Science (80-.)*. **344**,
337 1410–1414.
- 338 Poelstra, J.W., Vijay, N., Hoepfner, M.P. & Wolf, J.B.W. (2015). Transcriptomics of colour patterning and
339 coloration shifts in crows. *Mol. Ecol.* **24**, 4617–4628.
- 340 Rueffler, C., Van Dooren, T.J.M., Leimar, O. & Abrams, P.A. (2006). Disruptive selection and then what? *Trends*
341 *Ecol. Evol.* **21**, 238–245.

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- 342 Sandoval, L. & Barrantes, G. (2019). Is black plumage an adaptation to high elevations in a cosmopolitan bird
343 genus? *J. Avian Biol.* **50**, 1–8.
- 344 Schanda, J. (2007). *Colorimetry: Understanding the CIE System*. John Wiley Sons.
- 345 Schuch, A.P., Garcia, C.C.M., Makita, K. & Menck, C.F.M. (2013). DNA damage as a biological sensor for
346 environmental sunlight. *Photochem. Photobiol. Sci.* **12**, 1259–1272.
- 347 Schuch, A.P., Moreno, N.C., Schuch, N.J., Menck, C.F.M. & Garcia, C.C.M. (2017). Sunlight damage to cellular
348 DNA: Focus on oxidatively generated lesions. *Free Radic. Biol. Med.* **107**, 110–124.
- 349 Shahrokhi, G. & Patten, M.A. (2022), Linking Plumage Dimorphism and Environmental Stress, Mendeley Data, V1,
350 doi: 10.17632/jf4ffbnyc9.1
- 351 Stella, D., Pecháček, P., Meyer-Rochow, V.B. & Kleisner, K. (2018) UV reflectance is associated with
352 environmental conditions in Palearctic *Pieris napi* (Lepidoptera: Pieridae). *Insect Sci.* **25**, 508–518.
- 353 Sun, Y., Li, J., Zhang, W. & Wang, T.J. (2013). Local stress evolution in thermal barrier coating system during
354 isothermal growth of irregular oxide layer. *Surf. Coatings Technol.* **216**, 237–250.
- 355 Walsberg, G.E., Campbell, G.S. & King, J.R. (1978). Animal coat color and radiative heat gain: A re-evaluation. *J.*
356 *Comp. Physiol.* □ *B* **126**, 211–222.
- 357 Ward, J.M., Blount, J.D., Ruxton, G.D. & Houston, D.C. (2002). The adaptive significance of dark plumage for
358 birds in desert environments. *Ardea* **90**, 311–323.
- 359 Zimmerman, D.A., Turner, D.A. & Pearson, D.J. (1996). *Birds of Kenya and northern Tanzania*. Princeton
360 University Press.

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Table 1 The relative whiteness (L^*) body tracts within *Egretta* species, assessed using the BEST approach

	Little Egret (<i>E. garzetta</i>) <i>N</i> = 112				Wester Reef Heron (<i>E. gularis</i>) <i>N</i> = 11				Dimorphic Egret (<i>E. dimorpha</i>) <i>N</i> = 16			
	Belly	Vent	Tail	Back	Belly	Vent	Tail	Back	Belly	Vent	Tail	Back
Breast	>>	>	>	=	>	=	>>	=	>>	>>	=	<<
Belly		<<	<<	<<		=	>>	=		=	<<	<<<
Vent			<<	=			>>	=			<	<<<
Tail				=				<				=

The ">" or "<" means the posterior probability distribution was between 90.0 and 97.5% with absolute corresponding effect size, $|h|$, between 0.4 and 0.5. The ">>" or "<<" means more than 97.5% of the posterior probability distribution of estimated difference score was greater than zero with $|h|$ greater than 0.55. The ">>>" or "<<<<" means the $|h|$ is equal or greater than 1.0.

Table 2 The relative darkness (L^*) and blueness (b^*) body tracts within *Egretta* species, assessed using the BEST approach

	Wester Reef Heron <i>E. gularis</i> (L^*) <i>N</i> = 23				Dimorphic Egret <i>E. dimorpha</i> (L^*) <i>N</i> = 24				Western Reef Heron <i>E. gularis</i> (b^*) <i>N</i> = 23				Dimorphic Egret <i>E. dimorpha</i> (b^*) <i>N</i> = 24			
	Belly	Vent	Tail	Back	Belly	Vent	Tail	Back	Belly	Vent	Tail	Back	Belly	Vent	Tail	Back
Breast	=	=	=	<<<	=	>	=	<<	>	>>	>>	<<<	>>	>>	>	<<<
Belly		=	=	<<		=	=	<<		>>	>	<<<		=	=	<<<
Vent			=	<<			=	<<			=	<<<			<<	<<<
Tail				<<				<<				<<<				<<<

The ">" or "<" means the posterior probability distribution was between 90.0 and 97.5% with absolute corresponding effect size, $|h|$, between 0.4 and 0.5. The ">>" or "<<" means more than 97.5% of the posterior probability distribution of estimated difference score was greater than zero with $|h|$ greater than 0.55. The ">>>" or "<<<<" means the $|h|$ is equal or greater than 1.0.

Figure 1. An illustration of solar radiation absorption and reflection for the range of black to white feather coloration.

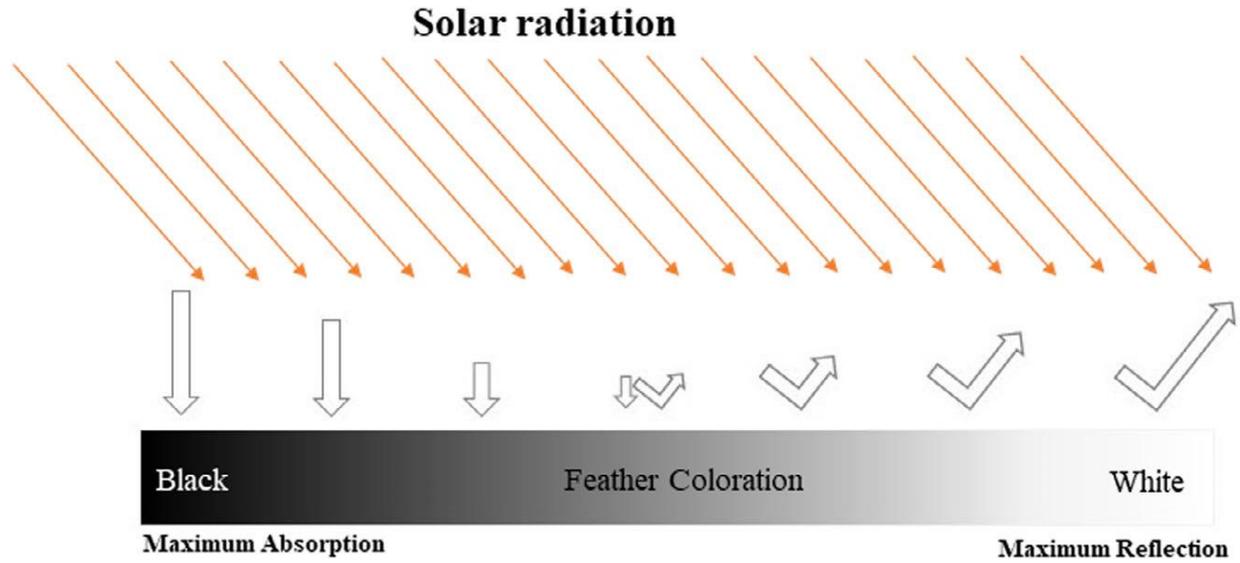
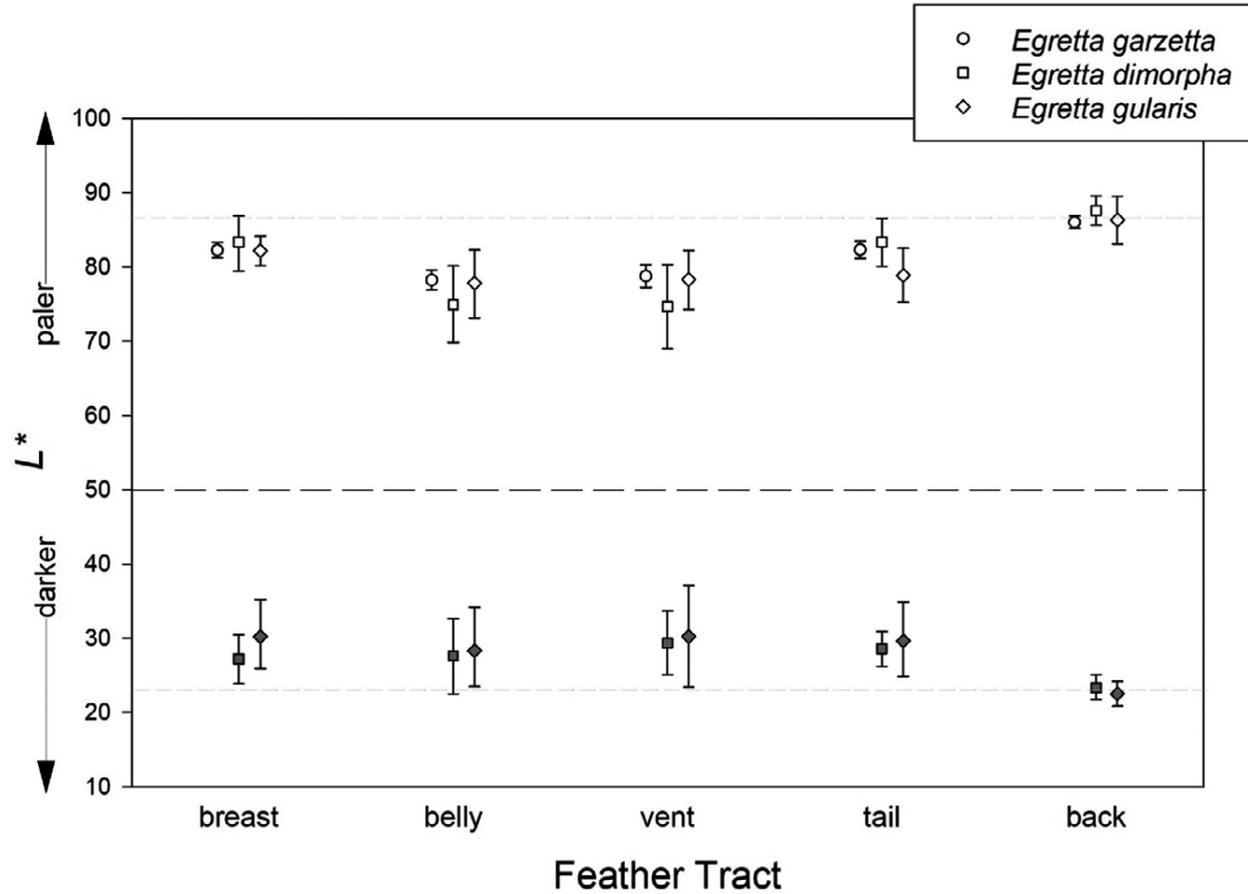


Figure 2. Plumage darkness (L^* values) of five feather tracts of three species *Egretta egretts*. Values shown are estimated means and associated 95% highest density Bayesian credible intervals. Note that back feathers are whiter that other tracts across all three species yet darker than other tracts in dark morphs of two species.



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Figure 3. Pairwise differences between body regions of *Egretta gularis* within each color morph (white = 11, dark = 23). A) The difference of whiteness (L^*) among white morphs. B) The difference of blueness (b^*) among dark morphs. C) The difference of darkness (L^*) among dark morphs. The yellow graphs represent pairwise differences between back, which we expect to be under the strongest selection, and other body regions, as indicated. The blue graphs indicate pairwise differences between other body regions. The dotted line indicated no difference.

