

1 **GLOBAL PATTERNS OF PLUMAGE COLOUR EVOLUTION IN ISLAND-LIVING PASSERIFORM BIRDS**

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11

12 **ABSTRACT**

13 Plumage coloration is an important trait involved communication and is shaped by a variety of  
14 ecological pressures. Island residency has the potential to change the evolutionary trajectory of  
15 plumage colour by differences in habitat and resources, or by altering predation pressure and  
16 social selection intensity. Latitude, island size, and isolation may further influence colour  
17 evolution by biasing colonization. Therefore, general patterns of plumage evolution are difficult  
18 to disentangle. We used phylogenetically controlled analyses to assess the influence of island  
19 residency on plumage colouration, by calculating chromaticity values from red, blue, green  
20 scores extracted from photos of Order Passeriformes birds. Importantly, we controlled for  
21 ecological factors hypothesized to influence colour evolution and assessed family-level effects.  
22 We found 1) colour varied between islands and mainlands in females, but not males, and both  
23 sexes were affected by several ecological factors; 2) patterns of colour evolution varied among  
24 families; 3) island size and distance to the mainland and other islands significantly influenced  
25 colour; and 4) interactions between ecological factors and latitude were consistently influenced  
26 colour, supporting a latitudinal gradient hypothesis. Our results indicate although island  
27 residency influences female colour evolution, a myriad of ecological factors drive plumage  
28 colour and the patterns vary among families.

29 **Keywords:** plumage colour, Passeriformes, ecology and evolution, islands, comparative  
30 phylogenetics

31 **INTRODUCTION**

32           Animal colour is an important and complex signal used in both inter- and intraspecific  
33 interactions (1) and is thought to evolve in response to a variety of evolutionary mechanisms  
34 including natural selection, sexual selection, genetic drift, environmental conditions, arbitrary  
35 mate choice (2), or some combination of these factors (3). In birds, plumage coloration varies  
36 widely among species (4), and colour signals may play important evolutionary roles by  
37 mediating mate choice, species recognition, and predator avoidance (5). As such, there is  
38 considerable interest in understanding the factors driving global patterns of plumage colour (6),  
39 (7),(8),(9),(10),(11).

40           Island systems provide unique opportunities to explore patterns of plumage colouration.  
41 Compared to continental habitats, islands are isolated, relatively small, and are replicated across  
42 a broad geographic scale, making them ideal systems to study the evolutionary processes that  
43 shape variation in traits (12). In response to insular environments, a number of “island  
44 syndrome” studies have documented the parallel evolution of island vertebrates when compared  
45 to mainland populations (13),(14). According to the “island rule” (15), body sizes in large  
46 vertebrates trend towards dwarfism while small vertebrates trend towards gigantism when  
47 comparing island populations to mainland populations (16),(14),(17),(18). Relative to their  
48 mainland counterparts, island vertebrates also exhibit K-selected life history strategies, as  
49 evidenced by low fecundity, relatively longer developmental periods, and high survival (16),  
50 (19). However, island studies have mostly focused on body size and life history traits, while the  
51 impact of island environments on ornamental traits is less understood.

52           Analyses of plumage colouration reveal a general pattern of dull-colouration in island  
53 birds, but most of these studies are constrained by small geographic scope and use of relatively

54 few species (7),(8),(10), but see (6). However, a recent worldwide analysis (11) compared  
55 plumage colouration of 116 island species to closely related mainland species and found a  
56 reduction in plumage brightness and colour intensity as well as a reduction in the number of  
57 colour patches in island species. Another large-scale study (20) found colour differences between  
58 mainland and island birds in 731 species across three families (Meliphagidae, Fringillidae, and  
59 Monarchidae), but the direction of this effect was complex and varied by family: Meliphagidae  
60 shifted towards melanin-based plumage while Fringillidae shifted away from carotenoid plumage  
61 on island environments. Together, these results suggest different selective pressures may be  
62 operating in different lineages or vary geographically.

63         Several hypotheses have been proposed to explain colour loss in island birds. If plumage  
64 colour functions in interspecific interactions, island birds may be duller coloured due to reduced  
65 selection for species recognition as island systems typically contain fewer sympatric species than  
66 continental areas (7),(8). Alternatively, if exaggerated color expression is under condition  
67 dependent sexual selection (21), then island species may become less colourful because of  
68 reduced sexual selection pressure on islands (8),(22). Sexual selection is predicted to be relaxed  
69 on islands because of reduced genetic diversity from founder effects (23) and/or reduced parasite  
70 pressure (24), diminishing the indirect fitness benefits from extra-pair copulations (25). The idea  
71 of reduced sexual selection pressure on islands is supported by lower extra-pair paternity rates in  
72 island species (26). Changes in the costs of bright plumage may also vary between island and  
73 continental habitats. For example, predation pressure on islands is often lower (27) and thus  
74 could promote elaboration of plumage colouration rather than camouflage (28),(29). Island  
75 species may also show decreased territoriality in part due to fewer con- and heterospecifics,  
76 relaxed sexual selection pressure, and/or increased resource availability (11), possibly reducing

77 the need to signal territoriality during species interactions (30). Food resources on islands may  
78 differ from those on the mainland, and carotenoid-deficient diets may reduce carotenoid-based  
79 (red, orange, yellow) plumage expression (21). Finally, some combination of these effects may  
80 result in colour differences between mainland and island birds.

81         Assessing colour variation in island birds can be challenging due to confounding  
82 ecological and natural history factors. First, colour evolution may be affected by latitudinal  
83 differences among species. Known as Gloger’s Rule, this biogeographic rule predicts animal  
84 coloration will covary with latitudinal changes in body temperature regulation, colours needed  
85 for camouflage, parasite loads, or some combination of these factors (31). Second, differences in  
86 habitat may influence ambient light in the environment, so there may be selection for or against  
87 ornate plumage given habitat-specific light conditions (32). Third, island characteristics such as  
88 geographic size and isolation (i.e., distance from mainland) may affect the evolutionary  
89 trajectory of colour evolution by biasing colonization or by limiting population sizes, thereby  
90 diminishing or exacerbating genetic drift effects (23). Finally, macroevolutionary studies often  
91 assess higher-level taxonomic processes, but because selection pressures likely vary among  
92 families, the directionality of the effects may change at lower taxonomic levels (33),(34).  
93 Therefore, to unravel the mechanisms mediating plumage evolution, it is important for studies to  
94 assess the biological and ecological factors contributing to colour at a global scale and across a  
95 broad range of taxa.

96         Although previous studies have documented colour differences between mainland and  
97 island bird populations using a few families or subsets of species (e.g., (11),(20)), no study has  
98 comprehensively assessed the selective pressures driving plumage colour evolution in island  
99 birds using an entire order of birds—while also simultaneously controlling for confounding

100 biotic and abiotic factors—calling into question the generalizability of an island effect on  
101 plumage coloration. Using a phylogenetic statistical framework, in this study we leveraged a  
102 global and comprehensive dataset of plumage colour in the Order Passeriformes to test the  
103 hypothesis that colour would differ between mainland and island populations. The Passeriformes  
104 is an ideal order to test hypotheses on plumage colour evolution because 1) it is a speciose order  
105 (more than half of all living birds), 2) passeriform species generally exhibit relatively ornate  
106 plumage colouration (6), 3) there is high variation in plumage colour among species, and 4)  
107 passeriform birds are broadly distributed throughout the world in both mainland and island  
108 habitats (35). We specifically tested the prediction that male and female passerines occupying  
109 islands would be less colourful than those occupying the mainland (*sensu* (11)), while also  
110 controlling for covariates such as latitude (i.e. “Gloger’s Rule”, (31)), diet (3), and variation in  
111 ambient light in the habitat (32). Given that selection pressures may vary among species within  
112 Passeriformes, we also tested for colour differences between mainland and islands species at the  
113 family-level. Finally, because island size and island isolation may influence species richness,  
114 resource availability, predation pressure, and/or bias island colonization (*sensu* (11),(29)), we  
115 also tested the effect of island size and isolation on plumage coloration.

## 116 **MATERIALS AND METHODS**

### 117 *Data Collection*

118 We classified 5,693 extant Passeriformes species (Dryad Data Respository) as mainland  
119 or island dwelling (Fig. 1) using global range maps from the International Union of Conservation  
120 of Nature’s Red List of Threatened Species (36). We considered mainland to be a land mass  
121 larger or equal to 7.7 million km<sup>2</sup> (approximately the area of mainland Australia, the smallest  
122 defined continent (37)). We defined islands as smaller or equal to 2.2 million km<sup>2</sup>

123 (approximately the size of Greenland, the largest defined island (37),(38). Passerines where 80%  
124 of their range covered non-continental landmasses (such as the Hawaiian islands or New  
125 Zealand) were classified as “island” species (n=1183). Species were classified as “mainland”  
126 when approximately 80% or more of the range covered a continent (such as North America or  
127 Australia) (n=4510). Throughout, we use the term land classification to refer to designation of a  
128 species as either an island or continental species Using IUCN classifications, we also collected  
129 the latitude centroid of each species range. Diet, habitat type, and geographic region were taken  
130 from (39) based on (40), (41), and (42). These factors may influence plumage colouration  
131 differences between island and continental species because of variation in pressures associated  
132 with thermoregulation, resource availability, dietary precursors, or light environments. We  
133 obtained data on island size, distance to nearest mainland, and distance to nearest other islands  
134 from the UN Environmental Programme island directory (38). Island size may influence colour  
135 evolution because there may be a greater diversity of predators on larger islands (29), while a  
136 lower diversity of congeneric species on smaller islands may reduce species recognition  
137 pressures (11). Distance to continents and other islands may influence the evolutionary trajectory  
138 of colouration of island birds through founder effects of relatively few individuals and alleles  
139 (35). Collectively, our dataset included land classification (island vs. continental), habitat, diet,  
140 global geographic region, range latitude for all extant passerines, and island size, distance to  
141 mainland, and distance to other islands for passerines found on islands (Dryad Data Repository).

142 We used plumage colour data from (43), who quantified red, green, and blue (RGB)  
143 values from images of the crown, forehead, nape, throat, upper breast and lower breast of all the  
144 Passeriformes species listed in the Birds of the World (44). Because carotenoid- and structural-  
145 based colouration lead to elaborate colouration through different physiological mechanisms, we

146 used colour scores extracted from the RGB values (43) to calculate chromaticity. Red  
147 chromaticity was calculated using the equation:  $R/(R+G+B)$ , and blue chromaticity was  
148 calculated using the equation:  $B/(R+G+B)$ , where R is the red value, G is the green value, and B  
149 is the blue value from (43). Chromaticity provides an estimate of the relative short and long  
150 wavelengths and is a reliable estimate of carotenoid and structural plumage coloration (45).

151 To assess the efficacy of using chromaticity to estimate “carotenoid” and “structural”  
152 plumage coloration, a single, independent observer categorized the colour for multiple plumage  
153 patches in males and females of all species in the Family Thraupidae (n=346 species/sex) using  
154 the publicly available visual media source Birds of the World by the Cornell Lab of Ornithology  
155 (44). In this analysis, we used 10 patches: auricular, crown, back, rump, throat, breast, belly,  
156 crissum, wingtip (color of the tip of the longest primary flight feather), and dorsal side of the  
157 rectrices. Patches were chosen to mirror (46), who measured the reflectance spectrum of each  
158 patch colour using a spectrophotometer for most members in Thraupidae. We then compared the  
159 chromaticity values to these classifications and found the distribution of red and blue  
160 chromaticity scores did not overlap in plumage patches classified as “blue” or “red.” This  
161 suggests that our chromaticity values effectively captured the variation in structural blue and  
162 carotenoid red plumage coloration (Fig. S1).

### 163 *Phylogenetic Methods*

164 To control for phylogenetic relationships in our analyses, we downloaded 1000 potential  
165 phylogenies from birdtree.org (47),(48) for the 5,693 passerine species included in the dataset.  
166 We used TreeAnnotator in BEAST v1.10.1 (49) to construct a maximum clade credibility tree  
167 using 1% burn in and mean node heights. We repeated these steps with the 1,183 island  
168 passerines to test the effect of island characteristics on passerine colour.

169 *Statistical Analysis*

170 We performed all analyses in R 3.5.3 (50) using phylogenetic generalized least squares  
171 (PGLS) in the *nlme* package (51). We tested how male and female passerine colour variation was  
172 explained by land classification, diet, habitat, latitude, and region using stepwise model reduction  
173 based on Akaike Information Criterion (AIC). We first built a full model, which included either  
174 red or blue chromaticity as the response variable, and land classification, diet, habitat, latitude,  
175 region, and their interactions (land classification x latitude, land classification x diet, land  
176 classification x habitat, and habitat x diet) as the main effects. We built separate models for each  
177 sex. We then undertook model reduction for all possible models using the *StepAIC* function in  
178 the *MASS* package and selected the top model based on the change in AIC ( $\Delta AIC$ , (52))  
179 between the full model and each reduced model. We considered  $\Delta AIC$  values within 4 to  
180 be competitive and chose our final model based on the lowest AIC (52). To assess  
181 differences in directionality among families, we included family as a fixed effect in the final  
182 model and plotted the results for each family. We then repeated these steps using only island  
183 passerines and included island size, distance to mainland, and distance to other islands and two-  
184 way interactions between all terms. We used phylogenetic path analyses using the R package  
185 *phylopath* to assess the direct and indirect effects of the variables from the top PGLS models. We  
186 first built candidate path analyses informed by the PGLS models and then ranked models using  
187 an information theory approach based on C-statistics (53). Information theory evaluates the  
188 conditional independencies of each model and assigns a C statistic. The models are ranked based  
189 on the change in C statistic ( $\Delta CICc$ ) between models, where lower C scores are optimized  
190 models and  $\Delta CICc < 2$  are competitive. The top phylogenetic path analysis model was then  
191 selected as the model with lowest C statistic and  $< 2 \Delta CICc$ .



## 192 **RESULTS**

### 193 *Effect of island residency and ecological factors on Passeriformes colour evolution*

194 We identified the reduced PGLS model as the top models for female red chromaticity  
195 (Table S1) that included land classification (F=57.21, P<0.0001), habitat (F=22.40, P<0.0001),  
196 diet guild (F=5.69, P=0.003), latitude (F=65.39, P<0.0001), region (F=15.54, P<0.0001), and the  
197 interactions between land classification and latitude (F=5.51, P=0.001), land classification and  
198 diet guild (F=10.60, P<0.0001), and habitat and diet guild (Table 1, F=4.55, P<0.0001).

199 Similarly, the top model for male red chromaticity was the reduced model (Table S1) and  
200 included land classification (F=0.05, P=0.82), habitat (F=1.17, P=0.32), diet guild (F=22.46,  
201 P<0.0001), latitude (F=15.81, P<0.0001), region (F=11.28, P<0.0001), and the interactions  
202 between land classification and latitude (F=2.17, P=0.14), land classification and diet guild  
203 (F=25.06, P<0.0001), and habitat and diet guild (Table 1, F=2.61, P=0.02).

204 The top model for female blue chromaticity was the reduced model (Table S1) and was  
205 explained by land classification (F=23.72, P<0.0001), habitat (F=20.09, P<0.0001), diet guild  
206 (F=3.0, P=0.05), latitude (F=75.58, P<0.0001), region (F=7.31, P<0.0001), the interactions  
207 between land classification and diet guild (F=17.93, P<0.0001), and habitat and diet guild (Table  
208 1, F=3.72, P<0.0001), but not land classification and latitude (F=2.54, P=0.11). Blue  
209 chromaticity in males was best explained by the reduced model (Table S1) and included diet  
210 guild (F=30.09, P<0.0001), latitude (F=14.01, P<0.0001), region (F=7.55, P<0.0001), and the  
211 interactions between land classification and guild (F=21.13, P<0.0001), and habitat and diet  
212 guild (Table 1, F=2.72, P=0.01), but not land classification (F=2.21, P=0.14) or habitat (F=1.96,  
213 P=0.12).

214 In general, we found mixed support for our prediction that island birds have reduced  
215 coloration. Colour differed significantly between mainland and island females, but not males  
216 (Fig. 1). Female red chromaticity was higher on the mainland than on islands (Fig. 1,  $F=57.21$ ,  
217  $P<0.0001$ ) while female blue chromaticity was lower on the mainland relative to islands (Fig. 1,  
218  $F=23.72$ ,  $P<0.0001$ ).

219 Apart from the effects of islands on plumage, we found colour varied with several  
220 ecological and natural history covariates and their interactions, underscoring the complexity of  
221 the macroevolutionary processes driving plumage colour evolution (Table 1). In support of  
222 Gloger's Rule, colour varied by latitude (Fig. S2): red chromaticity was higher and blue  
223 chromaticity was lower near the equator for both males ( $F=15.81$ ,  $P<0.0001$ ) and females  
224 ( $F=65.39$ ,  $P<0.0001$ ). However, the interaction between land classification and latitude revealed  
225 red chromaticity in island females was positively related to latitude, while mainland red  
226 chromaticity was negatively related to latitude (Fig. S2,  $F=5.51$ ,  $P=0.001$ ).

227 Colour also varied with diet, where both invertivore and omnivore guilds had higher red  
228 chromaticity (female:  $F=5.69$ ,  $P=0.003$ ; male:  $F=22.46$ ,  $P<0.0001$ ) and blue chromaticity (Table  
229 1, male:  $F=30.09$ ,  $P<0.0001$ ). However, the interactions between diet guild and land  
230 classification indicated that red chromaticity in invertivores was lower on islands (female:  
231  $F=10.60$ ,  $P<0.0001$ ; male:  $F=25.06$ ,  $P<0.0001$ ). Blue chromaticity in invertivores and herbivores  
232 was higher on islands but did not vary between islands and mainlands for omnivores (Fig. S3,  
233 female:  $F=17.93$ ,  $P<0.0001$ ; male:  $F=21.13$ ,  $P<0.0001$ ).

234 Colour varied among habitat types in females, with species in open habitats having higher  
235 red chromaticity ( $F=22.40$ ,  $P<0.0001$ ) while those in dense habitats had lower blue chromaticity  
236 (Table 1,  $F=20.09$ ,  $P<0.0001$ ). The interaction between habitat and guild indicates red

237 chromaticity in herbivorous birds was higher in dense and open habitats, but lower in aquatic  
238 habitats ( $F=4.55$ ,  $P<0.0001$ ). Similarly, blue chromaticity in herbivorous birds was lower in  
239 dense and open habitats but higher in aquatic habitats (Table 1,  $F=3.72$ ,  $P<0.0001$ ).

#### 240 *Phylogenetic Path Analyses*

241 Our phylogenetic path analyses indicated that plumage colour in the Passeriformes is  
242 influenced by several factors (Table S2). The top models predicting red chromaticity in females  
243 were explained by the direct effects of habitat and land classification and the indirect effect of  
244 habitat on land classification (Fig. 2,  $CICc=451.6$ ), while female blue chromaticity was  
245 explained by geographic region (Fig. 2,  $CICc=506.2$ ). The top model predicting red chromaticity  
246 in males was explained by the direct effects of land classification and latitude, and the indirect  
247 effect of latitude on land classification (Fig. 2,  $CICc=399.6$ ). Blue chromaticity in males was  
248 explained by the direct effect of diet and land classification and the indirect effect of diet on land  
249 classification (Fig. 2,  $CICc=486.9$ ).

#### 250 *The Island Effect varies among Passeriformes families*

251 The direction of colour change between mainland and island birds varied among families  
252 in the Passeriformes (Fig. 3). Red chromaticity increased in island females and males in  
253 Fringillidae, Meliphagidae, and Sturnidae but decreased in Estrildidae, Pellorneidae,  
254 Pycnonotidae, Tyrannidae, and Vireonidae (Fig. S4). Additionally, red chromaticity in females in  
255 the Parulidae and Turdidae, and in males in the Muscicapidae and Oriolidae decreased on islands  
256 (Fig. S4). Blue chromaticity increased in island females and males in Oriolidae, Pellornidae,  
257 Pycnonotidae, Turdidae, Tyrannidae, and Vireonidae but decreased in Sturnidae and  
258 Zosteropidae (Fig. S4). Blue chromaticity in island females increased in Campephagidae and

259 decreased in Meliphagidae (Fig. S4). Male blue chromaticity increased in Muscicapidae and  
260 decreased in Fringillidae and Ploceidae between the mainland and islands (Fig. S4).

### 261 *Island characteristics predict colour evolution within island Passeriformes*

262 In our analyses restricted to only island birds, we found the top models for red and blue  
263 chromaticity were the reduced models (Table S3) and included island size, island isolation (i.e.  
264 distance to the mainland and other islands), and other ecological covariates as above (Table S4).  
265 In females, red and blue chromaticity varied with island size, where red was lower and blue was  
266 higher on larger islands (Table S4, red:  $F=17.64$ ,  $P<0.0001$ ; blue:  $F=12.33$ ,  $P<0.0001$ ) and by  
267 island isolation (Fig. S5). Whereas female red chromaticity increased on more distant islands  
268 (distance to the mainland:  $F=5.69$ ,  $P=0.02$ ; distance to other islands:  $F=25.35$ ,  $P<0.0001$ , Fig.  
269 S5), blue chromaticity decreased on more isolated islands (Fig. S5, distance to other islands:  
270  $F=18.84$ ,  $P<0.0001$ ). We found two-way interactions between latitude and island size and  
271 latitude and island isolation, which revealed that red chromaticity increased at higher latitudes  
272 regardless of island size (Table S4,  $F=10.74$ ,  $P<0.0001$ ), and on more isolated islands, regardless  
273 of latitude (Table S4, latitude x nearest mainland:  $F=8.93$ ,  $P<0.0001$ ; latitude x nearest islands:  
274  $F=9.11$ ,  $P<0.0001$ ). Blue chromaticity decreased on larger islands (Table S4,  $F=12.33$ ,  
275  $P<0.0001$ ) and on more isolated islands (Fig. S5, nearest island:  $F=18.84$ ,  $P<0.0001$ ). We also  
276 found an interaction between island area and island isolation in blue, indicating blue chromaticity  
277 was lower on more distant islands regardless of island size (Table S4, nearest island:  $F=5.24$ ,  
278  $P=0.02$ ). Further, there was an interaction between latitude and geographic region (Table S4).  
279 While birds in most regions showed increases in red chromaticity and decreases in blue  
280 chromaticity, birds in Australasia exhibited decreases in red and increases in blue across latitude  
281 (Table S4,  $F=4.96$ ,  $P<0.0001$ ). Additionally, there was an interaction between land classification

282 and diet in female blue chromaticity, indicating blue decreased across latitude in herbivores and  
283 increased in invertivores, but blue did not in omnivores ( $F=4.21$ ,  $P=0.02$ ).

284 Similarly in males, red and blue chromaticity varied by island size, island isolation, and  
285 other ecological covariates (Table S3). Male red chromaticity was lower and blue chromaticity  
286 was higher on larger islands (Table S4, red:  $F=18.92$ ,  $P<0.0001$ , blue:  $F=12.37$ ,  $P<0.0001$ ). In  
287 contrast, red was higher, and blue was lower on more isolated islands (Fig. S5, red nearest  
288 mainland:  $F=10.45$ ,  $P<0.0001$ ; blue nearest mainland:  $F=7.75$ ,  $P=0.01$ ; red nearest islands:  
289  $F=10.29$ ,  $P<0.0001$ ; blue nearest islands:  $F=12.26$ ,  $P<0.0001$ ). There were also interactions  
290 between island area and distance to the nearest mainland, indicating red chromaticity was higher  
291 ( $F=10.29$ ,  $P<0.0001$ ) and blue was lower ( $F=6.38$ ,  $P=0.01$ ) on more distant islands regardless of  
292 island size (Table S4). For male blue chromaticity, there was an interaction between island area  
293 and geographic region, indicating that although blue chromaticity in male passerines in the  
294 Palearctic decreased on larger islands, it increased in males in Afrotropical and Australasian  
295 regions (Table S4,  $F=3.03$ ,  $P=0.02$ ).

## 296 **DISCUSSION**

297 Plumage coloration is an important phenotype involved in inter- and intraspecific  
298 communication signals, crypsis, and thermoregulation. As it is shaped by a variety of ecological  
299 and biological pressures, general patterns of colour evolution, especially in an entire order of  
300 birds, are difficult to disentangle. Our phylogenetic comparative analysis revealed plumage  
301 colouration of island species differs from their mainland counterparts. However, this pattern is  
302 more complex than has been reported previously, is mediated by a number of ecological factors,  
303 and varies across taxa. Overall, female passerines on islands exhibited reduced red and enhanced  
304 blue colouration but this effect varied among families, with some families showing significant

305 decreases, while others increased in red and blue chromaticity between the mainland and islands.  
306 Female and male colour variation was also related to ecological covariates, including diet,  
307 latitude, habitat, and geographic region. Further, among island species, colour variation was  
308 affected by island size and isolation. Our results support the hypothesis that colour is affected by  
309 biological and ecological factors (diet, resource availability, temperature, predation and  
310 competition) as well as evolutionary history (family lineages), highlighting the complexity of  
311 colour evolution in birds.

312         The reduced red colour in island females suggests a reduction in carotenoid-based  
313 colouration. Carotenoid-based colouration is obtained through the consumption, metabolic  
314 conversion, and deposition of carotenoid pigments, so our observed reduction in red chromaticity  
315 may reflect variation in diet rather than an adaptation to the island environment. The reduction in  
316 red colouration could be attributed to reduced availability of carotenoid precursors in the  
317 environment or reflect increased intraspecific competition for sources rich in carotenoid  
318 precursors (54). As an example, when introduced to the Hawaiian Islands, house finches  
319 (*Carpodacus mexicanus*), which typically exhibit a red head and breast patches, became orange  
320 or yellow soon after being established and carotenoid-restricted diet experiments resulted in the  
321 loss of red plumage in male house finches (21). Alternatively, the decrease in red chromaticity  
322 may be a result of relaxed social and/or sexual selection. As islands generally exhibit lower  
323 species diversity, the reduction in sympatric species may diminish the necessity of plumage  
324 elaboration for species recognition (11). Our results also revealed an increase in female blue  
325 chromaticity on islands. If island birds are carotenoid-deficient, populations may have adapted  
326 colouration strategies by shifting endogenous precursors to melanin-based colour. One study (11)  
327 previously reported that the reduction in plumage brightness in island birds was not associated

328 with increased black coloured plumage, such as through status signals like melanin-based badges  
329 (55),(56), but rather a continuous shift toward duller colours. This shift may be caused by  
330 increased melanin or carotenoid content in the feathers, both of which could create thicker  
331 keratin cortexes in feathers and reduce the incoherent scattering of light necessary for blue-  
332 shifted reflectance (57),(58). Whether island birds are indeed carotenoid deficient is not known;  
333 however, supplemental feeding experiments on dull island birds would be a useful study. Further  
334 research is also needed to investigate the mechanisms of reduced structural colouration and  
335 spectrometry along with microscopy of feather nanostructure to elucidate this finding.

336 One ecological factor that was consistently identified in our analyses as an important  
337 predictor of colour was latitude. Gloger's rule predicts lighter coloured individuals are found at  
338 higher latitudes and darker individuals at lower latitudes (31). This rule is broadly supported in  
339 birds (59); however, the few comprehensive studies assessing latitudinal effects on colour failed  
340 to consider the consequences of island habitats or other ecological and biological explanations.  
341 Our results from phylogenetic path analyses indicate that in male Passeriformes, the direct and  
342 indirect effects of latitude on land classification are the best predictors of colour. In females,  
343 although there was an overall difference in colour between island and mainland species, this  
344 varied by latitude, where red chromaticity in island females was positively related to latitude,  
345 while mainland red chromaticity was negatively related to latitude. However, neither land  
346 classification or latitude was selected in the top path analysis model for blue chromaticity. One  
347 reason latitude may influence colour evolution is its link to temperature and precipitation, which  
348 may have direct or indirect effects on plumage coloration (60). Geographic region was the sole  
349 predictor of female blue chromaticity in our path analyses, which may be operating similarly to  
350 latitude. Habitat was another important variable identified in our PGLS models and in the path

351 analysis for female red colour. Ambient light may vary among habitats, so selection for crypsis  
352 or conspecific signalling may vary given light environment contexts (32).

353 An interesting result of our study was island living influenced colour in only females.  
354 Colour elaboration in female passerines may be an adaptation to non-migratory life histories  
355 (61), which is the case for many island species (6). Although our results for red chromaticity do  
356 not support this notion, blue chromaticity increased on islands supporting the hypothesis that  
357 sedentary island life increases at least some aspects of plumage elaboration. Male colouration  
358 was not affected by island living, based on our PGLS, but rather was dependent upon other  
359 ecological factors such as diet, habitat, and latitude. In island species, island size and the distance  
360 to other islands and the mainland were significant as others have found (20), however these were  
361 not identified as important in the path analyses. Taken together, our results suggest that male  
362 colouration is influenced more by ecological and biological factors such as diet and habitat,  
363 while female coloration is affected by the combination of island living and the other ecological  
364 and biological factors.

365 Macroevolutionary studies are powerful ways to investigate large scale evolutionary  
366 patterns; however, they can mask differences at finer taxonomic scales (33),(62). We addressed  
367 this issue by analyzing colour evolution at the family-level. Despite finding no overall difference  
368 between mainland and island male coloration, several families showed significant increases or  
369 decreases (Fig. S2). If we had not undertaken the additional family-level analyses, we may have  
370 rejected the hypothesis that male colour differed between mainland and island species. Similarly,  
371 in females we found an overall decrease in red and an increase in blue chromaticity; however,  
372 the family-level analyses revealed the direction of these effects varied among families (Fig. S2),  
373 further highlighting how complex phenotypes, such as plumage colour can be affected by



374 different selective forces at different taxonomic scales (63). Therefore, we join the call to urge  
375 future macroevolutionary studies to consider a range of taxonomic scales to elucidate the  
376 evolution of phenotypes that are likely being pulled in multiple directions due to differing  
377 selective pressures (33).

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522

Table 1. AIC selected model results demonstrating the effect of each fixed effect and interactions on female and male Passeriformes plumage coloration. Significant results are indicated in bold text.

Sex	Variable	Fixed effect	<i>df</i>	<i>F</i>	<i>P</i>	
Female	Red chromaticity	<b>Land classification</b>	<b>1</b>	<b>57.21</b>	<b>&lt;0.0001</b>	
		<b>Habitat</b>	<b>3</b>	<b>22.40</b>	<b>&lt;0.0001</b>	
		<b>Diet</b>	<b>2</b>	<b>5.69</b>	<b>0.003</b>	
		<b>Latitude</b>	<b>1</b>	<b>65.39</b>	<b>&lt;0.0001</b>	
		<b>Geographic region</b>	<b>6</b>	<b>15.54</b>	<b>&lt;0.0001</b>	
		<b>Land x Latitude</b>	<b>3</b>	<b>5.51</b>	<b>0.001</b>	
		<b>Land x diet</b>	<b>2</b>	<b>10.60</b>	<b>&lt;0.0001</b>	
			<b>Habitat x diet</b>	<b>6</b>	<b>4.55</b>	<b>&lt;0.0001</b>
	Blue chromaticity	<b>Land classification</b>	<b>1</b>	<b>23.72</b>	<b>&lt;0.0001</b>	
		<b>Habitat</b>	<b>3</b>	<b>20.09</b>	<b>&lt;0.0001</b>	
		Diet	2	3.00	0.05	
		<b>Latitude</b>	<b>1</b>	<b>75.58</b>	<b>&lt;0.0001</b>	
		<b>Geographic region</b>	<b>6</b>	<b>7.31</b>	<b>&lt;0.0001</b>	
		Land x Latitude	1	2.54	0.11	
<b>Land x diet</b>		<b>2</b>	<b>17.93</b>	<b>&lt;0.0001</b>		
		<b>Habitat x diet</b>	<b>6</b>	<b>3.72</b>	<b>&lt;0.0001</b>	
Male	Red chromaticity	Land classification	1	0.05	0.82	
		Habitat	3	1.17	0.32	
		<b>Diet</b>	<b>2</b>	<b>22.46</b>	<b>&lt;0.0001</b>	
		<b>Latitude</b>	<b>1</b>	<b>15.81</b>	<b>&lt;0.0001</b>	
		<b>Geographic region</b>	<b>6</b>	<b>11.28</b>	<b>&lt;0.0001</b>	
		Land x Latitude	1	2.17	0.14	
		<b>Land x diet</b>	<b>2</b>	<b>25.06</b>	<b>&lt;0.0001</b>	
			<b>Habitat x diet</b>	<b>6</b>	<b>2.61</b>	<b>0.02</b>
	Blue chromaticity	Land classification	1	2.21	0.14	
		Habitat	3	1.96	0.12	
		<b>Diet</b>	<b>2</b>	<b>30.09</b>	<b>&lt;0.0001</b>	
		<b>Latitude</b>	<b>1</b>	<b>14.01</b>	<b>&lt;0.0001</b>	
		<b>Geographic region</b>	<b>6</b>	<b>7.55</b>	<b>&lt;0.0001</b>	
		<b>Land x diet</b>	<b>2</b>	<b>21.13</b>	<b>&lt;0.0001</b>	
			<b>Habitat x diet</b>	<b>6</b>	<b>2.72</b>	<b>0.01</b>

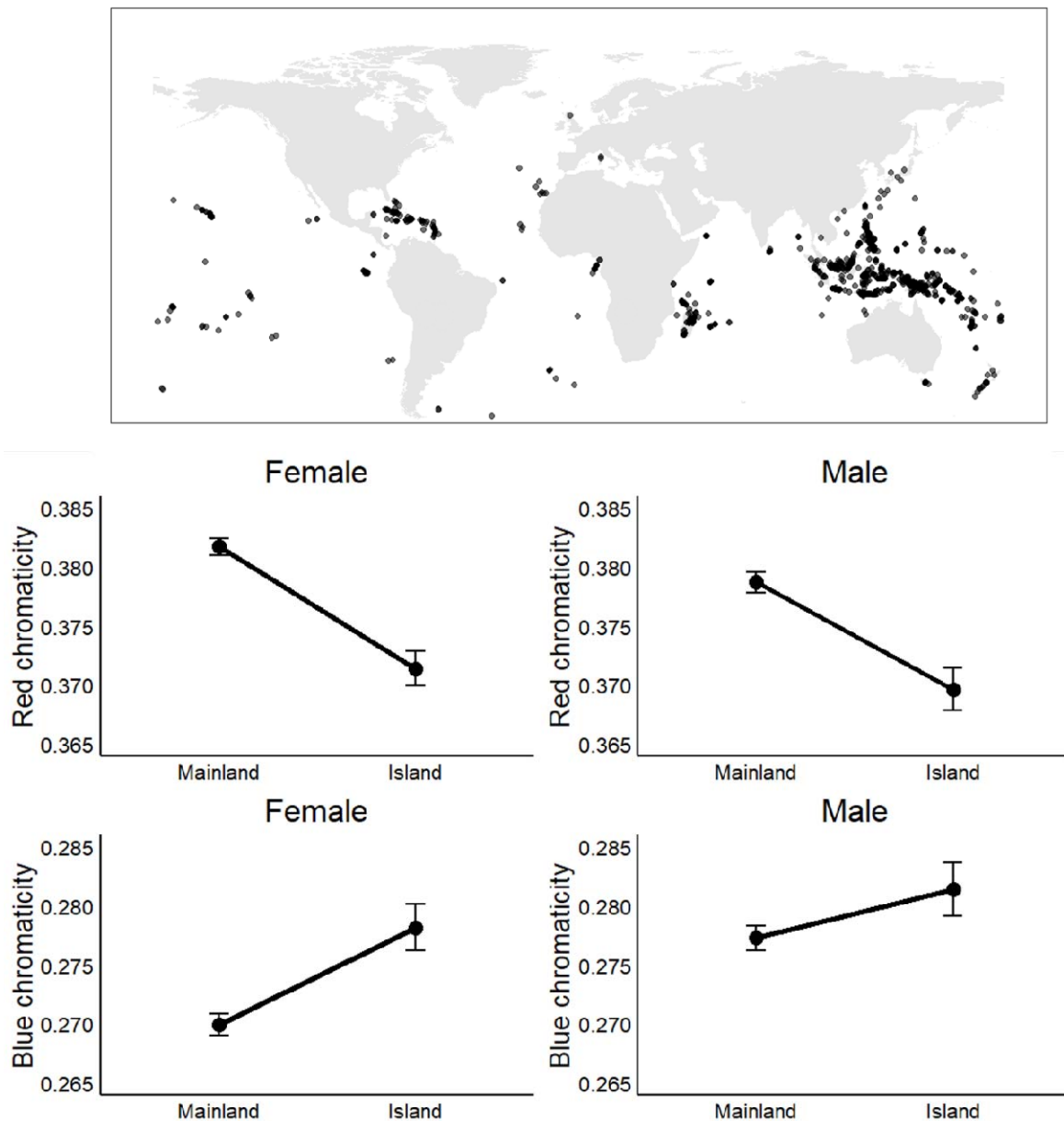


Fig. 1. Top panels: Global distribution of Passeriformes island species (n=1,183) used in the present study. Bottom panels: Female and male colour variation between mainland and island passerine birds (n=5,693). Red chromaticity ( $\pm$ SE) was significantly higher on the mainland for females ( $F=57.2$ ,  $P<0.0001$ ) but not in males ( $F=0.05$ ,  $P=0.82$ ). Blue chromaticity ( $\pm$ SE) was significantly lower on the mainland for females ( $F=23.7$ ,  $P<0.0001$ ) but did not differ in males ( $F=2.2$ ,  $P=0.14$ ).



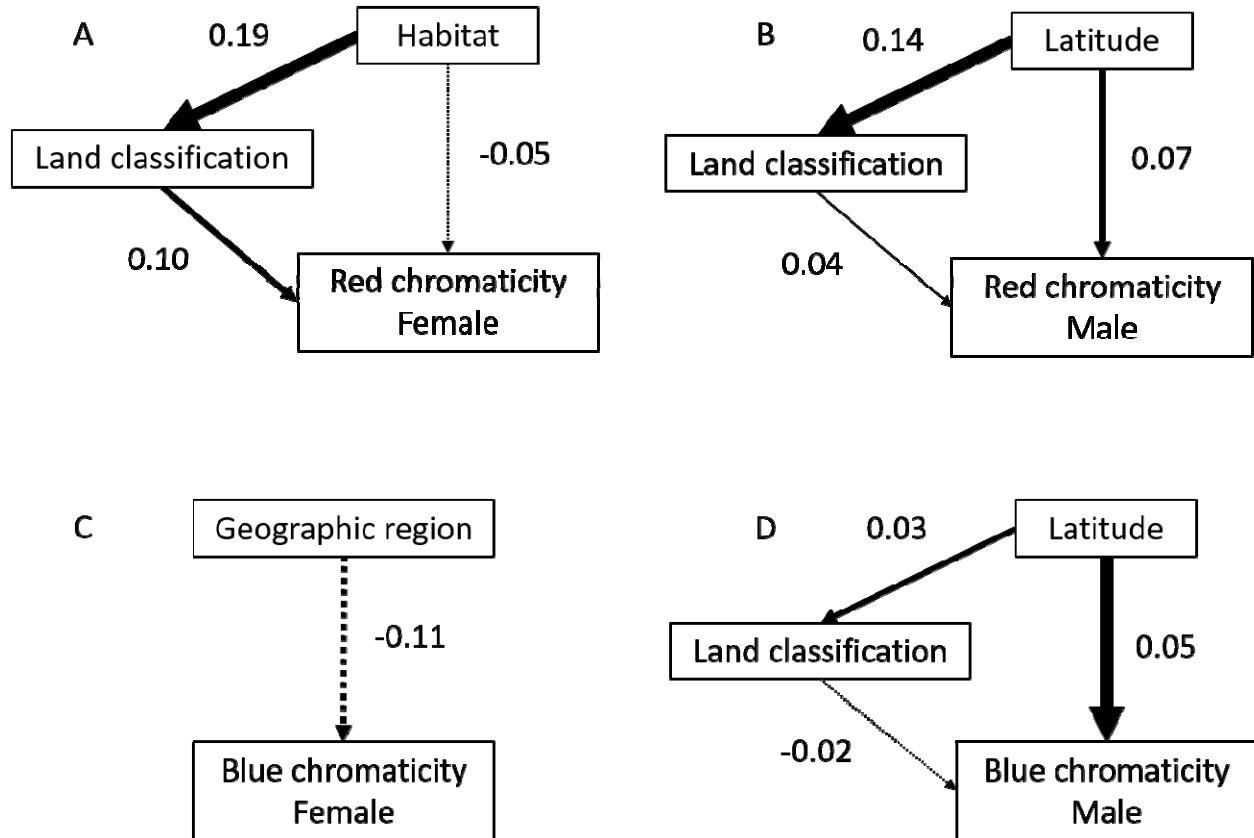


Fig. 2. Final path analysis models illustrating the effect of A) habitat and land classification (island/mainland) on female red chromaticity, B) geographic region on blue chromaticity, C) latitude and land classification on male red chromaticity, and D) male blue chromaticity. Solid lines indicate positive, while dashed lines indicate negative effects.

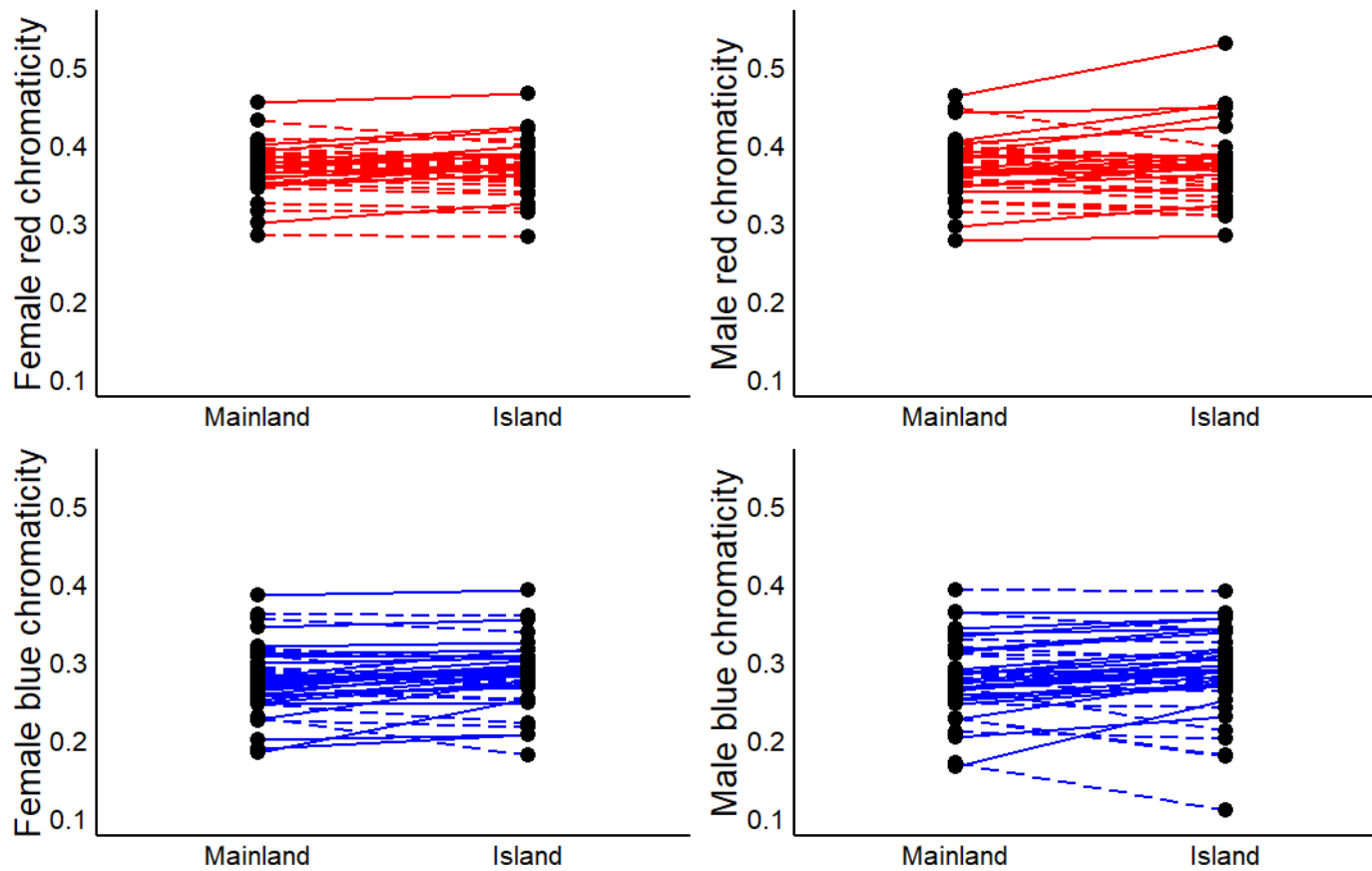


Fig. 3. Colour variation between mainland and island species among Passeriformes (dots). Solid lines represent increases in red (top panels) and blue chromaticity (bottom panels) and dashed lines indicate decreases. Although generally female red decreases and blue increases on islands, the direction of this effect varies among families.

Table S1. Full and reduced model selection results to assess the relationships between island and mainland classification, biological, and ecological variables on red and blue chromaticity in female and male Passeriformes birds.

Sex	Variable	Model	K	AICc	$\Delta$ AICc	Likelihood	AICcWt	LL	Cum.Wt
Female	Red chromaticity	Reduced	26	-18362.5	0	1	0.72	9207.40	0.72
		Full	27	-18360.6	1.88 <sup>1</sup>	0.39	0.28	9207.47	1
	Blue chromaticity	Reduced	24	-15856.7	0	1	0.59	7952.50	0.59
		Full	27	-15856	0.73 <sup>2</sup>	0.69	0.41	7955.16	1
Male	Red chromaticity	Reduced	24	-16349	0	1	0.77	8198.64	0.77
		Full	27	-16346.6	2.40 <sup>3</sup>	0.30	0.23	8200.47	1
	Blue chromaticity	Reduced	23	-14604.9	0	1	0.91	7325.58	0.91
		Full	27	-14600.3	4.59	0.10	0.09	7327.33	1

$\Delta$ AICc<4 model comparison results: <sup>1</sup>log ratio=0.14, P=0.7; <sup>2</sup>log ratio=5.33, P=0.15; <sup>3</sup>log ratio=3.66, P=0.3, indicating reduced models outperform full models. K=number of parameters, Likelihood=model likelihood, LL=log likelihood, Cum.Wt=cumulative model weight.

Table S2. Phylogenetic Path Analysis model selection results testing the effect of biological and ecological variables on Passeriformes island and mainland species colour. The top model appears in bold.

	Model	k	q	C	p	CICc	ΔCICc	L	w
Female Red Chromaticity	<b>six</b>	<b>12</b>	<b>9</b>	<b>433.6</b>	<b>0</b>	<b>451.61</b>	<b>0.00</b>	<b>1</b>	<b>1</b>
	five	14	7	486.7	0	500.71	49.10	2.17E-11	2.17E-11
	seven	12	9	519.1	0	537.17	85.56	2.64E-19	2.64E-19
	one	14	7	527.9	0	541.92	90.31	2.45E-20	2.45E-20
	eight	12	9	558.0	0	576.05	124.44	9.50E-28	9.50E-28
	two	14	7	565.9	0	579.88	128.27	1.40E-28	1.40E-28
	three	14	7	566.5	0	580.52	128.91	1.02E-28	1.02E-28
	four	14	7	568.3	0	582.36	130.75	4.06E-29	4.06E-29
Female Blue chromaticity	<b>five</b>	<b>14</b>	<b>7</b>	<b>492.2</b>	<b>0</b>	<b>506.19</b>	<b>0.00</b>	<b>1</b>	<b>1</b>
	six	12	9	524.9	0	542.92	36.73	1.06E-08	1.06E-08
	seven	12	9	527.2	0	545.23	39.04	3.33E-09	3.33E-09
	two	14	7	533.2	0	547.20	41.01	1.25E-09	1.25E-09
	one	14	7	533.2	0	547.25	41.06	1.21E-09	1.21E-09
	three	14	7	549.3	0	563.35	57.16	3.86E-13	3.86E-13
	four	14	7	549.8	0	563.84	57.65	3.03E-13	3.03E-13
Male Red Chromaticity	<b>five</b>	<b>12</b>	<b>9</b>	<b>381.6</b>	<b>0</b>	<b>399.64</b>	<b>0.00</b>	<b>1</b>	<b>1</b>
	two	14	7	466.8	0	480.82	81.18	2.35E-18	2.35E-18
	six	12	9	472.6	0	490.69	91.05	1.70E-20	1.70E-20
	one	14	7	483.0	0	497.02	97.38	7.15E-22	7.15E-22
	four	14	7	489.7	0	503.71	104.07	2.52E-23	2.52E-23
	seven	12	9	499.2	0	517.25	117.61	2.89E-26	2.89E-26
	eight	14	7	503.9	0	517.96	118.32	2.02E-26	2.02E-26
	three	14	7	506.4	0	520.46	120.82	5.81E-27	5.81E-27
Male Blue Chromaticity	<b>five</b>	<b>12</b>	<b>9</b>	<b>468.8</b>	<b>0</b>	<b>486.85</b>	<b>0.00</b>	<b>1.00</b>	<b>0.51</b>
	two	14	7	474.5	0	488.52	1.68	0.43	0.22
	four	14	7	475.5	0	489.49	2.64	0.27	0.14
	six	12	9	471.8	0	489.80	2.95	0.23	0.12
	seven	14	7	478.9	0	492.96	6.11	0.05	0.02
	one	14	7	486.2	0	500.24	13.39	0.00	0.00
	three	14	7	487.0	0	501.00	14.15	0.00	0.00

Table S3. Full and reduced model selection results to assess the relationships between classification, biological, and ecological variables on red and blue chromaticity in female and male Passeriformes island birds.

Sex	Variable	Model	K	AICc	$\Delta$ AICc	LL	AICcWt	LL	Cum.Wt
Female	Red chromaticity	Reduced	29	-1880.72	0	1	1.00	970.51	1.00
		Full	37	-1868.86	11.86	0.00	0.00	973.31	1
	Blue chromaticity	Reduced	27	-1463.26	0	1	1.00	759.63	1.00
		Full	37	-1446.89	16.38	0.00	0.00	762.32	1
Male	Red chromaticity	Reduced	26	-1665.93	0	1	1.00	859.89	1.00
		Full	37	-1649.28	16.65	0.00	0.00	863.52	1
	Blue chromaticity	Reduced	27	-1338.81	0	1	1.00	697.40	1.00
		Full	37	-1322.6	16.21	0.00	0.00	700.18	1

K=number of parameters, Likelihood=model likelihood, LL=log likelihood, Cum.Wt=cumulative model weight.

Table S4. AIC selected model results demonstrating the effect of fixed effects of biological, ecological, and island characteristics on island dwelling female and male Passeriformes plumage coloration.

Sex	Variable	Fixed effect	<i>df</i>	<i>F</i>	<i>P</i>	
Female	Red chromaticity	<b>Habitat</b>	<b>3</b>	<b>7.07</b>	<b>&lt;0.0001</b>	
		Diet	2	1.61	0.20	
		<b>Geographic region</b>	<b>4</b>	<b>3.75</b>	<b>0.01</b>	
		Latitude	1	0.84	0.36	
		<b>Island size</b>	<b>1</b>	<b>17.64</b>	<b>&lt;0.0001</b>	
		<b>Nearest mainland</b>	<b>1</b>	<b>5.69</b>	<b>0.02</b>	
		<b>Nearest Island group</b>	<b>1</b>	<b>25.35</b>	<b>&lt;0.0001</b>	
		<b>Diet x Latitude</b>	<b>2</b>	<b>4.59</b>	<b>0.01</b>	
		<b>Geographic region x latitude</b>	<b>4</b>	<b>4.03</b>	<b>&lt;0.0001</b>	
		<b>Latitude x islands size</b>	<b>1</b>	<b>10.74</b>	<b>&lt;0.0001</b>	
		<b>Latitude x Nearest mainland</b>	<b>1</b>	<b>8.93</b>	<b>&lt;0.0001</b>	
		<b>Latitude x nearest island group</b>	<b>1</b>	<b>9.11</b>	<b>&lt;0.0001</b>	
		Geographic region x island size	4	1.04	0.39	
		<b>Island size x nearest mainland</b>	<b>1</b>	<b>6.10</b>	<b>0.01</b>	
		Blue chromaticity	<b>Habitat</b>	<b>3</b>	<b>5.89</b>	<b>&lt;0.0001</b>
			Diet	2	1.68	0.19
			Geographic region	4	2.19	0.07
			Latitude	1	0.15	0.69
			<b>Island size</b>	<b>1</b>	<b>12.33</b>	<b>&lt;0.0001</b>
			Nearest mainland	1	2.98	0.08
<b>Nearest Island group</b>	<b>1</b>		<b>18.84</b>	<b>&lt;0.0001</b>		
<b>Diet x Latitude</b>	<b>2</b>		<b>4.21</b>	<b>0.02</b>		
<b>Geographic region x latitude</b>	<b>4</b>		<b>4.96</b>	<b>&lt;0.0001</b>		
Latitude x Nearest mainland	1		2.84	0.09		
<b>Geographic region x island size</b>	<b>4</b>		<b>5.13</b>	<b>&lt;0.0001</b>		
<b>Island size x nearest mainland</b>	<b>1</b>		<b>5.24</b>	<b>0.02</b>		
Red chromaticity	<b>Habitat</b>		<b>3</b>	<b>2.95</b>	<b>0.03</b>	
	Diet		2	0.48	0.62	
	<b>Geographic region</b>	<b>4</b>	<b>3.82</b>	<b>&lt;0.0001</b>		
	Latitude	1	1.04	0.31		
	<b>Island size</b>	<b>1</b>	<b>18.92</b>	<b>&lt;0.0001</b>		
	<b>Nearest mainland</b>	<b>1</b>	<b>10.45</b>	<b>&lt;0.0001</b>		
	<b>Nearest island group</b>	<b>1</b>	<b>10.29</b>	<b>&lt;0.0001</b>		
	Diet x Latitude	2	1.72	0.18		
	<b>Geographic region x latitude</b>	<b>4</b>	<b>8.24</b>	<b>&lt;0.0001</b>		
	Geographic region x island size	4	2.28	0.06		
	<b>Island size x nearest mainland</b>	<b>1</b>	<b>10.29</b>	<b>&lt;0.0001</b>		

	<b>Habitat</b>	<b>3</b>	<b>3.76</b>	<b>0.01</b>
	Diet	2	2.26	0.11
	<b>Geographic region</b>	<b>4</b>	<b>3.11</b>	<b>0.01</b>
	Latitude	1	0.80	0.37
	<b>Island size</b>	<b>1</b>	<b>12.37</b>	<b>&lt;0.0001</b>
	<b>Nearest mainland</b>	<b>1</b>	<b>7.75</b>	<b>0.01</b>
Blue chromaticity	<b>Nearest Island group</b>	<b>1</b>	<b>12.26</b>	<b>&lt;0.0001</b>
	Diet x Latitude	2	2.31	0.10
	<b>Geographic region x latitude</b>	<b>4</b>	<b>6.70</b>	<b>&lt;0.0001</b>
	Latitude x Nearest island group	1	0.49	0.48
	<b>Geographic region x island size</b>	<b>4</b>	<b>3.03</b>	<b>0.02</b>
	<b>Island size x nearest mainland</b>	<b>1</b>	<b>6.38</b>	<b>0.01</b>

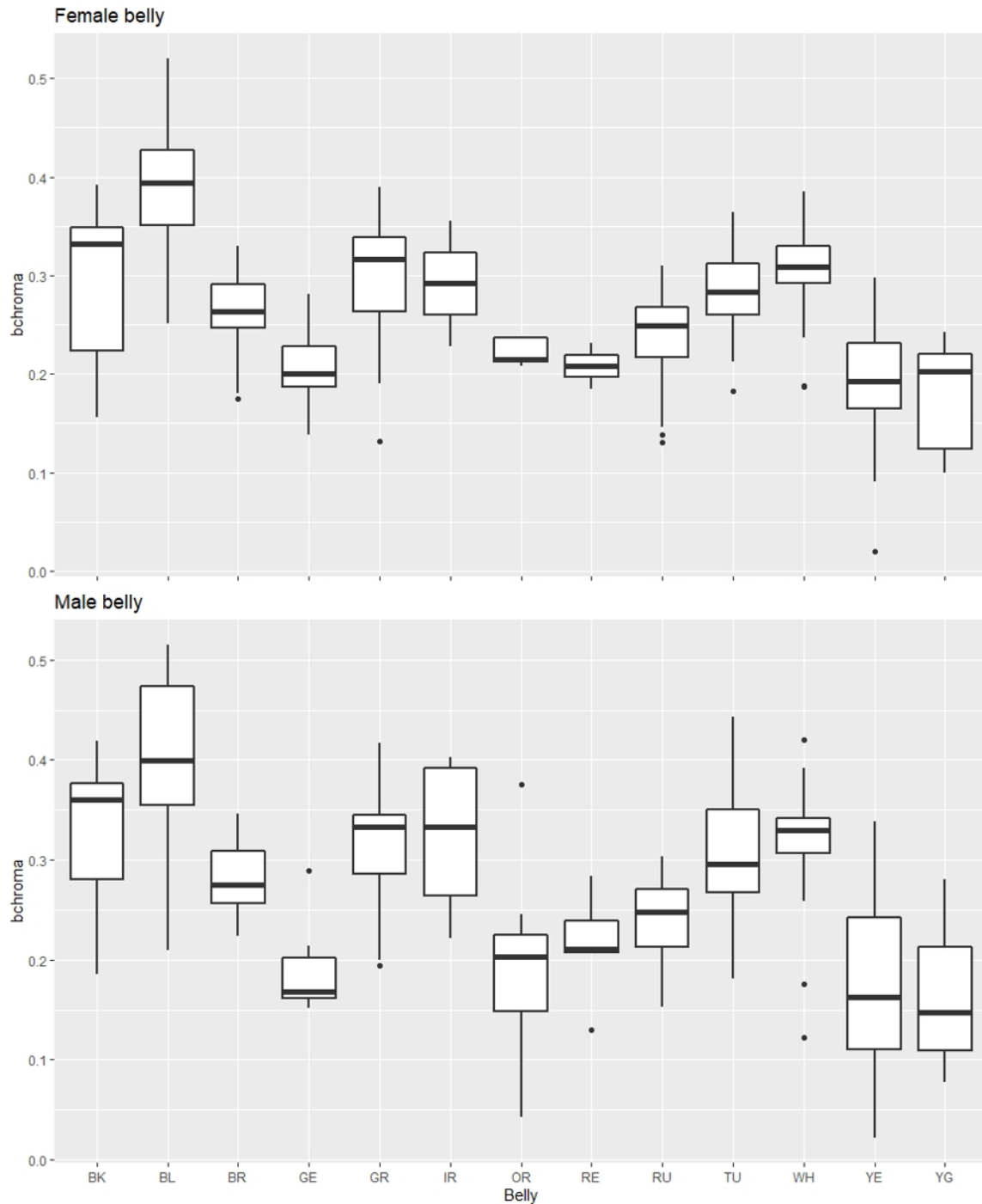


Fig. S1. Blue chromaticity (“bchroma”, y-axis) for Thraupidae plumage patches classified as red (“RE”) or blue (“BL”) by an independent observer. There is little overlap in the distribution of chromaticity values for patches classified as red or blue, suggesting that chromaticity effectively captures the variation in red and blue plumage colouration.



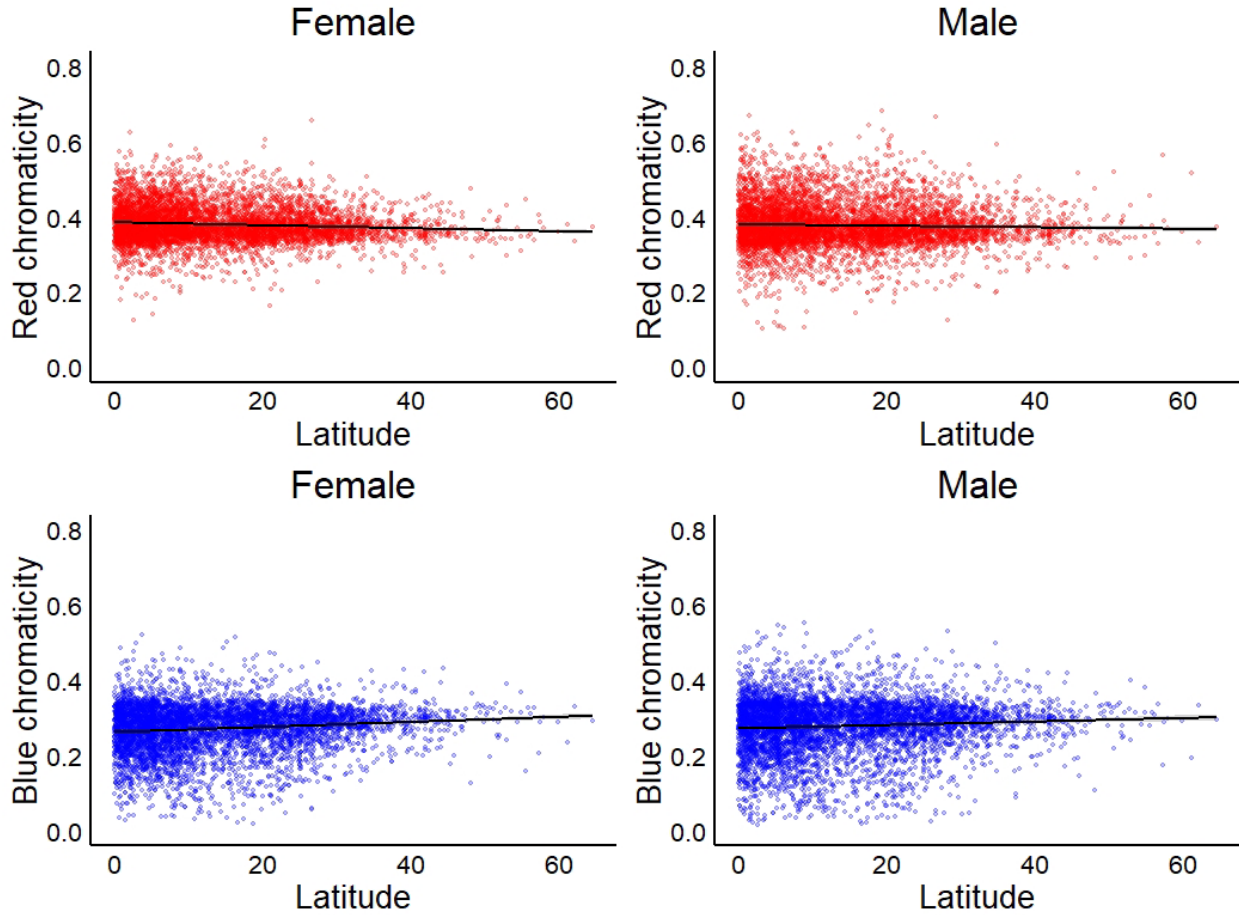


Fig. S2. Female and male colour variation of passerine birds ( $n=5,693$ ) across latitude. Top panels: Red chromaticity was significantly higher at lower latitudes for females ( $F=65.4$ ,  $P<0.0001$ ) and males ( $F=15.8$ ,  $P<0.0001$ ). Bottom panels: Blue chromaticity was positively related to latitude in females ( $F=75.6$ ,  $P<0.0001$ ) and males ( $F=14.01$ ,  $P<0.0001$ ).

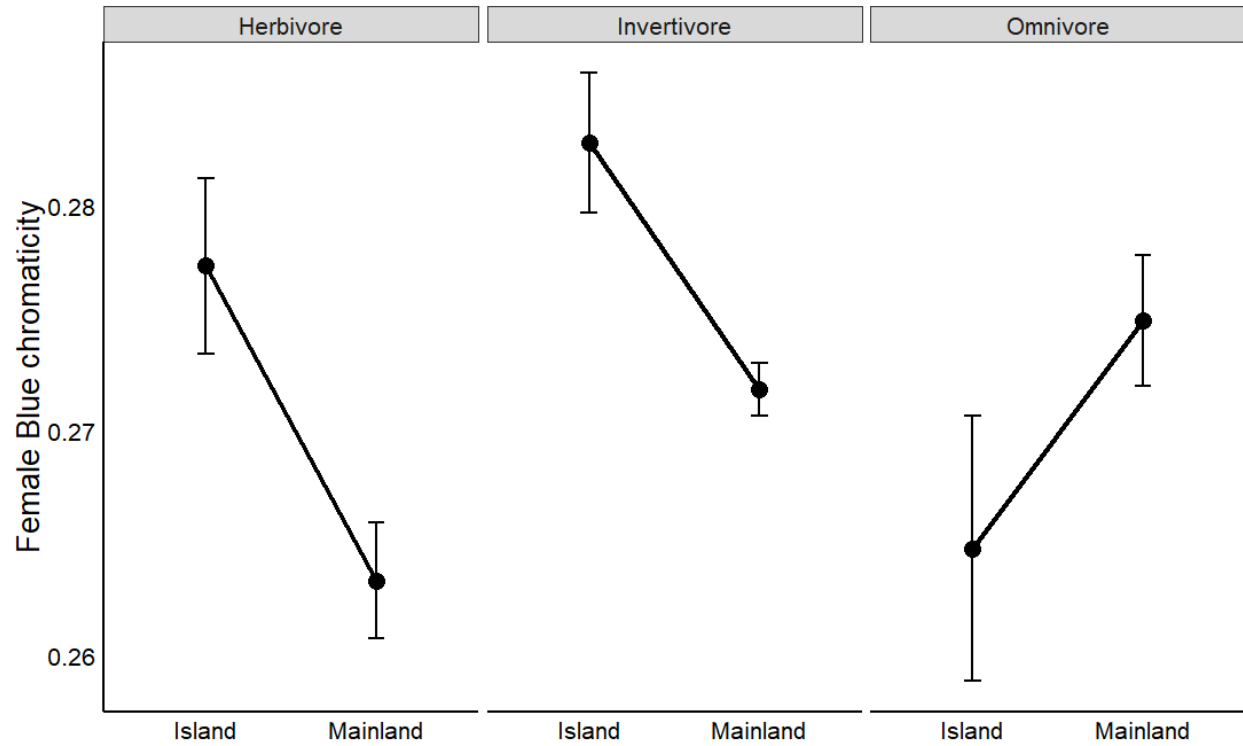


Fig. S3. Female blue chromaticity ( $\pm$ SE) of passerine birds ( $n=5,693$ ) of varying diets on islands and mainlands. The interaction between land type and diet indicated omnivore blue chromaticity did not vary between island and mainlands, but blue chromaticity was lower on mainland systems in herbivores and invertivores ( $F=17.93$ ,  $P<0.0001$ ).



Fig. S4. The island effect on colour evolution varied among Passeriformes families. Top panels: Red chromaticity; bottom panels: blue chromaticity. Red lines indicate decreases in chromaticity, while blue lines indicate increases in chromaticity between mainland and islands. Asterisks following family name indicate significant differences between mainlands and islands.

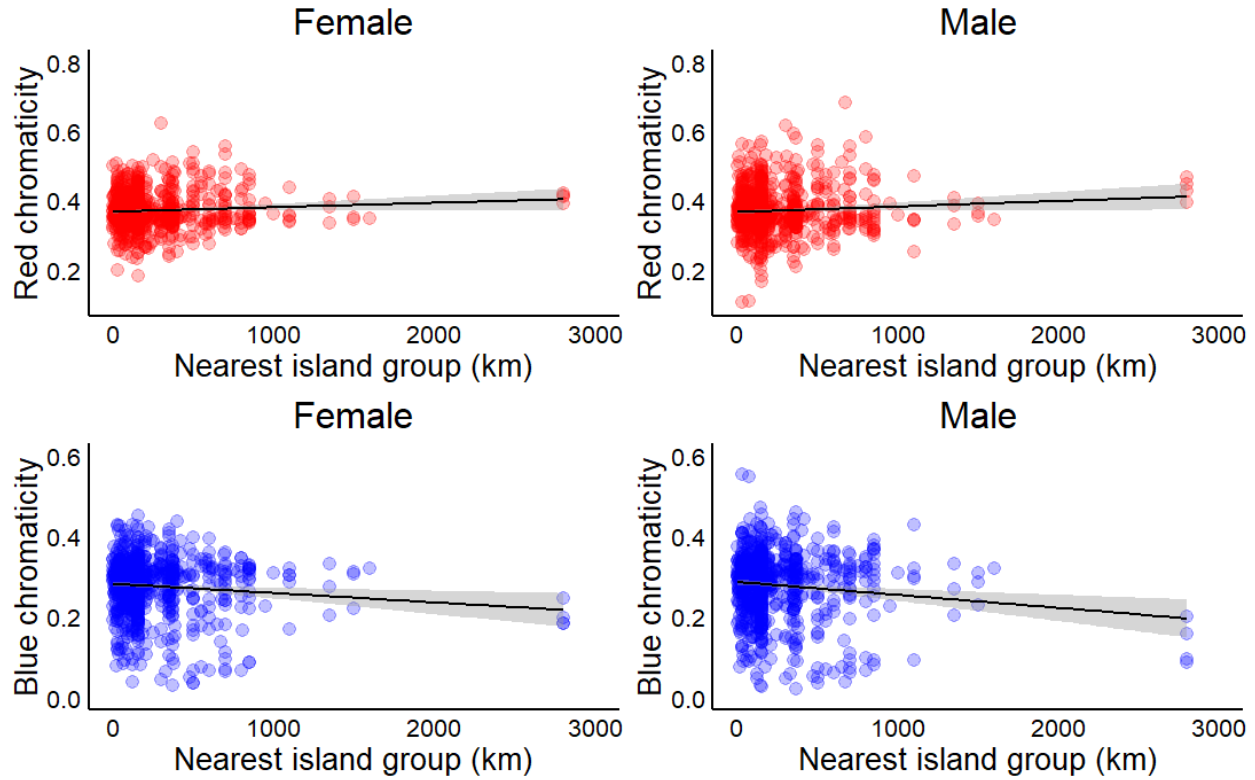


Fig. S5. The relationship between passerine female and male chromaticity ( $n=1,183$ ) and nearest island group (km). In females ( $F=25.4$ ,  $P<0.0001$ ) and males ( $F=10.3$ ,  $P<0.0001$ ), red chromaticity increased (top panels) and (bottom panels) blue chromaticity decreased (females:  $F=18.8$ ,  $P<0.0001$ ; males:  $F=12.3$ ,  $P<0.0001$ ) on more isolated islands.