

1 Pressure for rapid and accurate mate recognition promotes
2 avian-perceived plumage sexual dichromatism in true
3 thrushes (genus: *Turdus*)

4 Alec B. Luro^{1*}, Mark E. Hauber¹

5 ¹ Department of Evolution, Ecology and Behavior, School of Integrative Biology,
6 University of Illinois at Urbana-Champaign *alec.b.luro@gmail.com

7 **Abstract**

8 Ecological conditions limiting the time to find a compatible mate or increasing the difficulty in doing so
9 likely promote the evolution of traits used for species and mate recognition. Conspicuous traits that signal
10 an individual's species, sex, and breeding status reduce the challenge of identifying a compatible conspe-
11 cific mate, and should be present more frequently in species with limited time to find a mate and species
12 facing higher risk of making mate recognition errors, including migratory rather than sedentary species,
13 species shorter breeding seasons, and species breeding under high sympatry with many closely-related
14 heterospecifics. Here, we tested this recognition hypothesis for promoting plumage sexual dichromatism
15 in the true thrushes (*Turdus*), a large and diverse genus of passerine birds. We used receptor-noise limited
16 models of avian vision to quantify avian-perceived chromatic and achromatic visual contrasts between
17 male and female plumage patches and tested the influence of breeding season length, spatial distribu-
18 tion, and sympatry with other *Turdus* species on plumage dichromatism. As predicted, we found that
19 1) true thrush species with migratory behaviour have greater plumage sexual dichromatism than non-
20 migratory species, 2) species with longer breeding seasons have less plumage sexual dichromatism, and
21 3) the number of *Turdus* thrush species breeding in sympatry is associated with more plumage sexual
22 dichromatism. These results suggest that social recognition systems, including species and mate recogni-
23 tion, play a prominent role in the evolution of thrush plumage sexual dichromatism.

24 **Keywords**

25 *achromatic, chromatic, dichromatism, plumage, mate recognition*

26 **Introduction**

27 Species recognition is necessary in sexually reproducing lineages for individuals to find compatible mates
28 and produce viable offspring [1,2]. Conspicuous traits signaling species and sex identity increase the
29 ease and speed of mate recognition by reducing the effort, error, and time involved when searching for

30 compatible mates and lessen the likelihood of mating with heterospecifics [3]. Traits used in species
31 and mate recognition may also serve as signals of status to conspecifics and reduce costly conflicts over
32 resources and mates [4]. Accordingly, distinct traits facilitating mate recognition should be more likely to
33 arise and be maintained under conditions that increase both the difficulty of finding a compatible mate
34 and degree of resource competition among conspecifics and closely-related species. Conditions likely to
35 favour traits signaling individuals' species, sex, and breeding status include higher sympatry with many
36 closely-related species, limited time to find compatible breeding mates, and lower rates of encounter with
37 potential breeding mates [1].

38 In birds, plumage colour is a highly conspicuous trait signaling species and (often) sex identity [5,6].
39 Plumage sexual dichromatism, or the distinct set of differences in the appearance of male and female
40 feather colours and patterns, is common in birds and is usually attributed to different natural and sex-
41 ual selection pressures on males and females [7–11]. Plumage sexual dichromatism results in a visibly
42 perceivable trait useful for recognizing an individual's species, sex, and breeding status (e.g., in species
43 with sex-specific delayed plumage maturation, see [12]), reducing the time and effort expended to iden-
44 tify a suitable mate [13,14]. Evidence in favour of this recognition hypothesis for sexual dichromatism in
45 birds includes a positive association of greater plumage sexual dichromatism with migratory behaviour
46 and shorter breeding seasons [9], both of which reduce the amount of time available to search and find
47 suitable mates and successfully breed. Additional support for the recognition hypothesis includes a con-
48 sistent pattern of greater plumage sexual dichromatism and plumage colour elaboration in avian species
49 that reside on mainland continents and have large geographic ranges in comparison to species that do
50 not migrate, reside on islands, and have limited breeding ranges [10,15–23].

51 Moreover, plumage sexual dichromatism likely plays a role in hybridization avoidance via reproduc-
52 tive character displacement to facilitate species and mate recognition, especially among closely-related
53 species. For example, in *Ficedula* flycatchers, female choice selects for divergent male plumage coloura-
54 tion across populations and species, leading to male character displacement and reduced rates of in-
55 terspecific hybridization [24–26]. More broadly and across taxa, greater plumage dichromatism is posi-
56 tively associated with higher breeding sympatry with closely-related heterospecifics. Among a large sam-
57 ple of passerine sister species pairs, transitions from allopatry to parapatry and increases in geographic
58 range overlaps are positively correlated with greater plumage dichromatism [27]. Greater plumage sexual
59 dichromatism has also been found to be positively associated with greater avian species divergence and
60 richness [28,29]. Among passerine sister species pairs, more pronounced changes in male rather than
61 female plumage colouration in sexually-dichromatic species suggest that female choice and male-male
62 competition often lead to concurrent increases in sexual dichromatism and speciation events [28]. There-
63 fore, plumage sexual dichromatism may be a selected trait for facilitating species and mate recognition
64 when closely-related species have sympatric breeding ranges [5,30].

65 True thrushes (*Turdus* spp.) are an exceptionally diverse monophyletic genus of passerine birds con-
66 sisting of about ~86 species distributed across the globe (Fig. 1). The true thrushes are an ideal passerine
67 clade for examining the recognition hypothesis for plumage sexual dichromatism because plumage sexual
68 dichromatism and migratory behaviours vary substantially between species and sexual dichromatism has

69 evolved multiple times in thrushes across the world [31,32]. Hybridization also occurs in some, but not
70 all, *Turdus* species, indicating that some sympatric *Turdus* species can successfully interbreed. A partic-
71 ularly well-documented example of hybridization in true thrushes occurs at large hybrid zone between
72 four *Turdus* species (*T. atrogularis*, *T. eunomus*, *T. naumanni*, *T. ruficollis*) in north-central Asia [33]. Fur-
73 ther, plumage sexual dichromatism in true thrushes often coincides with age and breeding status in male
74 thrushes. Delayed plumage maturation in males is common among true thrushes [34–36], where males
75 have “female-like” plumage colouration during their first breeding season and develop typical breeding
76 adult male plumage for subsequent breeding seasons. The presence of delayed plumage maturation and
77 distinct juvenal plumage may serve as a signal of a young male’s sexual immaturity in order to reduce
78 levels conspecific aggression from older adults [36] and also suggests that female thrushes prefer older
79 males with prominent adult plumage as breeding mates.

80 Overall, ecological conditions that increase the time and degree of difficulty in finding a suitable con-
81 specific mate should select for phenotypic traits that reliably signal species and sex identity. Across
82 various bird lineages, greater plumage dichromatism is present in species that are i) migratory rather than
83 nonmigratory, ii) have shorter breeding seasons, iii) live on mainland rather than islands, iv) have larger
84 breeding ranges (distributions), and v) breed in sympatry with more closely-related species. These pat-
85 terns suggest that ecological circumstances where rapid and accurate mate recognition is challenging
86 strongly favour the evolution and maintenance of prominent plumage sexual dichromatism in birds. Here,
87 we test these predictions of the recognition hypothesis for plumage sexual dichromatism by evaluating
88 the potential influences of breeding timing, spacing, and sympatry on plumage dichromatism in *Turdus*
89 thrushes (Fig. 2).

90 Methods

91 Initial pre-registration of the study’s methods and analyses are available on Open Science Framework
92 [37].

93 Plumage sexual dichromatism

94 A total of N=77 *Turdus* thrush species (approximately ~89% of all known true thrush species) were sam-
95 pled for plumage spectral reflectance using prepared bird skin specimens at the American Museum of
96 Natural History in New York City and the Field Museum in Chicago, USA. Reflectance measurements
97 spanning 300-700nm were taken in triplicate from the belly, breast, throat, crown, and mantle plumage
98 patches [38] of each individual. N=3 male and N=3 female individuals were measured for most species
99 (exceptions: *T. lawrencii*, N=2 males and N=2 females; *T. swalesi*, N=1 male and N=1 female). Reflectance
100 spectra were measured using a 400 µm fiber optic reflection probe fitted with a rubber stopper to main-
101 tain a consistent measuring distance of 3 mm and area of 2 mm² at a 90° angle to the surface of the
102 feather patch. Measurements were taken using a JAZ spectrometer with a pulsed-xenon light source
103 (Ocean Optics, Dunedin, USA) and we used a diffuse 99% reflectance white standard (Spectralon WS-1-

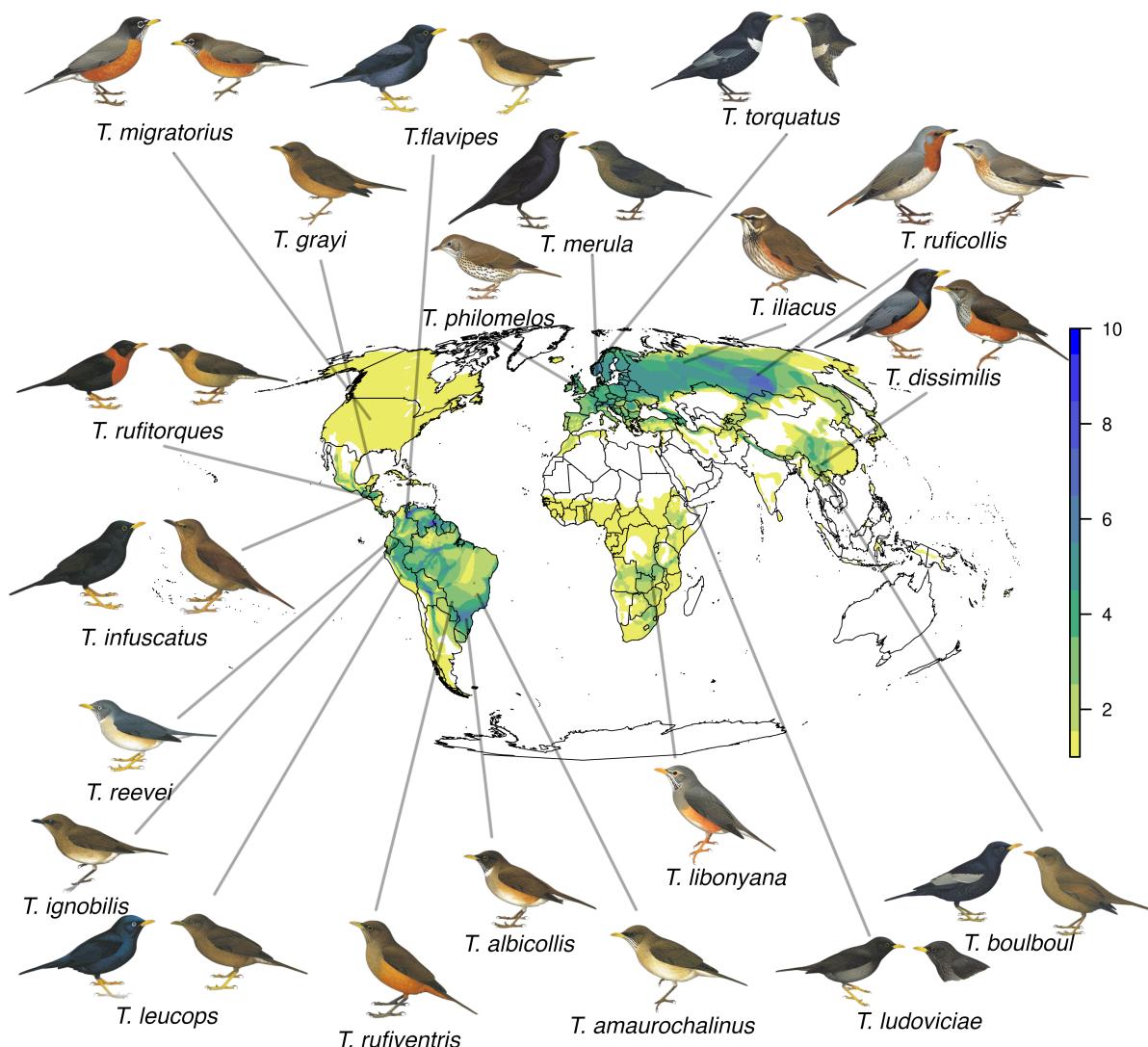


Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International, with representative species' males and females shown for species with plumage sexual dichromatism. The color scale indicates the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations used with permission from HBW Alive/Lynx Edicions

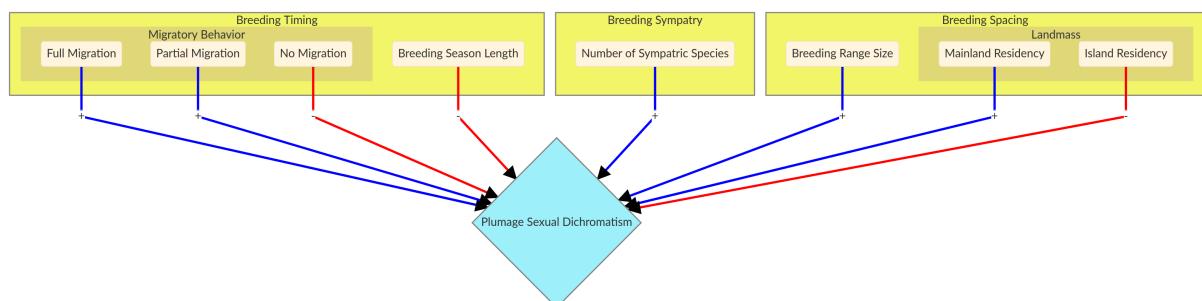


Figure 2: Hypotheses and predictions for each model (large yellow boxes). Arrow colours indicate predicted correlation, positive (blue) and negative (red)

104 SL, Labsphere, North Sutton NH, USA).

105 We applied a receptor-noise limited visual model [39] of the European Blackbird (*T. merula*) visual sys-
106 tem [40] in the *pavo* [41] package in R v4.0.0 [42] to calculate avian-perceived chromatic and achromatic
107 visual contrast (in units of “Just-Noticeable Differences”, or JNDs) of male vs. female plumage patches for
108 all sampled *Turdus* species. Chromatic and achromatic JNDs were calculated for male-female pairs within
109 each species (i.e., N=9 JND values calculated per patch for each species where N=3 males and N=3 fe-
110 males sampled), and then JND values were averaged for each species’ respective plumage patches. Under
111 ideal laboratory conditions, 1 JND is generally considered to be the discriminable threshold past which
112 an observer is predicted to be able to perceive the two colours as different. However, natural light envi-
113 ronments vary both spatially and temporally [43], bringing into question the accuracy of a 1 JND thresh-
114 old for generalizing visual contrast under natural conditions. Therefore, we calculated the total number
115 of sexually-dichromatic plumage patches per species (out of N=5 measured patches) as the number of
116 plumage patches with average JND values > 1, 2, or 3 to account for uncertainty in visual discrimination
117 thresholds due to variation in psychophysical and ambient lighting conditions affecting the strength of
118 between-sex plumage visual contrast [44]. Additionally, we modeled the number of divergent plumage
119 patches (at the three different JND thresholds listed above) within sexes and between different sympatric
120 species under different levels of breeding range overlap (10% increments between 0-90%; Fig. S1).

121 **Life History Data**

122 **Breeding Timing Model**

123 We collected data on migration behaviour and breeding season length from *Thrushes* [31] and the *Hand-
124 book of the Birds of the World* [45]. We assigned three different kinds of migratory behaviour: 1) *full
125 migration* when a species description clearly stated that a species “migrates”, 2) *partial migration* when a
126 species was described to have “altitudinal migration”, “latitudinal migration” or “movement during non-
127 breeding season”, or 3) *sedentary* when a species was described as “resident” or “sedentary”. Breeding
128 season length was defined as the number of months the species breeds each year.

129 **Breeding Sympatry Model**

130 Species’ breeding ranges were acquired from *BirdLife International* [46]. We calculated congener breeding
131 range overlaps (as percentages) using the *letsR* package in R [47]. We then calculated the number of sym-
132 patric species as the number of congeners with breeding ranges that overlap >30% with the focal species’
133 breeding range [27]. Comparisons of the number of sexually-dimorphic plumage patches vs. the number
134 of sympatric species among different breeding range overlap thresholds are provided in Supplementary
135 Figure 2.

136 **Breeding Spacing Model**

137 Species' breeding range sizes (in km²) were acquired using the *BirdLife International* breeding range maps.
138 Species' island vs. mainland residence was also determined using breeding ranges from *BirdLife Interna-*
139 *tional*. Mainland residence was assigned if the species had a breeding range on any continent and Japan.
140 Island residence was assigned to species having a breeding range limited to a non-continental landmass
141 entirely surrounded by a marine body of water.

142 **Statistical modeling**

143 We used phylogenetically-corrected Bayesian multilevel logistic regression models using the *brms* v2.13.0
144 package [48] in R v4.0.0 [42]. We modeled plumage sexual dichromatism responses as the number of
145 sexually-dichromatic patches > 1, 2, or 3 chromatic and achromatic JNDs. Plumage dichromatism re-
146 sponds were modeled as binomial trials (N=5 plumage patch "trials") to test for associations with breed-
147 ing timing, breeding sympatry and breeding spacing. For all phylogenetically-corrected models, we used
148 the *Turdus* molecular phylogeny from Nylander et al. (2008) [49] to create a covariance matrix of species'
149 phylogenetic relationships. All models used a dataset of N=67 out of the *Turdus* species for which all the
150 types of data (see above) were available.

151 Our *breeding timing* models included the following predictors: z-scores of breeding season length
152 (mean-centered by $\mu = 5.4$ months, and scaled by one standard deviation $\sigma = 2.3$ months), migratory
153 behaviour (no migration as the reference category versus partial or full migration), and their interaction.
154 *Breeding sympatry* models included the number of sympatric species with greater than 30% breeding range
155 overlap as the only predictor of the probability of having a sexually-dichromatic plumage patch. *Breeding*
156 *spacing* models included \log_e transformed breeding range size (km²) and breeding landmass (mainland
157 as the reference category versus island). We also ran null models (intercept only) for all responses. All
158 models' intercepts and response standard deviations were assigned a weakly informative prior (Student
159 T: df = 3, location = 0, scale = 10) [50], and predictor coefficients were assigned flat uninformative priors.
160 We ran each model for 6,000 iterations across 6 chains and assessed Markov Chain Monte Carlo (MCMC)
161 convergence using the Gelman-Rubin diagnostic (Rhat) [50]. We then performed k-fold cross-validation
162 [51] to assess each model's accuracy in predicting plumage sexual dichromatism of randomly-selected
163 samples of *Turdus* thrush species, refitting each model K=16 times. For each k-fold, the training dataset
164 included a randomly selected set of $N - N \frac{1}{K}$ or $N \approx 63$ species, and the testing dataset included $N \frac{1}{K}$ or
165 $N \approx 4$ species not included in the training dataset. Finally, we compared differences between the models'
166 expected log pointwise predictive densities (ELPD) to assess which model(s) best predicted the probability
167 of having a sexually-dichromatic plumage patch. [51].

168 Models' predictor effects were assessed using 90% highest-density intervals of the posterior distribu-
169 tions and probability of direction, the proportion of the posterior distribution that shares the same sign
170 (positive or negative) as the posterior median [52], to provide estimates of the probability of that a predic-
171 tor has an entirely positive or negative effect on the presence of sexually-dimorphic plumage patches. We
172 assume predictor estimates with a probability of direction ≥ 0.90 to be indicative of a reliable existence

173 of a predictor's effect on sexually-dimorphic plumage patches [52].

174 Results

175 Avian visual modeling

176 Among N=77 *Turdus* species, the following proportion have sexually monomorphic plumage (combined
177 achromatic and chromatic JND thresholds): 1.3% (n=1 species) have no sexually-dimorphic patches > 1
178 JND, 44% (n=34 species) have no dimorphic patches > 2 JND, and 63% (n=49 species) have no dimorphic
179 patches > 3 JND (Table S1). Additional proportions of *Turdus* species with sexually-dimorphic achromatic
180 or chromatic plumage patches are available in Table S2. When comparing within sexes between sympatric
181 species (i.e., following [27] at least a 30% overlap in breeding ranges: n=39 species with at least one
182 sympatric species and a median of n=6 sympatric species per focal species), the median number of avian-
183 discriminable plumage patches between species is 1 or greater for all three achromatic and chromatic
184 JND thresholds except for sympatric females at a chromatic JND threshold > 3 (Fig. S1).

185 Model comparisons

186 *Breeding sympathy*, *breeding timing*, and *breeding spacing* performed considerably better than *intercept-only*
187 (null models) in predicting the probability of a species having a sexually-dimorphic plumage patch. We
188 obtained N ≥ 4000 effective posterior samples for each model parameter and all models' Markov Chains
189 (MCMC) successfully converged (Rhat = 1 for all models' parameters). All *breeding sympathy*, *breeding tim-*
190 *ing*, and *breeding spacing* models performed similarly well and substantially better than *intercept only* mod-
191 els in predicting the probability of having a sexually-dimorphic plumage patch with achromatic JND values
192 > 1, 2, or 3 (Table 1; all models predicting achromatic plumage patches had ELPD values within 4, follow-
193 ing the convention of [53]). Among models predicting the probability of having a sexually-dichromatic
194 plumage patch with chromatic JND values >1, 2, or 3, all *breeding sympathy*, *breeding timing*, and *breeding*
195 *spacing* models performed much better than *intercept only* models, and *breeding sympathy* models had the
196 top predictive performance (Table 1; *breeding sympathy* models all have ELPD =0, only the *breeding spacing*
197 models predicting dichromatic plumage patches had similar predictive performance).

198 Achromatic plumage sexual dichromatism predictors

199 Migratory behaviour and shorter breeding season lengths were strongly associated with greater odds of
200 a species having achromatic plumage sexual dichromatism. All model predictors' effect estimates are pro-
201 vided as the posterior median odds-ratio (OR) and 90% highest-density interval (HDI) in Table 2. Among
202 predictors of achromatic sexually-dimorphic plumage patches, only predictors included in the *breeding*
203 *timing* model have predictors with probability of direction (*pd*) values ≥ 0.90 (Table 2). Specifically, longer
204 breeding season length was associated with lower odds of a species having a sexually-dimorphic plumage
205 patch with achromatic JND > 2 (breeding season length, OR [90% HDI] = 0.10 [0.01, 1.1], 89.5% decrease

206 in odds per 2.3-month increase in breeding season) and JND > 3 (breeding season length, OR [90% HDI]
207 = 0.25 [0.03, 1.5], 75% decrease in odds per 2.3-month increase in breeding season). Additionally, full
208 migratory behaviour, rather than no migratory behaviour, was associated with greater odds of a species
209 having a sexually-dimorphic plumage patch with achromatic JND > 1 (full migration, OR [90% HDI] = 4.97
210 [0.95, 24.4]), JND > 2 (full migration, OR [90% HDI] = 66.5 [3.2, 1802.4]) and JND > 3 (OR [90% HDI] =
211 22.3 [1.6, 307.9]). Finally, both full and partial migratory behaviour, rather than no migration behaviour,
212 in conjunction with longer breeding season lengths are associated with greater odds of a species having
213 a sexually-dimorphic plumage patch with achromatic JND > 1 (breeding season length x full migration,
214 OR [90% HDI] = 4.84 [0.67, 39.6]), JND > 2 (breeding season length x full migration, OR = 66.3 [0.59,
215 11415.7]; breeding season length x partial migration, OR [90% HDI] = 20.7 [0.9, 589.1]) and JND > 3
216 (breeding season length x partial migration, OR [90% HDI] = 8.28 [0.76, 109.1]).

217 **Chromatic plumage sexual dichromatism predictors**

218 Migratory behaviour, shorter breeding season lengths, and larger numbers of sympatric *Turdus* species
219 were strongly associated with greater odds of a species having chromatic plumage sexual dichromatism.
220 Among predictors of *breeding timing* models predicting chromatic sexually-dimorphic plumage patches,
221 longer breeding season length was associated with lower odds of a species having a plumage patch with
222 chromatic JND > 2 (OR [90% HDI] = 0.14 [0.01, 1.42], 86% reduction in odds per 2.3 month increase
223 in breeding season). Both full and partial migratory behaviour rather than no migration are associated
224 with greater odds of a species having a plumage patch JND > 1 (partial migration, OR [90% HDI] = 2.2
225 [0.94, 4.9]), JND > 2 (full migration, OR [90% HDI] = 80.51 [2.8, 3432.9]) and JND > 3 (partial migration,
226 OR [90% HDI] = 71.2 [0.32, 59062.9]; full migration, OR [90% HDI] = 234.7 [0.51, 300382.6]). For
227 *breeding spacing models*, island residency rather than mainland residency was associated with lower odds
228 of having a plumage patch > 1 chromatic JND (island, OR [90% HDI] = 0.27 [0.09, 0.89]). Finally, more
229 *Turdus* species in sympatry was associated with higher odds of a species having a sexually-dimorphic
230 chromatic plumage patch with JND > 1 (number of sympatric species, OR [90% HDI] = 1.4 [1.18, 1.67],
231 40% increase in odds per each additional sympatric species), JND > 2 (sympatric species, OR [90% HDI]
232 = 1.59 [1.01, 2.52], 59% increase in odds per each additional sympatric species), and JND > 3 (sympatric
233 species, OR [90% HDI] = 2.11 [1.03, 4.46], 111% increase in odds per each additional sympatric species).

Table 1: Expected log pointwise predictive densities (ELPD) differences and kfold information criterion values of models (ELPD Difference \pm standard error (kfold IC \pm standard error)). Values closest to zero indicate greater model prediction performance.

Plumage Metric	JND Threshold	Model			
		Breeding Sympatry	Breeding Timing	Breeding Spacing	Intercept Only
Achromatic					
	1 JND	0 \pm 0 (-122.17 \pm 0.67)	-2.51 \pm 2.49 (-124.68 \pm 2.38)	-2.59 \pm 1.01 (-124.76 \pm 1.04)	-21.69 \pm 7.36 (-143.87 \pm 7.51)
	2 JND	0 \pm 0 (-98.94 \pm 7.56)	-1.19 \pm 3.95 (-100.13 \pm 9.22)	-0.7 \pm 1.34 (-99.64 \pm 7.92)	-52.42 \pm 12.67 (-151.36 \pm 13.4)
	3 JND	-0.04 \pm 1.4 (-85.4 \pm 8.91)	-1.7 \pm 4.41 (-87.07 \pm 10.71)	0 \pm 0 (-85.37 \pm 8.76)	-28.54 \pm 10.02 (-113.91 \pm 13.65)
Chromatic					
	1 JND	0 \pm 0 (-115.75 \pm 2.95)	-5.67 \pm 3.55 (-121.42 \pm 2.28)	-2.73 \pm 3.4 (-118.49 \pm 2.67)	-14.8 \pm 7.22 (-130.55 \pm 7.05)
	2 JND	0 \pm 0 (-88.47 \pm 8.77)	-3.8 \pm 4.46 (-92.27 \pm 10.01)	-3.32 \pm 5.29 (-91.79 \pm 10.91)	-50.53 \pm 14.49 (-139 \pm 16.77)
	3 JND	0 \pm 0 (-62.77 \pm 10.41)	-8 \pm 4.32 (-70.77 \pm 12.29)	-4.43 \pm 3.9 (-67.2 \pm 11.72)	-47.63 \pm 15.34 (-110.4 \pm 20.01)

Table 2: Model predictor effect estimates (posterior median odds ratio and 90% highest-density interval) on the presence of a plumage patch with achromatic or chromatic visual contrast values > 1 , 2, and 3 JND. Model effects with a probability of direction (pd) value ≥ 0.90 are bolded in **red** for a negative effect and **blue** for a positive effect on plumage dichromatism. Phylogenetic signal (λ) for each model is provided as the median and 90% credible interval of the intraclass correlation coefficient among species.

Model	Parameter	Achromatic, JND > 1	Achromatic, JND > 2	Achromatic, JND > 3	Chromatic, JND > 1	Chromatic, JND > 2	Chromatic, JND > 3
Breeding Timing							
	Intercept	0 (0, 0.54), pd = 0.98	0 (0, 0.19), pd = 0.99	0 (0, 0.19), pd = 0.99	0.41 (0.05, 2.79), pd = 0.78	0 (0, 1.73), pd = 0.95	0 (0, 1.37), pd = 0.96
	Breeding Season Length	0.1 (0.01, 1.05), pd = 0.97	0.25 (0.03, 1.49), pd = 0.91	0.25 (0.03, 1.49), pd = 0.91	0.89 (0.56, 1.4), pd = 0.66	0.14 (0.01, 1.42), pd = 0.94	0.08 (0, 9.14), pd = 0.83
	Partial Migration vs. No Migration	0.76 (0.31, 2.75), pd = 0.53	4.11 (0.44, 33.64), pd = 0.83	3.65 (0.44, 33.64), pd = 0.85	2.2 (0.24, 4.89), pd = 0.94	6.7 (0.42, 134.8), pd = 0.88	71.16 (0.32, 59062.92), pd = 0.92
	Full Migration vs. No Migration	4.37 (0.95, 24.41), pd = 0.96	66.52 (3.19, 1802.4), pd = 0.99	22.34 (1.59, 307.9), pd = 0.98	2.29 (0.69, 7.31), pd = 0.88	80.31 (2.81, 343.86), pd = 0.99	234.71 (0.51, 200382.62), pd = 0.95
	Breeding Season Length x Partial Migration	1.34 (0.48, 3.92), pd = 0.68	20.71 (0.87, 589.09), pd = 0.96	8.28 (0.76, 109.11), pd = 0.94	1.39 (0.65, 3.12), pd = 0.76	9.03 (0.44, 251.36), pd = 0.9	34.46 (0.08, 68228.71), pd = 0.85
	Breeding Season Length x Full Migration	4.34 (0.67, 39.63), pd = 0.9	66.3 (0.59, 11415.7), pd = 0.93	16.41 (0.27, 824.69), pd = 0.89	1.68 (0.31, 8.33), pd = 0.7	160.6 (0.84, 67791.13), pd = 0.95	433.67 (0.01, 371945.69), pd = 0.85
	Phylogenetic Signal λ , Median (90% Credible Interval)	0.29 (0.16, 0.43)	0.72 (0.56, 0.86)	0.61 (0.42, 0.8)	0.17 (0.08, 0.28)	0.74 (0.57, 0.88)	0.89 (0.77, 0.97)
Breeding Spacing							
	Intercept	0 (0, 2.44), pd = 0.95	0 (0, 0.14), pd = 0.98	0 (0, 0.14), pd = 0.98	0.51 (0.03, 9.7), pd = 0.65	0 (0, 7.63), pd = 0.92	0 (0, 8.19), pd = 0.91
	Island vs. Mainland	1.08 (0.25, 4.79), pd = 0.54	0.53 (0.01, 17.83), pd = 0.61	0.92 (0.05, 19.32), pd = 0.52	0.27 (0.09, 0.89), pd = 0.97	0.03 (0, 3.99), pd = 0.89	0.04 (0, 67.59), pd = 0.77
	Breeding Range Size	1.08 (0.88, 1.32), pd = 0.75	1.23 (0.76, 2.01), pd = 0.77	1.3 (0.87, 1.93), pd = 0.87	1.02 (0.87, 1.19), pd = 0.58	1.24 (0.75, 2.05), pd = 0.77	1.26 (0.54, 2.99), pd = 0.69
	Phylogenetic Signal λ , Median (90% Credible Interval)	0.27 (0.15, 0.41)	0.71 (0.56, 0.85)	0.6 (0.42, 0.77)	0.15 (0.07, 0.25)	0.72 (0.55, 0.86)	0.85 (0.71, 0.95)
Breeding Sympatry							
	Intercept	0.41 (0.03, 5.83), pd = 0.72	0 (0, 0.98), pd = 0.95	0 (0, 0.34), pd = 0.98	0.25 (0.04, 1.35), pd = 0.91	0 (0, 1.12), pd = 0.95	0 (0, 0.29), pd = 0.98
	Number of Sympatric Species ($\geq 30\%$ Breeding Range Overlap)	1.03 (0.84, 1.27), pd = 0.61	1.15 (0.74, 1.75), pd = 0.71	1.13 (0.76, 1.63), pd = 0.71	1.4 (1.18, 1.67), pd = 0.99	1.59 (1.01, 2.52), pd = 0.96	2.11 (1.03, 4.46), pd = 0.97
	Phylogenetic Signal λ , Median (90% Credible Interval)	0.26 (0.14, 0.39)	0.7 (0.54, 0.83)	0.59 (0.41, 0.77)	0.13 (0.06, 0.23)	0.69 (0.52, 0.83)	0.82 (0.67, 0.94)

234 Discussion

235 Our results provide comparative correlative evidence in support of predictions of the recognition hypothesis
236 for plumage sexual dichromatism in true thrushes. We used a receptor-noise limited model of *Turdus*
237 *merula* vision [39,40] to measure avian-perceivable visual contrast of plumage colours and found that the
238 odds of plumage sexual dichromatism are much greater for *Turdus* thrush species that have full or partial
239 migration rather than no migration, have relatively short breeding seasons, and are in sympatry with many
240 other true thrush species (Table 1,2). Our results align with prior comparative studies of avian plumage
241 sexual dichromatism where strong associations of sexual dichromatism with greater migratory behaviour
242 [10] and more sympatric taxa [27] were found among many species of different passerine families.

243 Further, we determined that sympatric *Turdus* species have distinguishable plumage colouration differences
244 from one another when measuring plumage appearance from the avian visual perspective (Fig. S1).
245 Divergent plumage colouration within sexes between closely-related species indicates that plumage sexual
246 dichromatism may have evolved to facilitate species and mate recognition in *Turdus* species breeding
247 under higher sympatry with other true thrushes. However, we cannot directly determine if the plumage
248 sexual dichromatism in sympatric *Turdus* species is the result of reproductive character displacement. We
249 do not know if past changes in species' plumage sexual dichromatism occurred before or during periods of
250 sympatry with other *Turdus* species. Regardless, present-day plumage sexual dichromatism and perceivable
251 differences in plumage colouration between sympatric species likely reduces the challenge of finding
252 compatible mates by signaling an individual's sex, breeding status, and species. For example, the four
253 species *Turdus* hybrid zone in north-central Asia [33] is a particularly striking example where reproductive
254 character displacement has likely occurred and all four species exhibit strong plumage sexual dichromatism
255 (Fig. S3). Comparing within sexes between sister species pairs of *T.ruficollis* and *T.atrogularis*, and
256 *T.naumanni* and *T.eunomus* [49], plumage patterns of the species pairs are nearly identical except for a divergence
257 in colour. *T.ruficollis* and *T.atrogularis* share similar facial and throat colouring patterns, with the
258 main difference being red colouration in *T.ruficollis* in opposition to the black colouration of *T.atrogularis*.
259 In the second species pair, *T.naumanni* has red ventral plumage colouration and *T.eunomus* has black ventral
260 plumage colouration.

261 Previous studies have found that closely-related sympatric species tend to have more similar plumage
262 appearance than expected if plumage colouration patterns had evolved to facilitate species recognition
263 via reproductive character displacement [54,55]. The potential lack of major plumage colour divergence
264 among closely-related sympatric species may be attributable to constraints imposed by a shared light environment
265 on colour signal efficiency [56], or similar natural selection pressures (e.g., predators, parasites,
266 and weather). Generally, despite greater similarity in plumage appearance in comparison to allopatric
267 species, closely-related sympatric species can still have substantially different and biologically-relevant
268 differences in achromatic or chromatic interspecific visual contrast of plumage patches when measuring
269 plumage colouration differences from the avian visual perspective (as we have found in our analyses).

270 Conclusions

271 Patterns of plumage sexual dichromatism in true thrushes (*Turdus*) are consistent with select predictions
272 of the recognition hypothesis for plumage sexual dichromatism. Migratory behaviour and limited breed-
273 ing seasons reduce the amount of time available to find a mate, and greater plumage sexual dichromatism
274 may help migratory species find compatible mates more rapidly. Greater plumage sexual dichromatism
275 in *Turdus* species under sympatry with other true thrush species also supports the possibility that in-
276 creased plumage sexual dichromatism may be the result of reproductive character displacement. There-
277 fore, greater plumage sexual dichromatism likely increases the speed and accuracy of finding a compatible
278 breeding mate, reduces species and mate recognition errors, and decreases hybridization.

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285 Data Accessibility

286 Data and code used for the analyses can be found at <https://github.com/aluro2/Turdus-Dichromatism>.

287 Author Contributions

288 **Alec Luro:** Conceptualization, Investigation, Methodology, Software, Formal Analysis, Data Curation,
289 Visualization, Writing-Original Draft, Writing-Review & Editing. **Mark Hauber:** Conceptualization, Re-
290 sources, Supervision, Project administration, Funding acquisition, Writing-Review & Editing.

291 References

- 292 1. Andersson M. 1994 Species Recognition, Sexual Selection, and Speciation. In *Sexual Selection*, pp.
293 207–226. Princeton University Press. (doi:[10.2307/j.ctvs32s1x.13](https://doi.org/10.2307/j.ctvs32s1x.13))
- 294 2. Grönig J, Hochkirch A. 2008 Reproductive Interference Between Animal Species. *The Quarterly
295 Review of Biology* **83**, 257–282. (doi:[10.1086/590510](https://doi.org/10.1086/590510))
- 296 3. Pfennig KS, Hurlbert AH. 2012 Heterospecific interactions and the proliferation of sexually dimor-
297 phic traits. *Current Zoology* **58**, 453–462. (doi:[10.1093/czoolo/58.3.453](https://doi.org/10.1093/czoolo/58.3.453))

- 298 4. West-Eberhard MJ. 1983 Sexual Selection, Social Competition, and Speciation. *The Quarterly Re-*
299 *view of Biology* **58**, 155–183. (doi:[10.1086/413215](https://doi.org/10.1086/413215))
- 300 5. Martin PR, Montgomerie R, Lougheed SC. 2015 Color Patterns of Closely Related Bird Species Are
301 More Divergent at Intermediate Levels of Breeding-Range Sympatry. *The American Naturalist* **185**,
443–451. (doi:[10.1086/680206](https://doi.org/10.1086/680206))
- 302 6. Bitton P-P, Doucet SM. 2016 Sympatric black-headed and elegant trogons focus on dif-
303 ferent plumage characteristics for species recognition. *Animal Behaviour* **116**, 213–221.
(doi:[10.1016/j.anbehav.2016.03.035](https://doi.org/10.1016/j.anbehav.2016.03.035))
- 304 7. Martin TE, Badyaev AV. 1996 Sexual Dichromatism in Birds: Importance of Nest Predation and
305 Nest Location for Females Versus Males. *Evolution* **50**, 2454–2460. (doi:[10.2307/2410712](https://doi.org/10.2307/2410712))
- 306 8. Burns KJ. 1998 A Phylogenetic Perspective on the Evolution of Sexual Dichromatism in Tan-
307 agers (thraupidae): The Role of Female Versus Male Plumage. *Evolution* **52**, 1219–1224.
(doi:[10.1111/j.1558-5646.1998.tb01849.x](https://doi.org/10.1111/j.1558-5646.1998.tb01849.x))
- 308 9. Badyaev AV, Hill GE. 2003 Avian Sexual Dichromatism in Relation to Phylogeny
309 and Ecology. *Annual Review of Ecology, Evolution, and Systematics* **34**, 27–49.
(doi:[10.1146/annurev.ecolsys.34.011802.132441](https://doi.org/10.1146/annurev.ecolsys.34.011802.132441))
- 310 10. Dale J, Dey C, Delhey K, Kempenaers B, Valcu M. 2015 The effects of life-history and social selec-
311 tion on male and female plumage coloration. *Nature* **000**, 1–17. (doi:[10.1038/nature15509](https://doi.org/10.1038/nature15509))
- 312 11. Dunn PO, Armenta JK, Whittingham LA. 2015 Natural and sexual selection act on different axes
313 of variation in avian plumage color. *Science Advances* **1**, e1400155. (doi:[10.1126/sciadv.1400155](https://doi.org/10.1126/sciadv.1400155))
- 314 12. Hawkins GL, Hill GE, Mercadante A. 2012 Delayed plumage maturation and delayed reproductive
315 investment in birds. *Biological Reviews* **87**, 257–274. (doi:[10.1111/j.1469-185X.2011.00193.x](https://doi.org/10.1111/j.1469-185X.2011.00193.x))
- 316 13. Hamilton TH. 1961 On the Functions and Causes of Sexual Dimorphism in Breeding Plumage
317 Characters of North American Species of Warblers and Orioles. *The American Naturalist* **45**, 64–
73. (doi:[10.1086/282167](https://doi.org/10.1086/282167))
- 318 14. Saetre G-P, Slagsvold T. 1992 Evidence for sex recognition from plumage colour by the pied fly-
319 catcher, *Ficedula hypoleuca*. *Animal Behaviour* **44**, 293–299. (doi:[10.1016/0003-3472\(92\)90035-8](https://doi.org/10.1016/0003-3472(92)90035-8))
- 320 15. Friedman NR, Hofmann CM, Kondo B, Omland KE. 2009 Correlated evolution of migra-
321 tion and sexual dichromatism in the new world orioles (*Icterus*). *Evolution* **63**, 3269–3274.
(doi:[10.1111/j.1558-5646.2009.00792.x](https://doi.org/10.1111/j.1558-5646.2009.00792.x))
- 322 16. Simpson RK, Johnson MA, Murphy TG. 2015 Migration and the evolution of sexual dichromatism:
323 Evolutionary loss of female coloration with migration among wood-warblers. *Proceedings of the
Royal Society B: Biological Sciences* **282**, 20150375. (doi:[10.1098/rspb.2015.0375](https://doi.org/10.1098/rspb.2015.0375))
- 324 17. Matysioková B, Remeš V, Cockburn A. 2017 Broad-scale variation in sexual dichromatism in song-
325 birds is not explained by sex differences in exposure to predators during incubation. *Journal of
Avian Biology* **48**, 1322–1330. (doi:[10.1111/jav.01144](https://doi.org/10.1111/jav.01144))

- 326 18. Badyaev AV, Ghalambor CK. 1998 Does a Trade-Off Exist between Sexual Ornamentation and
Ecological Plasticity? Sexual Dichromatism and Occupied Elevational Range in Finches. *Oikos* **82**,
319–324. (doi:[10.2307/3546972](https://doi.org/10.2307/3546972))
- 327
- 328 19. Figuerola J, Green AJ. 2000 The evolution of sexual dimorphism in relation to mating patterns,
cavity nesting, insularity and sympatry in the Anseriformes. *Functional Ecology* **14**, 701–710.
(doi:[10.1046/j.1365-2435.2000.00474.x](https://doi.org/10.1046/j.1365-2435.2000.00474.x))
- 330 20. Tobias JA, Seddon N. 2009 Sexual selection and ecological generalism are correlated in antbirds.
Journal of Evolutionary Biology **22**, 623–636. (doi:[10.1111/j.1420-9101.2008.01678.x](https://doi.org/10.1111/j.1420-9101.2008.01678.x))
- 331
- 332 21. Roulin A, Salamin N. 2010 Insularity and the evolution of melanism, sexual dichromatism and
body size in the worldwide-distributed barn owl. *Journal of Evolutionary Biology* **23**, 925–934.
(doi:[10.1111/j.1420-9101.2010.01961.x](https://doi.org/10.1111/j.1420-9101.2010.01961.x))
- 333
- 334 22. Doutrelant C, Paquet M, Renault JP, Grégoire A, Crochet P-A, Covas R. 2016 Worldwide patterns
of bird colouration on islands. *Ecology Letters* **19**, 537–545. (doi:[10.1111/ele.12588](https://doi.org/10.1111/ele.12588))
- 335
- 336 23. Kearns AM, Joseph L, Austin JJ, Driskell AC, Omland KE. 2020 Complex mosaic of sexual dichro-
matism and monochromatism in Pacific robins results from both gains and losses of elaborate
coloration. *Journal of Avian Biology* **51**. (doi:[10.1111/jav.02404](https://doi.org/10.1111/jav.02404))
- 337
- 338 24. Alatalo RV, Gustafsson L, Lundberg A. 1994 Male coloration and species recognition in sympatric
flycatchers. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **256**, 113–118.
(doi:[10.1098/rspb.1994.0057](https://doi.org/10.1098/rspb.1994.0057))
- 339
- 340 25. Saetre G-P, Moum T, Bureš S, Král M, Adamjan M, Moreno J. 1997 A sexually selected
character displacement in flycatchers reinforces premating isolation. *Nature* **387**, 589–592.
(doi:[10.1038/42451](https://doi.org/10.1038/42451))
- 341
- 342 26. Laaksonen T et al. 2015 Sympatric divergence and clinal variation in multiple coloration traits of
Ficedula flycatchers. *Journal of Evolutionary Biology* **28**, 779–790. (doi:[10.1111/jeb.12604](https://doi.org/10.1111/jeb.12604))
- 343
- 344 27. Cooney CR, Tobias JA, Weir JT, Botero CA, Seddon N. 2017 Sexual selection, specia-
tion and constraints on geographical range overlap in birds. *Ecology Letters* **20**, 863–871.
(doi:[10.1111/ele.12780](https://doi.org/10.1111/ele.12780))
- 345
- 346 28. Seddon N et al. 2013 Sexual selection accelerates signal evolution during speciation in birds. *Pro-
ceedings of the Royal Society B: Biological Sciences* **280**, 20131065. (doi:[10.1098/rspb.2013.1065](https://doi.org/10.1098/rspb.2013.1065))
- 347
- 348 29. Cooney CR, Varley ZK, Nouri LO, Moody CJA, Jardine MD, Thomas GH. 2019 Sexual selection pre-
dicts the rate and direction of colour divergence in a large avian radiation. *Nature Communications*
10, 1773. (doi:[10.1038/s41467-019-09859-7](https://doi.org/10.1038/s41467-019-09859-7))
- 349
- 350 30. Martin PR, Montgomerie R, Lougheed SC. 2010 Rapid Sympatry Explains Greater Color
Pattern Divergence in High Latitude Birds. *Evolution* **64**, 336–347. (doi:[10.1111/j.1558-5646.2009.00831.x](https://doi.org/10.1111/j.1558-
5646.2009.00831.x))
- 351
- 352 31. Clement P, Hathaway R. 2000 *Thrushes*. London: A&C Black Publishers Ltd.
- 353

- 354 32. Nagy J, Végvári Z, Varga Z. 2019 Phylogeny, migration and life history: Filling the gaps in
the origin and biogeography of the *Turdus* thrushes. *Journal of Ornithology* **160**, 529–543.
(doi:[10.1007/s10336-019-01632-3](https://doi.org/10.1007/s10336-019-01632-3))
- 355 33. McCarthy EM. 2006 *Handbook of avian hybrids of the world*. Oxford ; New York: Oxford University
Press.
- 356 34. Escalona-Segura G, Peterson AT. 1997 Variable plumage ontogeny in the Black (*Turdus infuscatus*)
and Glossy-black Robins (*T. serranus*). *The Wilson Bulletin* **109**, 182–184.
- 359 35. Peterson AT, Navarro-Siguenza AG, Chen G. 2003 Delayed plumage maturation in Asian thrushes,
genus *Turdus*. *Forktail* **19**, 152–153.
- 360 36. Ligon RA, Hill GE. 2013 Is the juvenal plumage of altricial songbirds an honest signal of age? Ev-
idence from a comparative study of thrushes (Passeriformes: Turdidae). *Journal of Zoological Sys-
tematics and Evolutionary Research* **51**, 64–71. (doi:[10.1111/j.1439-0469.2012.00668.x](https://doi.org/10.1111/j.1439-0469.2012.00668.x))
- 361 37. Luro A, Hauber ME. 2019 Plumage dichromatism in *Turdus* thrushes.
(doi:[10.17605/OSF.IO/ZUM6D](https://doi.org/10.17605/OSF.IO/ZUM6D))
- 362 38. Andersson S, Prager M. 2006 Quantifying Colors. In *Bird coloration, Volume 1: Mechanisms and
Measurements* (eds GE Hill, KJ McGraw), pp. 76–77. Cambridge, MA: Harvard University Press.
- 363 39. Vorobyev M, Osorio D. 1998 Receptor noise as a determinant of colour thresholds. *Proceedings.
Biological sciences / The Royal Society* **265**, 351–8. (doi:[10.1098/rspb.1998.0302](https://doi.org/10.1098/rspb.1998.0302))
- 364 40. Hart NS, Partridge JC, Cuthill IC, Bennett AT. 2000 Visual pigments, oil droplets, ocular media and
cone photoreceptor distribution in two species of passerine bird: The blue tit (*Parus caeruleus*
L.) And the blackbird (*Turdus merula* L.). *Journal of comparative physiology. A, Sensory, neural, and
behavioral physiology* **186**, 375–387. (doi:[10.1007/s003590050437](https://doi.org/10.1007/s003590050437))
- 365 41. Maia R, Gruson H, Endler JA, White TE. 2019 Pavo 2: New tools for the spectral and spatial analysis
of colour in r. *Methods in Ecology and Evolution* **10**, 1097–1107. (doi:[10.1111/2041-210X.13174](https://doi.org/10.1111/2041-210X.13174))
- 366 42. R Core Team. 2020 *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R
Foundation for Statistical Computing.
- 367 43. Endler JA. 1993 The Color of Light in Forests and Its Implications. *Ecological Monographs* **63**, 1–27.
(doi:[10.2307/2937121](https://doi.org/10.2307/2937121))
- 368 44. Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall
J, Whiting MJ. 2015 An Integrative Framework for the Appraisal of Coloration in Nature. *The
American Naturalist* **185**, 705–724. (doi:[10.1086/681021](https://doi.org/10.1086/681021))
- 369 45. del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E. 2017 *Handbook of the birds of the world
alive*.
- 370 46. BirdLife International and Handbook of the Birds of the World. 2018 *Bird species distribution maps
of the world. Version 2018.1*.
- 371 47. Vilela B, Villalobos F. 2015 letsR: A new R package for data handling and analysis in macroecology.
Methods in Ecology and Evolution **6**, 1229–1234. (doi:[10.1111/2041-210X.12401](https://doi.org/10.1111/2041-210X.12401))

- 386 48. Bürkner PC. 2017 Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **80**, 1–28. (doi:[10.18637/jss.v080.i01](https://doi.org/10.18637/jss.v080.i01))
- 387
- 388 49. Nylander JAA, Olsson U, Alström P, Sanmartín I. 2008 Accounting for phylogenetic uncertainty in biogeography: A bayesian approach to dispersal-vicariance analysis of the thrushes (Aves: Turdus). *Systematic Biology* **57**, 257–268. (doi:[10.1080/10635150802044003](https://doi.org/10.1080/10635150802044003))
- 389
- 390 50. Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. 2013 *Bayesian data analysis, third edition*. Third. Boca Raton, FL: CRC Press. (doi:[10.1201/b16018](https://doi.org/10.1201/b16018))
- 391
- 392 51. Vehtari A, Gelman A, Gabry J. 2017 Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* **27**, 1413–1432. (doi:[10.1007/s11222-016-9696-4](https://doi.org/10.1007/s11222-016-9696-4))
- 393
- 394 52. Makowski D, Ben-Shachar MS, Chen SHA, Lüdecke D. 2019 Indices of Effect Existence and Significance in the Bayesian Framework. *Frontiers in Psychology* **10**. (doi:[10.3389/fpsyg.2019.02767](https://doi.org/10.3389/fpsyg.2019.02767))
- 395
- 396 53. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: A practical information-theoretic approach*. 2nd ed. New York: Springer.
- 397
- 398 54. Simpson RK, Wilson DR, Mistakidis AF, Mennill DJ, Doucet SM. 2021 Sympatry drives colour and song evolution in wood-warblers (Parulidae). *Proceedings of the Royal Society B: Biological Sciences* **288**, 20202804. (doi:[10.1098/rspb.2020.2804](https://doi.org/10.1098/rspb.2020.2804))
- 399
- 400 55. Miller ET, Leighton GM, Freeman BG, Lees AC, Ligon RA. 2019 Ecological and geographical overlap drive plumage evolution and mimicry in woodpeckers. *Nature Communications* **10**, 1602. (doi:[10.1038/s41467-019-09721-w](https://doi.org/10.1038/s41467-019-09721-w))
- 401
- 402 56. McNaught MK, Owens IPF. 2002 Interspecific variation in plumage colour among birds: Species recognition or light environment? *Journal of Evolutionary Biology* **15**, 505–514. (doi:[10.1046/j.1420-9101.2002.00431.x](https://doi.org/10.1046/j.1420-9101.2002.00431.x))
- 403