

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

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7 **Abstract**

8 Ecological conditions limiting the time to find a compatible mate or increasing the difficulty in doing
9 so likely promote the evolution of traits used for species and mate recognition. Here, we tested this
10 recognition hypothesis for promoting plumage sexual dichromatism in the true thrushes (*Turdus*), a large
11 and diverse genus of passerine birds. We used receptor-noise limited models of avian vision to quantify
12 avian-perceived chromatic and achromatic visual contrasts between male and female plumage patches
13 and tested the influence of breeding season length, spatial distribution, and sympatry with other *Turdus*
14 species on plumage dichromatism. As predicted, we found that 1) true thrush species with migratory
15 behaviour have greater plumage sexual dichromatism than non-migratory species, 2) species with longer
16 breeding seasons have less plumage sexual dichromatism, and 3) the number of *Turdus* thrush species
17 breeding in sympatry is associated with more plumage sexual dichromatism. These results suggest that
18 social recognition systems, including species and mate recognition, play a prominent role in the evolution
19 of thrush plumage sexual dichromatism.

20 **Keywords**

21 *achromatic, chromatic, dichromatism, plumage, species recognition*

22 **Introduction**

23 Species recognition is necessary in sexually reproducing lineages for individuals to find compatible mates
24 and produce viable offspring [1,2]. Conspicuous traits signaling species and sex identity increase the
25 ease and speed of mate recognition by reducing the effort, error, and time involved when searching for
26 compatible mates and lessen the likelihood of mating with heterospecifics [3]. Traits used in species
27 and mate recognition may also serve as signals of status to conspecifics and reduce costly conflicts over
28 resources and mates [4]. Accordingly, distinct traits facilitating mate recognition should be more likely to
29 arise and be maintained under conditions that increase both the difficulty of finding a compatible mate

30 and degree of resource competition among conspecifics and closely-related species. Conditions likely to
31 favour traits signaling individuals' species, sex, and breeding status include higher sympatry with many
32 closely-related species, limited time to find compatible breeding mates, and lower rates of encounter with
33 potential breeding mates [1].

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

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

59 True thrushes (*Turdus* spp.) are an exceptionally diverse monophyletic genus of passerine birds con-
60 sisting of about ~86 species distributed across the globe (Fig. 1). The true thrushes are an ideal passer-
61 ine clade for examining the species recognition hypothesis for plumage sexual dichromatism because
62 plumage sexual dichromatism and migratory behaviours vary substantially between species and sexual
63 dichromatism has evolved multiple times in thrushes across the world [31,32]. Hybridization also occurs
64 in some, but not all, *Turdus* species. There is a large hybrid zone between four *Turdus* species (*T. atrogu-*
65 *laris*, *T. eunomus*, *T. naumanni*, *T. ruficollis*) in north-central Asia [33], indicating that some sympatric *Turdus*
66 species can successfully interbreed.

67 Overall, ecological conditions that increase the time and degree of difficulty in finding a suitable con-
68 specific mate should select for phenotypic traits that reliably signal species and sex identity. Across

69 various bird lineages, greater plumage dichromatism is present in species that are i) migratory rather than
 70 nonmigratory, ii) have shorter breeding seasons, iii) live on mainlands rather than islands, iv) have larger
 71 breeding ranges (distributions), and v) breed in sympatry with more closely-related species. These pat-
 72 terns suggest that ecological circumstances where rapid and accurate mate recognition is challenging
 73 strongly favour the evolution and maintenance of prominent plumage sexual dichromatism in birds. Here,
 74 we test these predictions of the recognition hypothesis for sexually-dimorphic avian plumage by evaluat-
 75 ing the potential influences of breeding timing, spacing, and sympatry on plumage dichromatism in *Turdus*
 76 thrushes (Fig. 2).

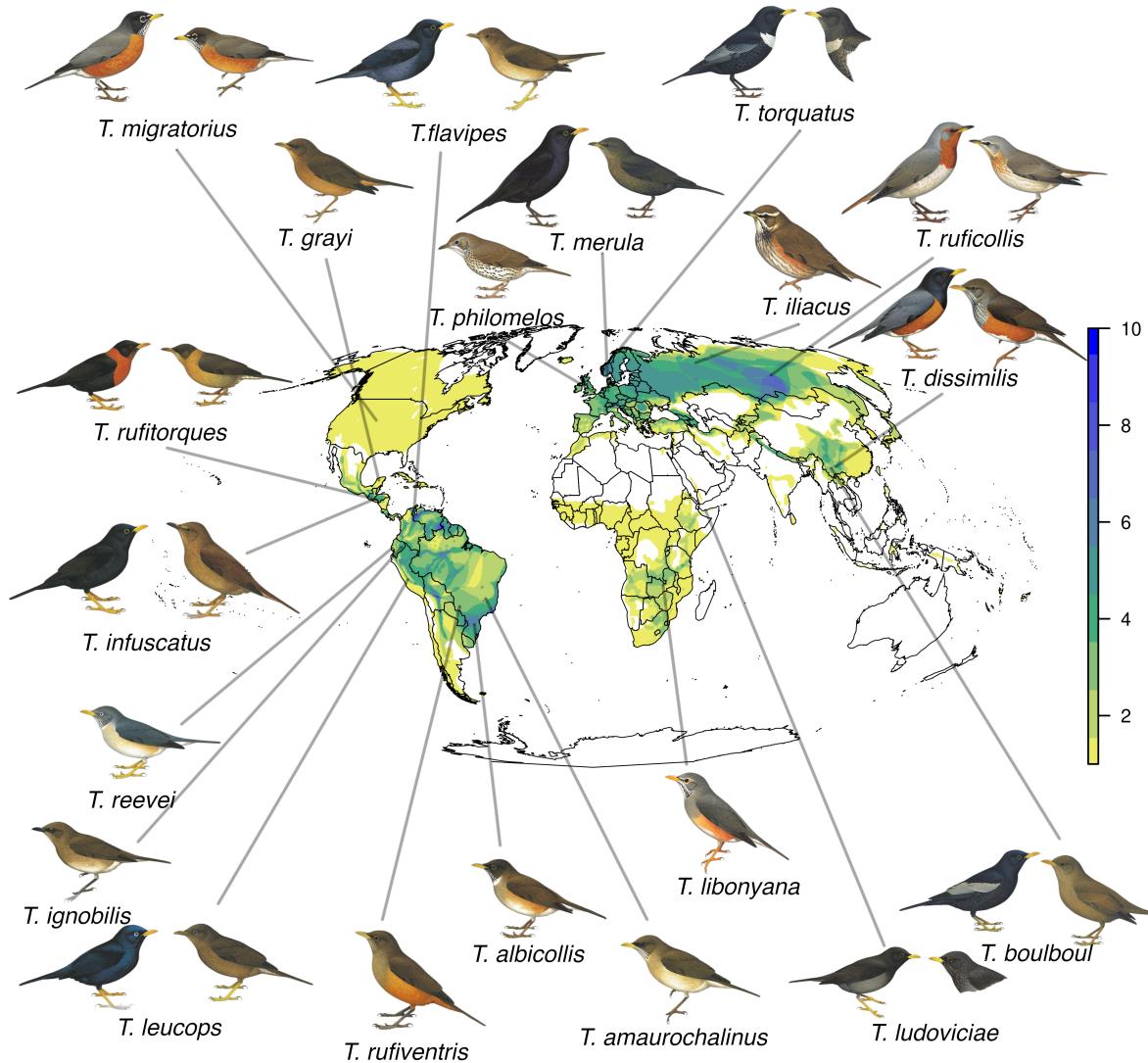


Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International, with representative species' males and females shown for species with sexually dimorphic plumage. The color scale indicates the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations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

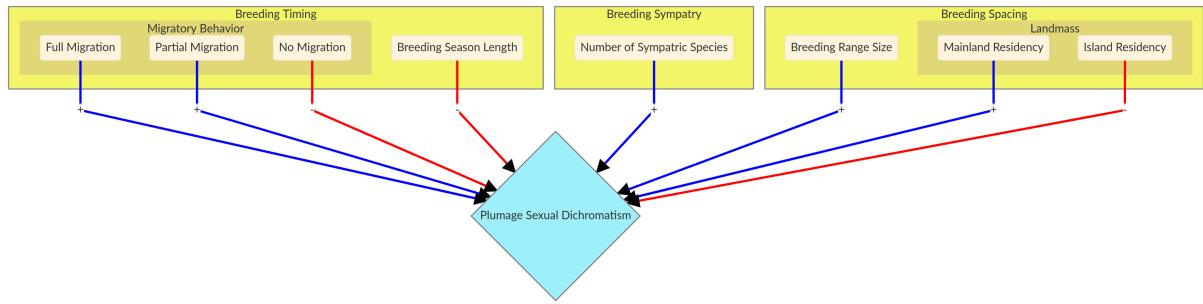


Figure 2: Hypotheses and predictions for each model (large yellow boxes). Arrow colours indicate predicted correlation, positive (blue) and negative (red)

Methods

Initial pre-registration of the study's methods and analyses are available on [Open Science Framework \[34\]](#).

Plumage sexual dichromatism

A total of N=77 *Turdus* thrush species (approximately ~89% of all known true thrush species) were sampled for plumage spectral reflectance using prepared bird skin specimens at the American Museum of Natural History in New York City and the Field Museum in Chicago, USA. Reflectance measurements spanning 300-700nm were taken in triplicate from the belly, breast, throat, crown, and mantle plumage patches [35] of each individual. N=3 male and N=3 female individuals were measured for most species (exceptions: *T. lawrencii*, N=2 males and N=2 females; *T. swalesi*, N=1 male and N=1 female). Reflectance spectra were measured using a 400 µm fiber optic reflection probe fitted with a rubber stopper to maintain a consistent measuring distance of 3 mm and area of 2 mm² at a 90° angle to the surface of the feather patch. Measurements were taken using a JAZ spectrometer with a pulsed-xenon light source (Ocean Optics, Dunedin, USA) and we used a diffuse 99% reflectance white standard (Spectralon WS-1-SL, Labsphere, North Sutton NH, USA).

We applied a receptor-noise limited visual model [36] of the European Blackbird (*T. merula*) visual system [37] in the *pavo* [38] package in R v4.0.0 [39] to calculate avian-perceived chromatic and achromatic visual contrast (in units of "Just-Noticeable Differences", or JNDs) of male vs. female plumage patches for all sampled *Turdus* species. Chromatic and achromatic JNDs were calculated for male-female pairs within each species (i.e., N=9 JND values calculated per patch for each species where N=3 males and N=3 females sampled), and then JND values were averaged for each species' respective plumage patches. Under ideal laboratory conditions, 1 JND is generally considered to be the discriminable threshold past which an observer is predicted to be able to perceive the two colours as different. However, natural light environments vary both spatially and temporally [40], bringing into question the accuracy of a 1 JND threshold for generalizing visual contrast under natural conditions. Therefore, we calculated the total number of sexually-dichromatic plumage patches per species (out of N=5 measured patches) as the number of plumage patches with average JND values > 1, 2, or 3 to account for uncertainty in visual discrimination

104 thresholds due to variation in psychophysical and ambient lighting conditions affecting the strength of
105 between-sex plumage visual contrast [41]. Additionally, we modeled the number of divergent plumage
106 patches (at the three different JND thresholds listed above) within sexes and between different sympatric
107 species under different levels of breeding range overlap (10% increments between 0-90%).

108 **Life History Data**

109 **Breeding Timing Model**

110 We collected data on migration behaviour and breeding season length from *Thrushes* [31] and the *Hand-*
111 *book of the Birds of the World* [42]. We assigned three different kinds of migratory behaviour: 1) *full*
112 *migration* when a species description clearly stated that a species “migrates”, 2) *partial migration* when a
113 species was described to have “altitudinal migration”, “latitudinal migration” or “movement during non-
114 breeding season”, or 3) *sedentary* when a species was described as “resident” or “sedentary”. Breeding
115 season length was defined as the number of months the species breeds each year.

116 **Breeding Sympatry Model**

117 Species’ breeding ranges were acquired from *BirdLife International* [43]. We calculated congener breeding
118 range overlaps (as percentages) using the *letsR* package in R [44]. We then calculated the number of sym-
119 patric species as the number of congeners with breeding ranges that overlap >30% with the focal species’
120 breeding range [27]. Comparisons of the number of sexually-dimorphic plumage patches vs. the number
121 of sympatric species among different breeding range overlap thresholds are provided in Supplementary
122 Figure 1.

123 **Breeding Spacing Model**

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

129 **Statistical modeling**

130 We used phylogenetically-corrected Bayesian multilevel logistic regression models using the *brms* v2.13.0
131 package [45] in R v4.0.0 [39]. We modeled plumage sexual dichromatism responses as the number of
132 sexually-dichromatic patches > 1, 2, or 3 chromatic and achromatic JNDs. Plumage dichromatism re-
133 sponses were modeled as binomial trials (N=5 plumage patch “trials”) to test for associations with breed-
134 ing timing, breeding sympatry and breeding spacing. For all phylogenetically-corrected models, we used
135 the *Turdus* molecular phylogeny from Nylander et al. (2008) [46] to create a covariance matrix of species’

136 phylogenetic relationships. All models used a dataset of N=67 out of the *Turdus* species for which all the
137 types of data (see above) were available.

138 Our breeding timing models included the following predictors: z-scores of breeding season length
139 (mean-centered by $\mu = 5.4$ months, and scaled by one standard deviation $\sigma = 2.3$ months), migratory
140 behaviour (no migration as the reference category versus partial or full migration), and their interaction.
141 Breeding sympatry models included the number of sympatric species with greater than 30% breeding range
142 overlap as the only predictor of the probability of having a sexually-dichromatic plumage patch. Breeding
143 spacing models included \log_e transformed breeding range size (km²) and breeding landmass (mainland
144 as the reference category versus island). We also ran null models (intercept only) for all responses. All
145 models' intercepts and response standard deviations were assigned a weakly informative prior (Student
146 T: df = 3, location = 0, scale = 10) [47], and predictor coefficients were assigned flat uninformative priors.
147 We ran each model for 6,000 iterations across 6 chains and assessed Markov Chain Monte Carlo (MCMC)
148 convergence using the Gelman-Rubin diagnostic (Rhat) [47]. We then performed k-fold cross-validation
149 [48] to refit each model K=16 times. For each k-fold, the training dataset included a randomly selected set
150 of $N - N \frac{1}{K}$ or $N \approx 63$ species, and the testing dataset included $N \frac{1}{K}$ or $N \approx 4$ species not included in the
151 training dataset. Finally, we compared differences between the models' expected log pointwise predictive
152 densities (ELPD) to assess which model(s) best predicted the probability of having a sexually-dichromatic
153 plumage patch. [48].

154 Models' predictor effects were assessed using 90% highest-density intervals of the posterior distribu-
155 tions and probability of direction, the proportion of the posterior distribution that shares the same sign
156 (positive or negative) as the posterior median [49], to provide estimates of the probability of that a predic-
157 tor has an entirely positive or negative effect on the presence of sexually-dimorphic plumage patches. We
158 assume predictor estimates with a probability of direction ≥ 0.90 to be indicative of a reliable existence
159 of a predictor's effect on sexually-dimorphic plumage patches [49].

160 Results

161 Avian visual modeling

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

171 **Model comparisons**

172 *Breeding sympathy, breeding timing, and breeding spacing* performed considerably better than *intercept-only*
173 (*null models*) in predicting the probability of a species having a sexually-dimorphic plumage patch. We
174 obtained $N \geq 4000$ effective posterior samples for each model parameter and all models' Markov Chains
175 (MCMC) successfully converged (Rhat = 1 for all models' parameters). All *breeding sympathy, breeding tim-*
176 *ing, and breeding spacing* models performed similarly well and substantially better than *intercept only* mod-
177 els in predicting the probability of having a sexually-dimorphic plumage patch with achromatic JND values
178 > 1, 2, or 3 (Table 1; all models predicting achromatic plumage patches had ELPD values within 4, follow-
179 ing the convention of [50]). Among models predicting the probability of having a sexually-dichromatic
180 plumage patch with chromatic JND values >1, 2, or 3, all *breeding sympathy, breeding timing, and breeding*
181 *spacing* models performed much better than *intercept only* models, and *breeding sympathy* models had the
182 top predictive performance (Table 1; *breeding sympathy* models all have ELPD =0, only the *breeding spacing*
183 models predicting dichromatic plumage patches had similar predictive performance).

184 **Achromatic plumage sexual dichromatism predictors**

185 Migratory behaviour and shorter breeding season lengths were strongly associated with greater odds of
186 a species having achromatic plumage sexual dichromatism. All model predictors' effect estimates are pro-
187 vided as the posterior median odds-ratio (OR) and 90% highest-density interval (HDI) in Table 2. Among
188 predictors of achromatic sexually-dimorphic plumage patches, only predictors included in the *breeding*
189 *timing* model have predictors with probability of direction (pd) values ≥ 0.90 (Table 2). Specifically, longer
190 breeding season length was associated with lower odds of a species having a sexually-dimorphic plumage
191 patch with achromatic JND > 2 (breeding season length, OR [90% HDI] = 0.10 [0.01, 1.1], 89.5% decrease
192 in odds per 2.3-month increase in breeding season) and JND > 3 (breeding season length, OR [90% HDI]
193 = 0.25 [0.03, 1.5], 75% decrease in odds per 2.3-month increase in breeding season). Additionally, full
194 migratory behaviour, rather than no migratory behaviour, was associated with greater odds of a species
195 having a sexually-dimorphic plumage patch with achromatic JND > 1 (full migration, OR [90% HDI] = 4.97
196 [0.95, 24.4]), JND > 2 (full migration, OR [90% HDI] = 66.5 [3.2, 1802.4]) and JND > 3 (OR [90% HDI] =
197 22.3 [1.6, 307.9]). Finally, both full and partial migratory behaviour, rather than no migration behaviour,
198 in conjunction with longer breeding season lengths are associated with greater odds of a species having
199 a sexually-dimorphic plumage patch with achromatic JND > 1 (breeding season length x full migration,
200 OR [90% HDI] = 4.84 [0.67, 39.6]), JND > 2 (breeding season length x full migration, OR = 66.3 [0.59,
201 11415.7]; breeding season length x partial migration, OR [90% HDI] = 20.7 [0.9, 589.1]) and JND > 3
202 (breeding season length x partial migration, OR [90% HDI] = 8.28 [0.76, 109.1]).

203 **Chromatic plumage sexual dichromatism predictors**

204 Migratory behaviour, shorter breeding season lengths, and larger numbers of sympatric *Turdus* species
205 were strongly associated with greater odds of a species having chromatic plumage sexual dichromatism.
206 Among predictors of *breeding timing* models predicting chromatic sexually-dimorphic plumage patches,

longer breeding season length was associated with lower odds of a species having a plumage patch with chromatic JND > 2 (OR [90% HDI] = 0.14 [0.01, 1.42], 86% reduction in odds per 2.3 month increase in breeding season). Both full and partial migratory behaviour rather than no migration are associated with greater odds of a species having a plumage patch JND > 1 (partial migration, OR [90% HDI] = 2.2 [0.94, 4.9]), JND > 2 (full migration, OR [90% HDI] = 80.51 [2.8, 3432.9]) and JND > 3 (partial migration, OR [90% HDI] = 71.2 [0.32, 59062.9]; full migration, OR [90% HDI] = 234.7 [0.51, 300382.6]). For *breeding spacing models*, island residency rather than mainland residency was associated with lower odds of having a plumage patch > 1 chromatic JND (island, OR [90% HDI] = 0.27 [0.09, 0.89]). Finally, more *Turdus* species in sympatry was associated with higher odds of a species having a sexually-dimorphic chromatic plumage patch with JND > 1 (number of sympatric species, OR [90% HDI] = 1.4 [1.18, 1.67], 40% increase in odds per each additional sympatric species), JND > 2 (sympatric species, OR [90% HDI] = 1.59 [1.01, 2.52], 59% increase in odds per each additional sympatric species), and JND > 3 (sympatric 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.

Model					
Plumage Metric	JND Threshold	Breeding Sympathy	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	0.56 (0.31, 2.75), pd = 0.53	4.11 (0.3, 61.54), 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, 31.2), 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)

220 **Discussion**

221 Our results provide comparative correlative evidence in support of predictions of the recognition hypothesis
222 for plumage sexual dichromatism in true thrushes. We used a receptor-noise limited model of *Turdus*
223 *merula* vision [36,37] to measure avian-perceivable visual contrast of plumage colours and found that the
224 odds of plumage sexual dichromatism are much greater for *Turdus* thrush species that have full or partial
225 migration rather than no migration, have relatively short breeding seasons, and are in sympatry with many
226 other true thrush species (Table 1,2). Our results align with prior comparative studies of avian plumage
227 sexual dichromatism where strong associations of sexual dichromatism with greater migratory behaviour
228 [10] and more sympatric taxa [27] were found among many species of different passerine families.

229 Further, we determined that sympatric *Turdus* species have distinguishable plumage colouration differences
230 from one another when measuring plumage appearance from the avian visual perspective (Fig. S1).
231 Divergent plumage colouration within sexes between closely-related species indicates that plumage sexual
232 dichromatism may have evolved to facilitate species and mate recognition in *Turdus* species breeding
233 under higher sympatry with other true thrushes. However, we cannot directly determine if the plumage
234 sexual dichromatism in sympatric *Turdus* species is the result of reproductive character displacement. We
235 do not know if past changes in species' plumage sexual dichromatism occurred before or during periods of
236 sympatry with other *Turdus* species. Regardless, present-day plumage sexual dichromatism and perceivable
237 differences in plumage colouration between sympatric species likely reduces the challenge of finding
238 compatible mates by signaling an individual's sex, breeding status, and species. For example, the four
239 species *Turdus* hybrid zone in north-central Asia [33] is a particularly striking example where reproductive
240 character displacement has likely occurred and all four species exhibit strong plumage sexual dichromatism (Fig. S2). Comparing within sexes between sister species pairs of *T.ruficollis* and *T.atrogularis*, and
241 *T.naumanni* and *T.eunomus* [46], plumage patterns of the species pairs are nearly identical except for a divergence in colour. *T.ruficollis* and *T.atrogularis* share similar facial and throat colouring patterns, with the
243 main difference being red colouration in *T.ruficollis* in opposition to the black colouration of *T.atrogularis*.
244 In the second species pair, *T.naumanni* has red ventral plumage colouration and *T.eunomus* has black ventral
245 plumage colouration.

247 Previous studies have found that closely-related sympatric species tend to have more similar plumage
248 appearance than expected if plumage colouration patterns had evolved to facilitate species recognition
249 via reproductive character displacement [51,52]. The potential lack of major plumage colour divergence
250 among closely-related sympatric species may be attributable to constraints imposed by a shared light environment
251 on colour signal efficiency [53], or similar natural selection pressures (e.g., predators, parasites,
252 and weather). Generally, despite greater similarity in plumage appearance in comparison to allopatric
253 species, closely-related sympatric species can still have substantially different and biologically-relevant
254 differences in achromatic or chromatic interspecific visual contrast of plumage patches when measuring
255 plumage colouration differences from the avian visual perspective (as we have found in our analyses).

256 **Conclusions**

257 Patterns of plumage sexual dichromatism in true thrushes (*Turdus*) are consistent with select predictions
258 of the recognition hypothesis for plumage sexual dichromatism. Migratory behaviour and limited breed-
259 ing seasons reduce the amount of time available to find a mate, and greater plumage sexual dichroma-
260 tism may help migratory species find compatible mates more rapidly. Greater plumage sexual dichro-
261 matism in *Turdus* species under sympatry with other true thrush species also supports the possibility
262 that increased plumage sexual dichromatism may be the result of reproductive character displacement.
263 Therefore, greater plumage sexual dichromatism likely reduces species and mate recognition errors and
264 decreases hybridization.

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271 **Data Accessibility**

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

273 **Author Contributions**

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

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