

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 so  
9 likely promote the evolution of traits used for species and mate recognition. Conspicuous traits that  
10 signal an individual's species, sex, and breeding status reduce the challenge of identifying a compati-  
11 ble conspecific mate, and should be more common in migratory rather than sedentary species, species  
12 with shorter breeding seasons, and species breeding under high sympatry with many closely-related het-  
13 erospecifics. Here, we tested this recognition hypothesis for promoting plumage sexual dichromatism  
14 in the true thrushes (*Turdus* spp.), a large and diverse genus of passerine birds. We used receptor-noise  
15 limited models of avian vision to quantify avian-perceived chromatic and achromatic visual contrasts  
16 between male and female plumage patches and tested the influence of breeding season length, spatial  
17 distribution, and sympatry with other *Turdus* species on plumage dichromatism. As predicted, we found  
18 that 1) true thrush species with migratory behaviour have greater plumage sexual dichromatism than  
19 non-migratory species, 2) species with longer breeding seasons have less plumage sexual dichromatism,  
20 and 3) greater numbers of *Turdus* thrush species breeding in sympatry is associated with more plumage  
21 sexual dichromatism. These results suggest that social recognition systems, including species and mate  
22 recognition, play a prominent role in the evolution of plumage sexual dichromatism in true thrushes.

23 **Keywords**

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

25 **Introduction**

26 Species recognition is necessary in sexually reproducing lineages for individuals to find compatible mates  
27 and produce viable offspring [1,2]. Conspicuous traits signaling species and sex identity increase the  
28 ease and speed of mate recognition by reducing the effort, error, and time involved when searching for  
29 compatible mates and lessen the likelihood of mating with heterospecifics [3]. Traits used in species

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

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

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

64 True thrushes (*Turdus* spp.) are an exceptionally diverse monophyletic genus of passerine birds con-  
65 sisting of about ~86 species distributed across the globe (Fig. 1). The true thrushes are an ideal passerine  
66 clade for examining the recognition hypothesis for plumage sexual dichromatism because plumage sexual  
67 dichromatism and migratory behaviours vary substantially between species and sexual dichromatism has  
68 evolved multiple times in thrushes across the world [31,32]. Hybridization also occurs in some, but not

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

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

## 89 Methods

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

### 92 Plumage sexual dichromatism

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

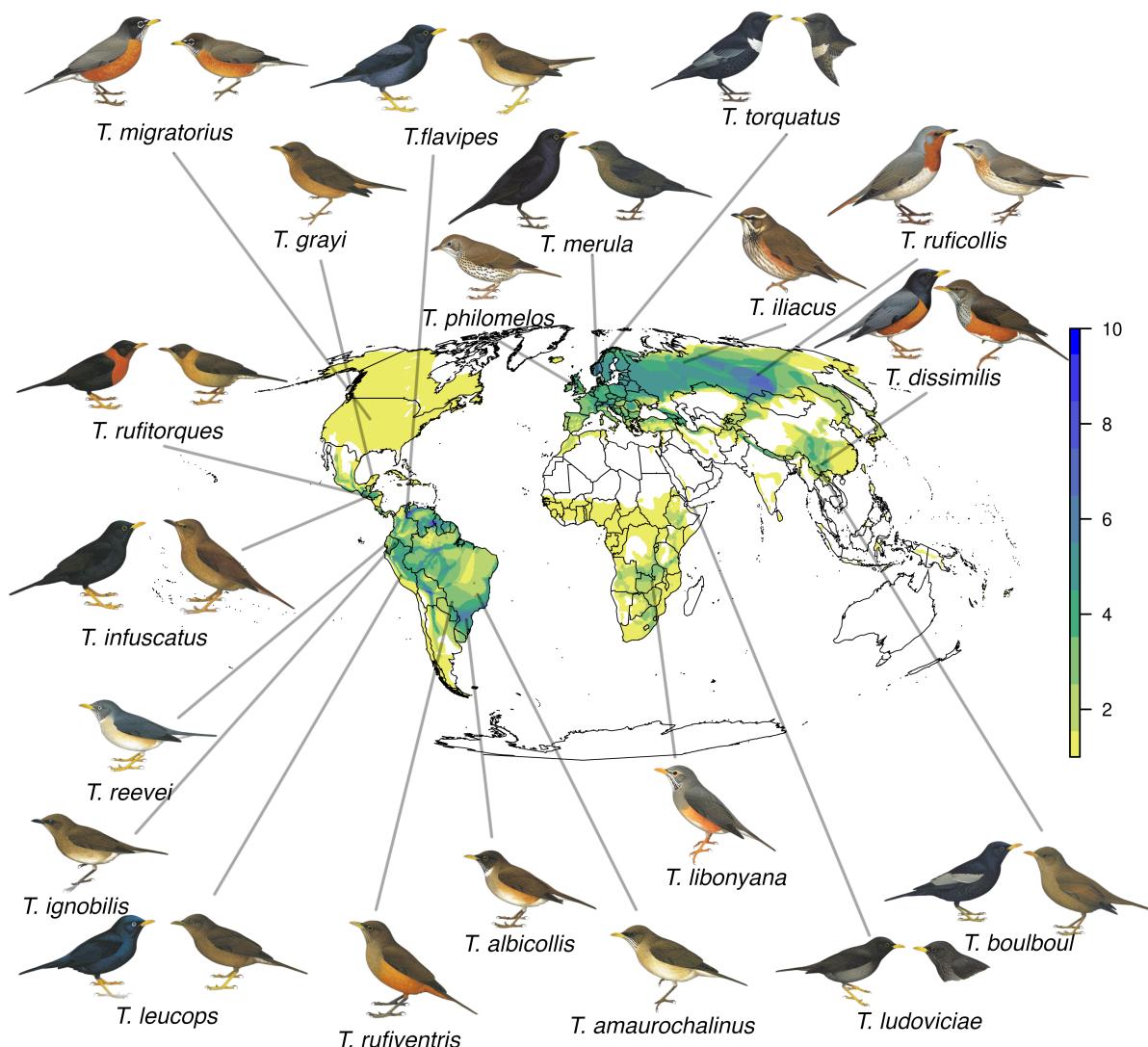


Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International, with representative species' males and females shown for species with plumage sexual dichromatism. The color scale indicates the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations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

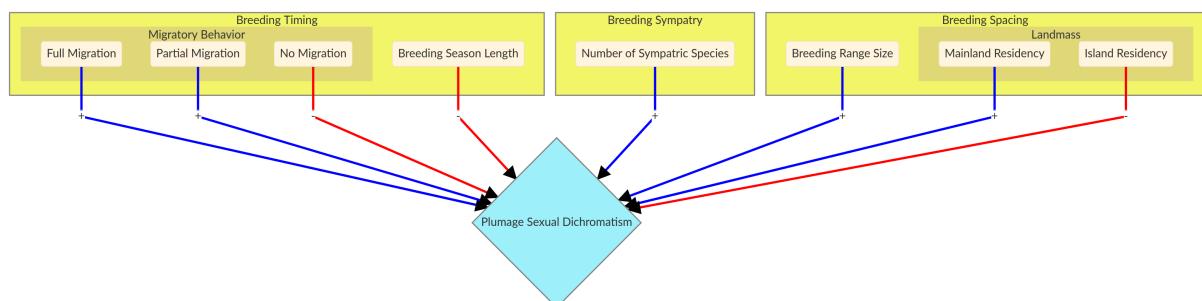


Figure 2: Hypotheses and predictions for each model (large yellow boxes). Arrow colours indicate predicted correlation, positive (blue) and negative (red)

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

## 120 **Life History Data**

### 121 **Breeding Timing Model**

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

### 128 **Breeding Sympatry Model**

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

### 135 **Breeding Spacing Model**

136 Species’ breeding range sizes (in km<sup>2</sup>) were acquired using the *BirdLife International* breeding range maps.  
137 Species’ island vs. mainland residence was also determined using breeding ranges from *BirdLife Interna-*

138 *tional*. Mainland residence was assigned if the species had a breeding range on any continent and Japan.  
139 Island residence was assigned to species having a breeding range limited to a non-continental landmass  
140 entirely surrounded by a marine body of water.

141 **Statistical modeling**

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

150 Our *breeding timing* models included the following predictors: z-scores of breeding season length  
151 (mean-centered by  $\mu = 5.4$  months, and scaled by one standard deviation  $\sigma = 2.3$  months), migratory  
152 behaviour (no migration as the reference category versus partial or full migration), and their interaction.  
153 *Breeding sympatry* models included the number of sympatric species with greater than 30% breeding range  
154 overlap as the only predictor of the probability of having a sexually-dichromatic plumage patch. *Breeding*  
155 *spacing* models included  $\log_e$  transformed breeding range size (km<sup>2</sup>) and breeding landmass (mainland  
156 as the reference category versus island). We also ran null models (intercept only) for all responses. All  
157 models’ intercepts and response standard deviations were assigned a weakly informative prior (Student  
158 T: df = 3, location = 0, scale = 10) [50], and predictor coefficients were assigned flat uninformative priors.  
159 We ran each model for 6,000 iterations across 6 chains and assessed Markov Chain Monte Carlo (MCMC)  
160 convergence using the Gelman-Rubin diagnostic (Rhat) [50]. We then performed k-fold cross-validation  
161 [51] to assess each model’s accuracy in predicting plumage sexual dichromatism of randomly-selected  
162 samples of *Turdus* thrush species, refitting each model K=16 times. For each k-fold, the training dataset  
163 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  
164  $N \approx 4$  species not included in the training dataset. Finally, we compared differences between the models’  
165 expected log pointwise predictive densities (ELPD) to assess which model(s) best predicted the probability  
166 of having a sexually-dichromatic plumage patch. [51].

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

173 **Results**

174 **Avian visual modeling**

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

184 **Model comparisons**

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

197 **Achromatic plumage sexual dichromatism predictors**

198 Migratory behaviour and shorter breeding season lengths were strongly associated with greater odds of  
199 a species having achromatic plumage sexual dichromatism. All model predictors' effect estimates are pro-  
200 vided as the posterior median odds-ratio (OR) and 90% highest-density interval (HDI) in Table 2. Among  
201 predictors of achromatic sexually-dimorphic plumage patches, only predictors included in the *breeding*  
202 *timing* model have predictors with probability of direction (*pd*) values ≥ 0.90 (Table 2). Specifically, longer  
203 breeding season length was associated with lower odds of a species having a sexually-dimorphic plumage  
204 patch with achromatic JND > 2 (breeding season length, OR [90% HDI] = 0.10 [0.01, 1.1], 89.5% decrease  
205 in odds per 2.3-month increase in breeding season) and JND > 3 (breeding season length, OR [90% HDI]  
206 = 0.25 [0.03, 1.5], 75% decrease in odds per 2.3-month increase in breeding season). Additionally, full  
207 migratory behaviour, rather than no migratory behaviour, was associated with greater odds of a species

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

### 216 ***Chromatic plumage sexual dichromatism predictors***

217 Migratory behaviour, shorter breeding season lengths, and larger numbers of sympatric *Turdus* species  
 218 were strongly associated with greater odds of a species having chromatic plumage sexual dichromatism.  
 219 Among predictors of *breeding timing* models predicting chromatic sexually-dimorphic plumage patches,  
 220 longer breeding season length was associated with lower odds of a species having a plumage patch with  
 221 chromatic JND > 2 (OR [90% HDI] = 0.14 [0.01, 1.42], 86% reduction in odds per 2.3 month increase  
 222 in breeding season). Both full and partial migratory behaviour rather than no migration are associated  
 223 with greater odds of a species having a plumage patch JND > 1 (partial migration, OR [90% HDI] = 2.2  
 224 [0.94, 4.9]), JND > 2 (full migration, OR [90% HDI] = 80.51 [2.8, 3432.9]) and JND > 3 (partial migration,  
 225 OR [90% HDI] = 71.2 [0.32, 59062.9]; full migration, OR [90% HDI] = 234.7 [0.51, 300382.6]). For  
 226 *breeding spacing models*, island residency rather than mainland residency was associated with lower odds  
 227 of having a plumage patch > 1 chromatic JND (island, OR [90% HDI] = 0.27 [0.09, 0.89]). Finally, more  
 228 *Turdus* species in sympatry was associated with higher odds of a species having a sexually-dimorphic  
 229 chromatic plumage patch with JND > 1 (number of sympatric species, OR [90% HDI] = 1.4 [1.18, 1.67],  
 230 40% increase in odds per each additional sympatric species), JND > 2 (sympatric species, OR [90% HDI]  
 231 = 1.59 [1.01, 2.52], 59% increase in odds per each additional sympatric species), and JND > 3 (sympatric  
 232 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
<b>Achromatic</b>					
	1 JND	0 ± 0 (-122.17 ± 0.67)	-2.51 ± 2.49 (-124.68 ± 2.38)	-2.59 ± 1.01 (-124.76 ± 1.04)	-21.69 ± 7.36 (-143.87 ± 7.51)
	2 JND	0 ± 0 (-98.94 ± 7.56)	-1.19 ± 3.95 (-100.13 ± 9.22)	-0.7 ± 1.34 (-99.64 ± 7.92)	-52.42 ± 12.67 (-151.36 ± 13.4)
	3 JND	-0.04 ± 1.4 (-85.4 ± 8.91)	-1.7 ± 4.41 (-87.07 ± 10.71)	0 ± 0 (-85.37 ± 8.76)	-28.54 ± 10.02 (-113.91 ± 13.65)
<b>Chromatic</b>					
	1 JND	0 ± 0 (-115.75 ± 2.95)	-5.67 ± 3.55 (-121.42 ± 2.28)	-2.73 ± 3.4 (-118.49 ± 2.67)	-14.8 ± 7.22 (-130.55 ± 7.05)
	2 JND	0 ± 0 (-88.47 ± 8.77)	-3.8 ± 4.46 (-92.27 ± 10.01)	-3.32 ± 5.29 (-91.79 ± 10.91)	-50.53 ± 14.49 (-139 ± 16.77)
	3 JND	0 ± 0 (-62.77 ± 10.41)	-8 ± 4.32 (-70.77 ± 12.29)	-4.43 ± 3.9 (-67.2 ± 11.72)	-47.63 ± 15.34 (-110.4 ± 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  $\geq 0.90$  are bolded in **red** for a negative effect and **blue** for a positive effect on plumage dichromatism. Phylogenetic signal ( $\lambda$ ) 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
<b>Breeding Timing</b>							
	Intercept	<b>0 (0, 0.54), pd = 0.98</b>	<b>0 (0, 0.19), pd = 0.99</b>	<b>0 (0, 0.19), pd = 0.99</b>	0.41 (0.05, 2.79), pd = 0.78	<b>0 (0, 1.73), pd = 0.95</b>	<b>0 (0, 1.37), pd = 0.96</b>
	Breeding Season Length	<b>0.1 (0.01, 1.05), pd = 0.97</b>	<b>0.25 (0.03, 1.49), pd = 0.91</b>	<b>0.25 (0.03, 1.49), pd = 0.91</b>	0.89 (0.56, 1.4), pd = 0.66	<b>0.14 (0.01, 1.42), pd = 0.94</b>	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	<b>4.37 (0.95, 24.41), pd = 0.96</b>	<b>66.52 (3.19, 1802.4), pd = 0.99</b>	<b>22.34 (1.59, 307.9), pd = 0.98</b>	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	<b>8.28 (0.76, 109.11), pd = 0.94</b>	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	<b>4.34 (0.67, 39.63), pd = 0.9</b>	<b>66.3 (0.59, 11415.7), pd = 0.93</b>	16.41 (0.27, 824.69), pd = 0.89	1.68 (0.31, 8.33), pd = 0.7	<b>160.6 (0.84, 67791.13), pd = 0.95</b>	433.67 (0.01, 371945.69), pd = 0.85
	Phylogenetic Signal $\lambda$ , 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)
<b>Breeding Spacing</b>							
	Intercept	<b>0 (0, 2.44), pd = 0.95</b>	<b>0 (0, 0.14), pd = 0.98</b>	<b>0 (0, 0.14), pd = 0.98</b>	0.51 (0.03, 9.7), pd = 0.65	<b>0 (0, 7.63), pd = 0.92</b>	<b>0 (0, 8.19), pd = 0.91</b>
	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	<b>0.27 (0.09, 0.89), pd = 0.97</b>	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 $\lambda$ , 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)
<b>Breeding Sympatry</b>							
	Intercept	0.41 (0.03, 5.83), pd = 0.72	<b>0 (0, 0.98), pd = 0.95</b>	<b>0 (0, 0.34), pd = 0.98</b>	<b>0.25 (0.04, 1.35), pd = 0.91</b>	<b>0 (0, 1.12), pd = 0.95</b>	<b>0 (0, 0.29), pd = 0.98</b>
	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	<b>1.4 (1.18, 1.67), pd = 0.99</b>	<b>1.59 (1.01, 2.52), pd = 0.96</b>	<b>2.11 (1.03, 4.46), pd = 0.97</b>
	Phylogenetic Signal $\lambda$ , 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)

## 233 Discussion

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

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

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

## 269 Conclusions

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

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## 284 Data Accessibility

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

## 286 Author Contributions

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

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