

1 Rapid mate recognition promotes greater avian-perceived  
2 plumage sexual dichromatism in true thrushes (genus:  
3 *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 the  
10 species recognition hypothesis for plumage sexual dimorphism in the true thrushes (*Turdus*), a large and  
11 diverse genus of passerine birds. We used receptor-noise limited models of avian vision to quantify  
12 avian-perceived chromatic and achromatic visual contrast between male and female plumage patches  
13 and tested the influence of breeding timing, spacing, and *Turdus* species sympatry on plumage sexual  
14 dimorphism. Time and opportunities for mate sampling are more limited in migratory rather than non-  
15 migratory species, and we found that true thrush species with migratory behaviour have greater plumage  
16 sexual dimorphism than non-migratory species. Additionally, we found that plumage sexual dimorphism is  
17 positively correlated with the number of *Turdus* thrush species breeding in sympatry. Our results suggest  
18 that species recognition plays a prominent role in the evolution of plumage sexual dimorphism.

## **19    Keywords**

## *dichromatism, plumage, species recognition*

21 **Introduction**

Species recognition is necessary in sexually reproducing lineages for individuals to find compatible mates and produce viable offspring [1,2]. Conspicuous traits signaling species and sex identity increase the ease of species recognition by reducing the time and effort expended when searching for compatible mates and lessen the likelihood of mating with heterospecifics [3]. Alternatively, traits used in species and mate recognition may also serve as signals of status to conspecifics and reduce costly conflicts over resources and mates [4]. Accordingly, distinct traits facilitating species and mate recognition should arise when closely-related species are highly sympatric, when the time to find a mate is limited, when potential mates are not encountered often, and when competition for mates and resources is high [1].

30 In birds, plumage colour is a highly conspicuous trait signaling species and (often) sex identity [5,6].  
31 Plumage sexual dichromatism, a distinct set of differences in the appearance of male and female feather  
32 colours, is common in birds and usually attributed to different selection pressures on males and females  
33 [7–11]. Fundamentally, plumage sexual dichromatism results in a visible trait useful for recognizing an  
34 individual's species, sex, and age (e.g., in species with delayed plumage maturation, see [12]), reducing  
35 the time and effort necessary to identify a suitable mate [13,14]. Evidence in favor of the species recog-  
36 nition hypothesis for sexual dichromatism includes a positive association between migratory behaviour,  
37 shorter breeding seasons, and plumage sexual dichromatism [9]. Specifically, bird species that migrate to  
38 and from their breeding territories and have large geographic ranges tend to have greater plumage sexual  
39 dichromatism than species that do not migrate and have limited breeding ranges [10,15–17]. Addition-  
40 ally, bird species that reside on mainland continents and have larger breeding ranges often have greater  
41 plumage colour elaboration and sexual dichromatism than species living on islands with limited breeding  
42 ranges [18–23].

43 Moreover, plumage sexual dichromatism likely plays a role in hybridization avoidance via reproduc-  
44 tive character displacement to facilitate species and mate recognition. For example, in European *Ficedula*  
45 flycatchers, female choice selects for divergent male plumage colouration, leading to character displace-  
46 ment between species and populations and reduced rates of hybridization [24–26]. More broadly and  
47 across taxa, greater plumage dichromatism is positively correlated with transitions from allopatry to para-  
48 patry and increases in geographic range overlaps among passerine sister species pairs [27]. Plumage  
49 sexual dichromatism has also been found to be positively associated with species richness among sister  
50 species pairs, and dichromatism mainly increases through changes in male plumage [28], suggesting that  
51 female choice and male-male competition lead to concurrent changes in male plumage colour and spe-  
52 ciation events. Further, plumage sexual dichromatism is positively associated with greater interspecific  
53 plumage colour evolution rate and divergence in *Tyrannida* suboscines [29]. Therefore, plumage sexual  
54 dichromatism may be an especially favourable trait for facilitating species and mate recognition when  
55 closely-related species have sympatric breeding ranges [5,30].

56 True thrushes (genus: *Turdus*) are an exceptionally diverse genus of passerine birds consisting of about  
57 ~86 species distributed across the globe (Fig. 1). Plumage sexual dimorphism and migratory behaviors  
58 vary substantially between species and have evolved multiple times in thrushes across the world [31,32].  
59 Interestingly, there have been several documented cases of hybridization in *Turdus* thrushes, and there  
60 is a large hybrid zone between four *Turdus* species (*T. atrogularis*, *T. eunomus*, *T. naumanni*, *T. ruficollis*)  
61 in north-central Asia [33], indicating that some sympatric *Turdus* species interbreed. Therefore, the true  
62 thrushes are an ideal passerine clade for examining the species recognition hypothesis for plumage sexual  
63 dimorphism.

64 Overall, ecological conditions that increase the time and degree of difficulty in finding a suitable con-  
65 specific mate should select for phenotypic traits that reliably signal species and sex identity. Taken to-  
66 gether, repeated findings across various bird lineages of greater plumage dichromatism in species that  
67 are i) migratory rather than nonmigratory, ii) have shorter breeding seasons, iii) live on mainlands rather  
68 than islands, iv) have larger breeding ranges, and v) breed in sympatry with closely-related species sug-

69  gests that circumstances where rapid species recognition is challenging strongly favour the evolution and  
 70  maintenance of prominent plumage sexual dichromatism in birds. Here, we test predictions of the species  
 71  recognition hypothesis for sexually-dimorphic traits. To this end, we evaluate the potential influences of  
 72  breeding timing, spacing, and sympatry on plumage dichromatism in the *Turdus* thrushes.

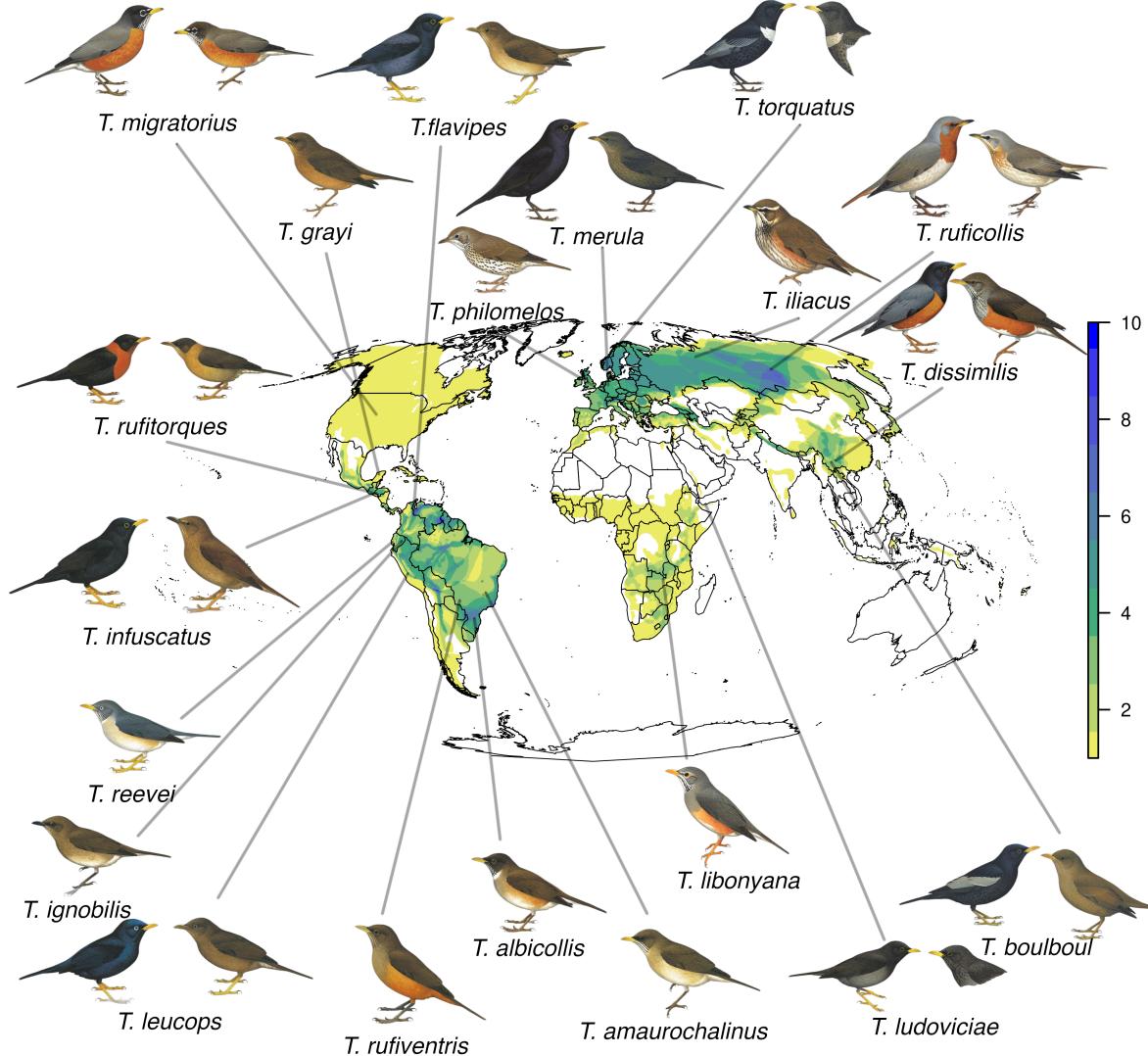


Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International. Colors indicate the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations © HBW Alive/Lynx Edicions

## 73 Methods

### 74 Plumage sexual dichromatism

75  A total of N=77 *Turdus* thrush species (approximately ~89% of all known true thrush species) were sam-  
 76  pled for plumage spectral reflectance using prepared bird skin specimens at the American Museum of  
 77  Natural History in New York City and the Field Museum in Chicago. Reflectance measurements spanning

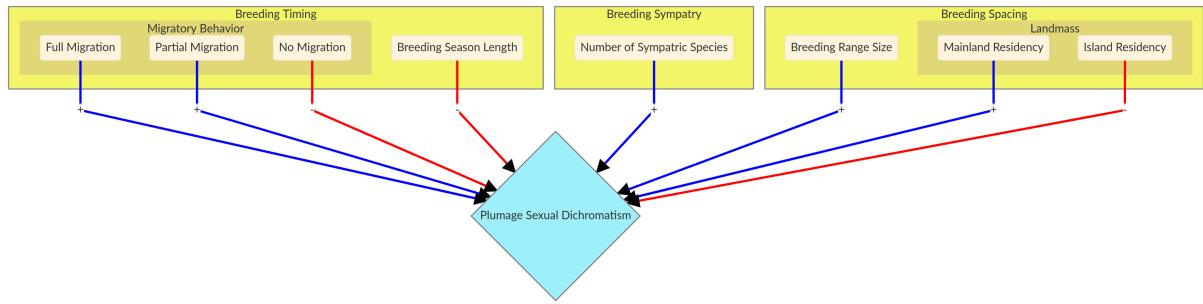


Figure 2: Hypotheses and predictions for each model. Arrow colours indicate predicted correlation, positive (blue) and negative (red).

300-700nm were taken in triplicate from the belly, breast, throat, crown and mantle plumage patches [34] 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  $\mu\text{m}$  fiber optic reflection probe fitted with a rubber stopper to maintain a consistent measuring distance of 3 mm and area of 2  $\text{mm}^2$  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 [35] of the European Blackbird (*T. merula*) visual system [36] in the *pavo* [37] package in R v4.0.0 [38] 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 colors as different. However, natural light environments vary both spatially and temporally [39], 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 thresholds due to variation in psychophysical and ambient lighting conditions affecting the strength of between-sex plumage visual contrast [40]. Additionally, we modeled the number of divergent plumage patches (JND >1, 2, and 3) within sexes and between different sympatric species under different levels of breeding range overlap (10% increments between 0-90%).

## 102 Life History Data

### 103 Breeding Timing Model

104 We collected data on migration behaviour and breeding season length from *Thrushes* [31] and the *Handbook of the Birds of the World* [41]. We assigned three different kinds of migratory behaviour: 1) full

106 migration when a species description clearly stated that a species “migrates”, 2) partial migration when a  
107 species was described to have “altitudinal migration”, “latitudinal migration” or “movement during non-  
108 breeding season”, or 3) sedentary when a species was described as “resident” or “sedentary”. Breeding  
109 season length was defined as the number of months the species breeds each year.

110 **Breeding Sympathy Model**

111 Species’ breeding ranges were acquired from *BirdLife International* [42]. We calculated congener breeding  
112 range overlaps (as percentages) using the *letsR* package in R [43]. We then calculated the number of sym-  
113 patric species as the number of congeners with breeding ranges that overlap >30% with the focal species’  
114 breeding range [27]. Comparisons of the number of sexually-dimorphic plumage patches vs. the number  
115 of sympatric species among different breeding range overlap thresholds are provided in Supplementary  
116 Figure 2.

117 **Breeding Spacing Model**

118 Species’ breeding range sizes (in km<sup>2</sup>) were acquired using the *BirdLife International* breeding range maps.  
119 Species’ island vs. mainland residence was also determined using breeding ranges from *BirdLife Interna-*  
120 *tional*. Mainland residence was assigned if the species had a breeding range on any continent and Japan.  
121 Island residence was assigned to species having a breeding range limited to a non-continental landmass  
122 entirely surrounded by an oceanic body of water.

123 **Statistical modeling**

124 We used phylogenetically-corrected Bayesian multilevel logistic regression models using the *brms* v2.13.0  
125 package [44] in R v4.0.0 [38] where responses, the number of sexually-dichromatic patches >1, 2, and  
126 3 chromatic and achromatic JNDs, were modelled as binomial trials (N=5 plumage patch “trials”) to test  
127 for associations with breeding timing, breeding sympathy and breeding spacing. For all phylogenetically-  
128 corrected models, we used the *Turdus* phylogeny from Nylander et al. (2008) [45] to create a covariance  
129 matrix of species’ phylogenetic relationships. All models used a dataset of N=67 out of the *Turdus* species  
130 for which all the types of data (see above) were available.

131 Our breeding timing models included the following predictors: z-scores of breeding season length  
132 (mean-centered by  $\mu = 5.4$  months, and scaled by one standard deviation  $\sigma = 2.3$  months), migratory  
133 behaviour (no migration as the reference category versus partial or full migration), and their interaction.  
134 Breeding sympathy models included the number of sympatric species with greater than 30% breeding range  
135 overlap as the only predictor of the probability of having a sexually-dichromatic plumage patch. Breeding  
136 spacing models included  $\log_e$  transformed breeding range size (km<sup>2</sup>) and breeding landmass (mainland as  
137 the reference category versus island). We also ran null models (intercept only) for all responses. All models’  
138 intercepts and response standard deviations were assigned a weak prior (Student T: df = 3, location = 0,  
139 scale = 10), and predictor coefficients were assigned flat priors. We ran each model for 6,000 iterations  
140 across 6 chains and assessed Markov Chain Monte Carlo (MCMC) convergence using the Gelman-Rubin

141 diagnostic (Rhat) [46]. We then performed k-fold cross-validation [47] to refit each model K=16 times.  
142 For each k-fold, the training dataset included a randomly selected set of  $N - N \frac{1}{K}$  or  $N \approx 63$  species,  
143 and the testing dataset included  $N \frac{1}{K}$  or  $N \approx 4$  species not included in the training dataset. Finally, we  
144 compared differences between the models' expected log pointwise predictive densities (ELPD) to assess  
145 which model(s) best predicted the probability of having a sexually-dichromatic plumage patch. [47].

146 Models' predictor effects were assessed using 90% highest-density intervals of the posterior distribu-  
147 tions and probability of direction, the proportion of the posterior distribution that shares the same sign  
148 (positive or negative) as the posterior median [48], to provide estimates of the probability of that a pre-  
149 dictor has an entirely positive or negative effect on the presence of sexually-dimorphic plumage patches.  
150 We assume predictor estimates with a probability of direction  $\geq 0.90$  to be indicative of a true existence  
151 of a predictor's effect on sexually-dimorphic plumage patches [48].

## 152 Results

### 153 Avian visual modeling

154 Among  $N=77$  *Turdus* species, the following proportion have sexually monomorphic plumage (combined  
155 achromatic and chromatic JND thresholds): 1.3% ( $n=1$  species) have no sexually-dimorphic patches  $> 1$   
156 JND, 44% ( $n=34$  species) have no dimorphic patches  $> 2$  JND, and 63% ( $n=49$  species) have no dimor-  
157 phic patches  $> 3$  JND (Table S1). Conversely, 98.7% ( $n=78$  species) have at least one sexually-dimorphic  
158 plumage patch  $> 1$  JND, 56% ( $n=43$  species) have at least one plumage patch  $> 2$  JND, and 37% ( $n=28$   
159 species) have at least one patch  $> 3$  JND (Table S1). Additional proportions of *Turdus* species with sexually-  
160 dimorphic achromatic or chromatic plumage patches are available in Table S2. When comparing within  
161 sexes between sympatric species (i.e., at least a 30% overlap in breeding ranges:  $n=39$  species with at  
162 least one sympatric species and a median of  $n=6$  sympatric species per focal species), the median number  
163 of avian-discriminable plumage patches between species is 1 or greater for all achromatic and chromatic  
164 JND thresholds except for sympatric females at a chromatic JND threshold  $> 3$  (Fig. S1).

### 165 Model comparisons

166 We obtained  $N \geq 4000$  effective posterior samples for each model parameter and all models' Markov  
167 Chains (MCMC) successfully converged (Rhat = 1 for all models' parameters) (Supplementary Figure 3,  
168 4). All *breeding sympathy*, *breeding timing*, and *breeding spacing* models performed similarly well and sub-  
169 stantially better than *intercept only* models in predicting the probability of having a sexually-dimorphic  
170 plumage patch with achromatic JND values  $> 1$ , 2, or 3 (Table 1; all models predicting achromatic plumage  
171 patches had ELPD values within 4, following the convention of Burnham and Anderson (2002)[49]).  
172 Among models predicting the probability of having a sexually-dichromatic plumage patch with chromatic  
173 JND values  $> 1$ , 2, or 3, all *breeding sympathy*, *breeding timing*, and *breeding spacing* models performed much  
174 better than *intercept only* models, and *breeding sympathy* models had the top predictive performance (Ta-  
175 ble 1; *breeding sympathy* models all have ELPD =0, only the *breeding spacing* models predicting dichromatic

176 plumage patches with had similar predictive performance).

### 177 **Achromatic plumage sexual dimorphism predictors**

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

### 195 **Chromatic plumage sexual dimorphism predictors**

196 Among predictors of *breeding timing* models predicting chromatic sexually-dimorphic plumage patches,  
197 longer breeding season length was associated with lower odds of a species having a plumage patch with  
198 chromatic JND  $> 2$  (OR [90% HDI] = 0.14 [0.01, 1.42], 86% reduction in odds per 2.3 month increase in  
199 breeding season), and both full and partial migratory behaviour rather than no migration are associated  
200 with greater odds of a species having a plumage patch JND  $> 1$  (partial migration, OR [90% HDI] = 2.2  
201 [0.94, 4.9]), JND  $> 2$  (full migration, OR [90% HDI] = 80.51 [2.8, 3432.9]) and JND  $> 3$  (partial migration,  
202 OR [90% HDI] = 71.2 [0.32, 59062.9]; full migration, OR [90% HDI] = 234.7 [ 0.51, 300382.6]). For  
203 *breeding spacing models*, island residency rather than mainland residency was associated with lower odds  
204 of having a plumage patch  $> 1$  chromatic JND (island, OR [90% HDI] = 0.27 [0.09, 0.89]). Finally, more  
205 *Turdus* species in sympatry was associated with higher odds of a species having a chromatic plumage  
206 patch with JND  $> 1$  (number of sympatric species, OR [90% HDI] = 1.4 [1.18, 1.67], 40% increase in odds  
207 per each additional sympatric species), JND  $> 2$  (sympatric species, OR [90% HDI] = 1.59 [1.01, 2.52], 59%  
208 increase in odds per each additional sympatric species), and JND  $> 3$  (sympatric species, OR [90% HDI]  
209 = 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 $\pm$ 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) |                |
| <b>Chromatic</b>  |                                    |                                       |                                       |  |                |
| 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  $\geq 0.90$  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                                | 0.76 (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)                   |

210 **Discussion**

211 Our results provide correlative evidence in support of the species recognition hypothesis for plumage sex-  
212 ual dimorphism in true thrushes. We used a receptor-noise limited model of *Turdus merula* vision [35,36]  
213 to measure avian-perceivable visual contrast of plumage colours and found that the odds of plumage sex-  
214 ual dimorphism are much greater for *Turdus* thrush species that have full or partial migration rather than  
215 no migration, have relatively short breeding seasons, and are in sympatry with many other true thrush  
216 species (Table 1,2). Our results align with broader comparative studies of plumage sexual dimorphism  
217 where strong associations between migratory behavior [10] and sympathy [27] were found among many  
218 species of different passerine families.

219 Further, we determined that sympatric *Turdus* species have distinguishable plumage colouration  
220 differences from one another when measuring plumage appearance from the avian visual perspective  
221 (Fig. S1). Therefore, plumage sexual dichromatism may have evolved to facilitate species recognition  
222 in species breeding under high sympathy with other true thrushes. However, we cannot directly deter-  
223 mine if plumage sexual dimorphism in sympatric *Turdus* species is the result of reproductive character  
224 displacement. Namely, we do not know if past changes in species' plumage sexual dimorphism occurred  
225 before or during periods of sympathy with other *Turdus* species. Regardless, present-day plumage  
226 sexual dimorphism and perceivable differences in plumage colouration between sympatric species likely  
227 reduces the challenge of finding compatible mates.

228 Previous studies have found that closely-related sympatric species tend to have more similar plumage  
229 appearance than expected if plumage colouration had evolved to facilitate species recognition via repro-  
230 ductive character displacement [50,51]. The potential lack of major plumage colour divergence among  
231 closely-related sympatric species may be attributable to constraints imposed by a shared light environ-  
232 ment on colour signal efficiency [52], or similar natural selection pressures (e.g., predators, parasites,  
233 and weather). Generally, despite greater similarity in plumage appearance in comparison to allopatric  
234 species, closely-related sympatric species can still have substantially different and biologically-relevant  
235 differences in achromatic or chromatic interspecific visual contrast of plumage patches when measuring  
236 plumage colouration differences from the avian visual perspective (as we have found in our analyses).

237 **Conclusions**

238 Patterns of plumage sexual dimorphism in true thrushes (*Turdus*) are consistent with predictions of the  
239 species recognition hypothesis for plumage sexual dimorphism. Migratory behaviour and limited breed-  
240 ing seasons reduce the amount of time available to find a mate, and greater plumage sexual dimorphism  
241 may help migratory species find compatible mates more rapidly. Greater plumage sexual dimorphism  
242 in *Turdus* species under sympathy with other true thrush species also supports the possibility that in-  
243 creased plumage sexual dichromatism may be the result of reproductive character displacement. There-  
244 fore, greater plumage sexual dimorphism likely reduces species recognition errors and hybridization.

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