

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

4      Alec B. Luro<sup>1\*</sup>, Mark E. Hauber<sup>1</sup>

5      <sup>1</sup> Department of Evolution, Ecology and Behavior, School of Integrative Biology,  
6      University of Illinois at Urbana-Champaign \*alec.b.luro@mail.com

7      **Abstract**

8      Ecological conditions limiting the time to find a compatible mate or increasing the difficulty in doing so  
9      likely promote the evolution of traits used for species and mate recognition. Here, we tested this species  
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 timing, spacing, and sympatry with other *Turdus* species on plumage  
14     dimorphism. As predicted, we found that 1) true thrush species with migratory behaviour have greater  
15     plumage sexual dimorphism than non-migratory species, 2) species with longer breeding seasons have less  
16     sexual dichromatism, and 3) the number of *Turdus* thrush species breeding in sympatry is associated with  
17     more plumage dimorphism. These results suggest that conspecific recognition systems, including species  
18     and mate recognition, play a prominent role in the evolution of thrush plumage sexual dimorphism.

19     **Keywords**

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

21     **Introduction**

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

29 the time to find a breeding mate is limited, when potential mates are not encountered often, and when  
30 competition for mates and resources is higher [1].

31 In birds, plumage colour is a highly conspicuous trait signaling species and (often) sex identity [5,6]  
32 . Plumage sexual dichromatism, or the distinct set of differences in the appearance of male and female  
33 feather colours, is common in birds and usually attributed to different natural and sexual selection pres-  
34 sures on males and females [7–11]. Fundamentally, plumage sexual dichromatism results in a visibly per-  
35 ceivable trait useful for recognizing an individual's species, sex, and (sometimes) age (e.g., in species with  
36 sex-specific delayed plumage maturation, see [12]). Therefore, plumage sexual dichromatism reduces the  
37 time and effort necessary to identify a suitable mate [13,14]. Evidence in favor of this recognition hypoth-  
38 esis for sexual dichromatism includes a positive association of greater plumage sexual dichromatism with  
39 migratory behaviour and shorter breeding seasons [9]. Specifically, bird species that migrate to and from  
40 their breeding territories and have large geographic ranges tend to have greater plumage sexual dichro-  
41 matism than species that do not migrate and have limited breeding ranges [10,15–17]. Additionally, bird  
42 species that reside on mainland continents and have larger breeding ranges often have greater plumage  
43 colour elaboration and sexual dichromatism than species living on islands with limited breeding ranges  
44 [18–23].

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

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

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

68 gether, across various bird lineages, greater plumage dichromatism is present in species that are i) migra-  
 69 tory rather than nonmigratory, ii) have shorter breeding seasons, ii) live on mainlands rather than islands,  
 70 iv) have larger breeding ranges (distributions), and v) breed in sympatry with more closely-related species  
 71 suggests that circumstances where rapid species recognition is challenging strongly favour the evolution  
 72 and maintenance of prominent plumage sexual dichromatism in birds. Here, we test these predictions of  
 73 the species recognition hypothesis for sexually-dimorphic avian plumage. To this end, we evaluate the  
 74 potential influences of breeding timing, spacing, and sympatry on plumage dichromatism in the *Turdus*  
 75 thrushes.

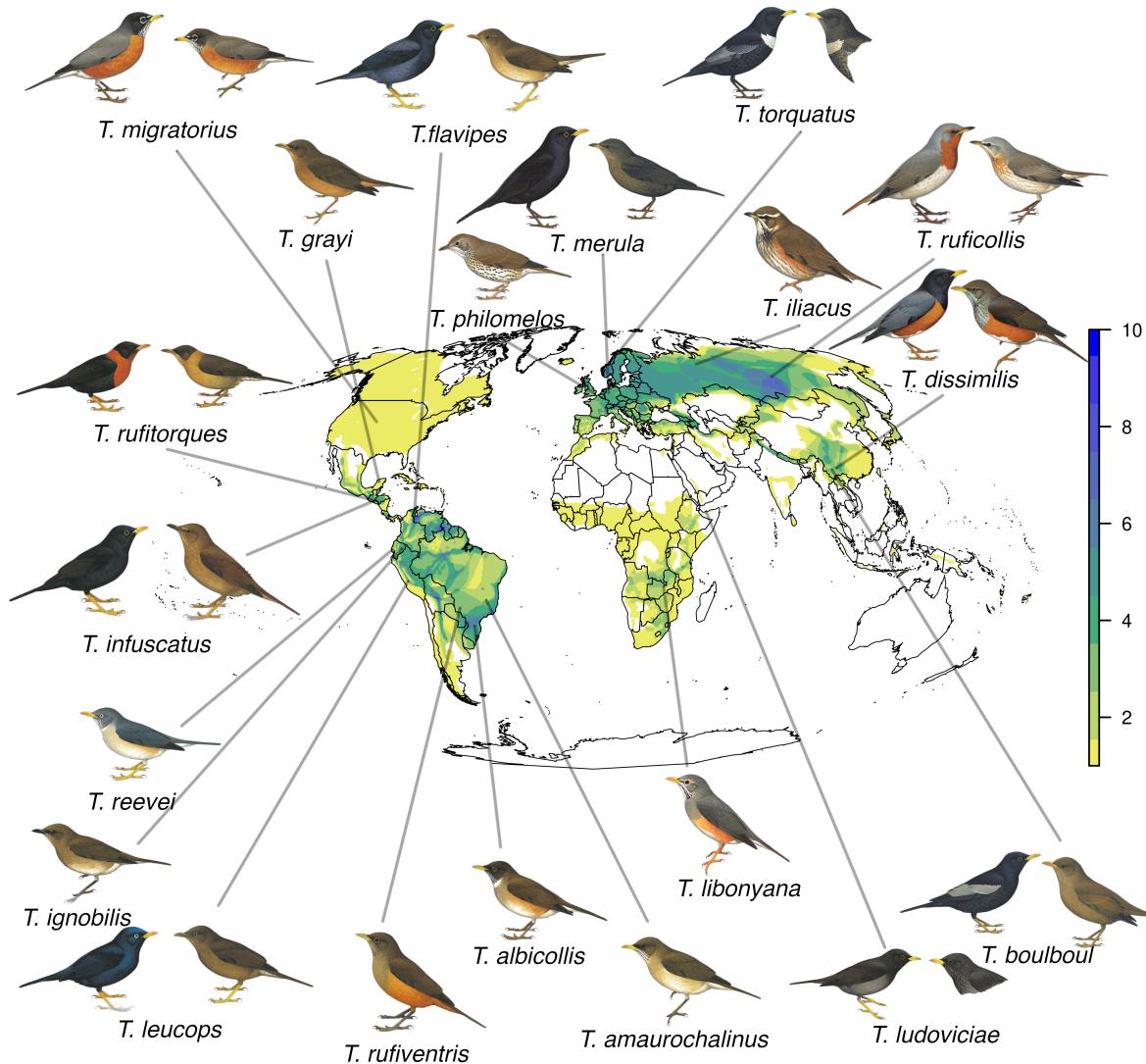


Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International. Colors indicate the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations © HBW Alive/Lynx Edicions

## 76 Methods

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

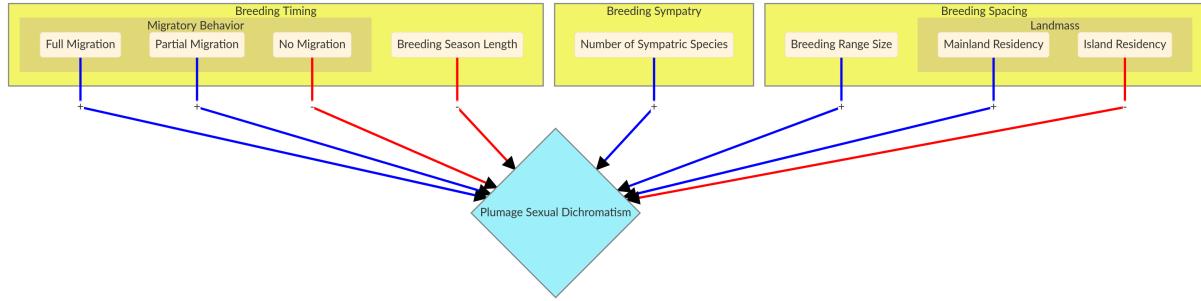


Figure 2: Hypotheses and predictions for each model. Arrow colours indicate predicted correlation, positive (blue) and negative (red).

### 78 **Plumage sexual dichromatism**

79 A total of N=77 *Turdus* thrush species (approximately ~89% of all known true thrush species) were sam-  
80 pled for plumage spectral reflectance using prepared bird skin specimens at the American Museum of  
81 Natural History in New York City and the Field Museum in Chicago. Reflectance measurements spanning  
82 300-700nm were taken in triplicate from the belly, breast, throat, crown and mantle plumage patches [34]  
83 of each individual. N=3 male and N=3 female individuals were measured for most species (exceptions: *T.*  
84 *lawrencii*, N=2 males and N=2 females; *T. swalesi*, N=1 male and N=1 female). Reflectance spectra were  
85 measured using a 400 µm fiber optic reflection probe fitted with a rubber stopper to maintain a consis-  
86 tent measuring distance of 3 mm and area of 2 mm<sup>2</sup> at a 90° angle to the surface of the feather patch.  
87 Measurements were taken using a JAZ spectrometer with a pulsed-xenon light source (Ocean Optics,  
88 Dunedin, USA) and we used a diffuse 99% reflectance white standard (Spectralon WS-1-SL, Labsphere,  
89 North Sutton NH, USA).

90 We applied a receptor-noise limited visual model [35] of the European Blackbird (*T. merula*) visual sys-  
91 tem [36] in the *pavo* [37] package in R v4.0.0 [38] to calculate avian-perceived chromatic and achromatic  
92 visual contrast (in units of “Just-Noticeable Differences”, or JNDs) of male vs. female plumage patches for  
93 all sampled *Turdus* species. Chromatic and achromatic JNDs were calculated for male-female pairs within  
94 each species (i.e., N=9 JND values calculated per patch for each species where N=3 males and N=3 fe-  
95 males sampled), and then JND values were averaged for each species’ respective plumage patches. Under  
96 ideal laboratory conditions, 1 JND is generally considered to be the discriminable threshold past which  
97 an observer is predicted to be able to perceive the two colors as different. However, natural light envi-  
98 ronments vary both spatially and temporally [39], bringing into question the accuracy of a 1 JND thresh-  
99 old for generalizing visual contrast under natural conditions. Therefore, we calculated the total number  
100 of sexually-dichromatic plumage patches per species (out of N=5 measured patches) as the number of  
101 plumage patches with average JND values > 1, 2, or 3 to account for uncertainty in visual discrimination  
102 thresholds due to variation in psychophysical and ambient lighting conditions affecting the strength of  
103 between-sex plumage visual contrast [40]. Additionally, we modeled the number of divergent plumage  
104 patches (JND >1, 2, and 3) within sexes and between different sympatric species under different levels  
105 of breeding range overlap (10% increments between 0-90%).

106 **Life History Data**

107 **Breeding Timing Model**

108 We collected data on migration behaviour and breeding season length from *Thrushes* [31] and the *Hand-  
109 book of the Birds of the World* [41]. We assigned three different kinds of migratory behaviour: 1) *full  
110 migration* when a species description clearly stated that a species “migrates”, 2) *partial migration* when a  
111 species was described to have “altitudinal migration”, “latitudinal migration” or “movement during non-  
112 breeding season”, or 3) *sedentary* when a species was described as “resident” or “sedentary”. Breeding  
113 season length was defined as the number of months the species breeds each year.

114 **Breeding Sympatry Model**

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

121 **Breeding Spacing Model**

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

127 **Statistical modeling**

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

135 Our *breeding timing* models included the following predictors: z-scores of breeding season length  
136 (mean-centered by  $\mu = 5.4$  months, and scaled by one standard deviation  $\sigma = 2.3$  months), migratory  
137 behaviour (no migration as the reference category versus partial or full migration), and their interaction.  
138 *Breeding sympathy* models included the number of sympatric species with greater than 30% breeding range  
139 overlap as the only predictor of the probability of having a sexually-dichromatic plumage patch. *Breeding*

spacing models included  $\log_e$  transformed breeding range size (km<sup>2</sup>) and breeding landmass (mainland as the reference category versus island). We also ran null models (intercept only) for all responses. All models' intercepts and response standard deviations were assigned a weak prior (Student T: df = 3, location = 0, scale = 10), and predictor coefficients were assigned flat priors. We ran each model for 6,000 iterations across 6 chains and assessed Markov Chain Monte Carlo (MCMC) convergence using the Gelman-Rubin diagnostic (Rhat) [46]. We then performed k-fold cross-validation [47] to refit each model K=16 times. For each k-fold, the training dataset 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  $N \approx 4$  species not included in the training dataset. Finally, we compared differences between the models' expected log pointwise predictive densities (ELPD) to assess which model(s) best predicted the probability of having a sexually-dichromatic plumage patch. [47].

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

## Results

### Avian visual modeling

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

### Model comparisons

We obtained  $N \geq 4000$  effective posterior samples for each model parameter and all models' Markov Chains (MCMC) successfully converged (Rhat = 1 for all models' parameters) (Supplementary Figure 3, 4). All *breeding sympathy*, *breeding timing*, and *breeding spacing* models performed similarly well and substantially better than *intercept only* models in predicting the probability of having a sexually-dimorphic plumage patch with achromatic JND values  $> 1$ , 2, or 3 (Table 1; all models predicting achromatic plumage

175 patches had ELPD values within 4, following the convention of Burnham and Anderson (2002)[49]).  
176 Among models predicting the probability of having a sexually-dichromatic plumage patch with chromatic  
177 JND values >1, 2, or 3, all *breeding sympatry*, *breeding timing*, and *breeding spacing* models performed much  
178 better than *intercept only* models, and *breeding sympatry* models had the top predictive performance (Ta-  
179 ble 1; *breeding sympatry* models all have ELPD =0, only the *breeding spacing* models predicting dichromatic  
180 plumage patches with had similar predictive performance).

### 181 **Achromatic plumage sexual dimorphism predictors**

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

### 199 **Chromatic plumage sexual dimorphism predictors**

200 Among predictors of *breeding timing* models predicting chromatic sexually-dimorphic plumage patches,  
201 longer breeding season length was associated with lower odds of a species having a plumage patch with  
202 chromatic JND  $> 2$  (OR [90% HDI] = 0.14 [0.01, 1.42], 86% reduction in odds per 2.3 month increase in  
203 breeding season), and both full and partial migratory behaviour rather than no migration are associated  
204 with greater odds of a species having a plumage patch JND  $> 1$  (partial migration, OR [90% HDI] = 2.2  
205 [0.94, 4.9]), JND  $> 2$  (full migration, OR [90% HDI] = 80.51 [2.8, 3432.9]) and JND  $> 3$  (partial migration,  
206 OR [90% HDI] = 71.2 [0.32, 59062.9]; full migration, OR [90% HDI] = 234.7 [ 0.51, 300382.6]). For  
207 *breeding spacing models*, island residency rather than mainland residency was associated with lower odds  
208 of having a plumage patch  $> 1$  chromatic JND (island, OR [90% HDI] = 0.27 [0.09, 0.89]). Finally, more  
209 *Turdus* species in sympatry was associated with higher odds of a species having a chromatic plumage  
210 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.

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	0.56 (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, 8.195), 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, 3.39), 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)

214 **Discussion**

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

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

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

242 **Conclusions**

243 Patterns of plumage sexual dimorphism in true thrushes (*Turdus*) are consistent with select predictions  
244 of the species recognition hypothesis for plumage sexual dimorphism. Migratory behaviour and limited  
245 breeding seasons reduce the amount of time available to find a mate, and greater plumage sexual dimor-  
246 phism may help migratory species find compatible mates more rapidly. Greater plumage sexual dimor-  
247 phism in *Turdus* species under sympatry with other true thrush species also supports the possibility that  
248 increased plumage sexual dichromatism may be the result of reproductive character displacement. There-  
249 fore, greater plumage sexual dimorphism likely reduces species recognition errors and hybridization.

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254 **References**

- 255 1. Andersson M. 1994 Species Recognition, Sexual Selection, and Speciation. In *Sexual Selection*, pp.  
256 207–226. Princeton University Press. (doi:[10.2307/j.ctvs32s1x.13](https://doi.org/10.2307/j.ctvs32s1x.13))
- 257 2. Gröning J, Hochkirch A. 2008 Reproductive Interference Between Animal Species. *The Quarterly  
258 Review of Biology* **83**, 257–282. (doi:[10.1086/590510](https://doi.org/10.1086/590510))
- 259 3. Pfennig KS, Hurlbert AH. 2012 Heterospecific interactions and the proliferation of sexually dimor-  
260 phic traits. *Current Zoology* **58**, 453–462. (doi:[10.1093/czoolo/58.3.453](https://doi.org/10.1093/czoolo/58.3.453))
- 261 4. West-Eberhard MJ. 1983 Sexual Selection, Social Competition, and Speciation. *The Quarterly Re-  
262 view of Biology* **58**, 155–183. (doi:[10.1086/413215](https://doi.org/10.1086/413215))
- 263 5. Martin PR, Montgomerie R, Lougheed SC. 2015 Color Patterns of Closely Related Bird Species Are  
264 More Divergent at Intermediate Levels of Breeding-Range Sympatry. *The American Naturalist* **185**,  
443–451. (doi:[10.1086/680206](https://doi.org/10.1086/680206))
- 265 6. Bitton P-P, Doucet SM. 2016 Sympatric black-headed and elegant trogons focus on dif-  
266 ferent plumage characteristics for species recognition. *Animal Behaviour* **116**, 213–221.  
(doi:[10.1016/j.anbehav.2016.03.035](https://doi.org/10.1016/j.anbehav.2016.03.035))
- 267 7. Martin TE, Badyaev AV. 1996 Sexual Dichromatism in Birds: Importance of Nest Predation and  
268 Nest Location for Females Versus Males. *Evolution* **50**, 2454–2460. (doi:[10.2307/2410712](https://doi.org/10.2307/2410712))
- 269 8. Burns KJ. 1998 A Phylogenetic Perspective on the Evolution of Sexual Dichromatism in Tan-  
270 agers (Thraupidae): The Role of Female Versus Male Plumage. *Evolution* **52**, 1219–1224.  
(doi:[10.1111/j.1558-5646.1998.tb01849.x](https://doi.org/10.1111/j.1558-5646.1998.tb01849.x))
- 271 9. Badyaev AV, Hill GE. 2003 Avian Sexual Dichromatism in Relation to Phylogeny  
272 and Ecology. *Annual Review of Ecology, Evolution, and Systematics* **34**, 27–49.  
(doi:[10.1146/annurev.ecolsys.34.011802.132441](https://doi.org/10.1146/annurev.ecolsys.34.011802.132441))
- 273 10. Dale J, Dey C, Delhey K, Kempenaers B, Valcu M. 2015 The effects of life-history and social selec-  
274 tion on male and female plumage coloration. *Nature* **000**, 1–17. (doi:[10.1038/nature15509](https://doi.org/10.1038/nature15509))
- 275 11. Dunn PO, Armenta JK, Whittingham LA. 2015 Natural and sexual selection act on different axes  
276 of variation in avian plumage color. *Science Advances* **1**, e1400155. (doi:[10.1126/sciadv.1400155](https://doi.org/10.1126/sciadv.1400155))
- 277 12. Hawkins GL, Hill GE, Mercadante A. 2012 Delayed plumage maturation and delayed reproductive  
278 investment in birds. *Biological Reviews* **87**, 257–274. (doi:[10.1111/j.1469-185X.2011.00193.x](https://doi.org/10.1111/j.1469-185X.2011.00193.x))

- 279 13. Hamilton TH. 1961 On the Functions and Causes of Sexual Dimorphism in Breeding Plumage  
Characters of North American Species of Warblers and Orioles. *The American Naturalist* **45**, 64-  
73. (doi:[10.1086/282167](https://doi.org/10.1086/282167))
- 280
- 281 14. Saetre G-P, Slagsvold T. 1992 Evidence for sex recognition from plumage colour by the pied fly-  
catcher, *Ficedula hypoleuca*. *Animal Behaviour* **44**, 293-299. (doi:[10.1016/0003-3472\(92\)90035-8](https://doi.org/10.1016/0003-3472(92)90035-8))
- 282
- 283 15. Friedman NR, Hofmann CM, Kondo B, Omland KE. 2009 Correlated evolution of migra-  
tion and sexual dichromatism in the new world orioles (*Icterus*). *Evolution* **63**, 3269-3274.  
(doi:[10.1111/j.1558-5646.2009.00792.x](https://doi.org/10.1111/j.1558-5646.2009.00792.x))
- 284
- 285 16. Simpson RK, Johnson MA, Murphy TG. 2015 Migration and the evolution of sexual dichromatism:  
Evolutionary loss of female coloration with migration among wood-warblers. *Proceedings of the  
Royal Society B: Biological Sciences* **282**, 20150375. (doi:[10.1098/rspb.2015.0375](https://doi.org/10.1098/rspb.2015.0375))
- 286
- 287 17. Matysioková B, Remeš V, Cockburn A. 2017 Broad-scale variation in sexual dichromatism in song-  
birds is not explained by sex differences in exposure to predators during incubation. *Journal of  
Avian Biology* **48**, 1322-1330. (doi:[10.1111/jav.01144](https://doi.org/10.1111/jav.01144))
- 288
- 289 18. Badyaev AV, Ghalambor CK. 1998 Does a Trade-Off Exist between Sexual Ornamentation and  
Ecological Plasticity? Sexual Dichromatism and Occupied Elevational Range in Finches. *Oikos* **82**,  
319-324. (doi:[10.2307/3546972](https://doi.org/10.2307/3546972))
- 290
- 291 19. Figuerola J, Green AJ. 2000 The evolution of sexual dimorphism in relation to mating patterns,  
cavity nesting, insularity and sympatry in the Anseriformes. *Functional Ecology* **14**, 701-710.  
(doi:[10.1046/j.1365-2435.2000.00474.x](https://doi.org/10.1046/j.1365-2435.2000.00474.x))
- 292
- 293 20. Tobias JA, Seddon N. 2009 Sexual selection and ecological generalism are correlated in antbirds.  
*Journal of Evolutionary Biology* **22**, 623-636. (doi:[10.1111/j.1420-9101.2008.01678.x](https://doi.org/10.1111/j.1420-9101.2008.01678.x))
- 294
- 295 21. Roulin A, Salamin N. 2010 Insularity and the evolution of melanism, sexual dichromatism and  
body size in the worldwide-distributed barn owl. *Journal of Evolutionary Biology* **23**, 925-934.  
(doi:[10.1111/j.1420-9101.2010.01961.x](https://doi.org/10.1111/j.1420-9101.2010.01961.x))
- 296
- 297 22. Doutrelant C, Paquet M, Renault JP, Grégoire A, Crochet P-A, Covas R. 2016 Worldwide patterns  
of bird colouration on islands. *Ecology Letters* **19**, 537-545. (doi:[10.1111/ele.12588](https://doi.org/10.1111/ele.12588))
- 298
- 299 23. Kearns AM, Joseph L, Austin JJ, Driskell AC, Omland KE. 2020 Complex mosaic of sexual dichro-  
matism and monochromatism in Pacific robins results from both gains and losses of elaborate  
coloration. *Journal of Avian Biology* **51**. (doi:[10.1111/jav.02404](https://doi.org/10.1111/jav.02404))
- 300
- 301 24. Alatalo RV, Gustafsson L, Lundberg A. 1994 Male coloration and species recognition in sympatric  
flycatchers. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **256**, 113-118.  
(doi:[10.1098/rspb.1994.0057](https://doi.org/10.1098/rspb.1994.0057))
- 302
- 303 25. Saetre G-P, Moum T, Bureš S, Král M, Adamjan M, Moreno J. 1997 A sexually selected  
character displacement in flycatchers reinforces premating isolation. *Nature* **387**, 589-592.  
(doi:[10.1038/42451](https://doi.org/10.1038/42451))
- 304

- 305 26. Laaksonen T et al. 2015 Sympatric divergence and clinal variation in multiple coloration traits of  
306 Ficedula flycatchers. *Journal of Evolutionary Biology* **28**, 779–790. (doi:[10.1111/jeb.12604](https://doi.org/10.1111/jeb.12604))
- 307 27. Cooney CR, Tobias JA, Weir JT, Botero CA, Seddon N. 2017 Sexual selection, specia-  
308 tion and constraints on geographical range overlap in birds. *Ecology Letters* **20**, 863–871.  
(doi:[10.1111/ele.12780](https://doi.org/10.1111/ele.12780))
- 309 28. Seddon N et al. 2013 Sexual selection accelerates signal evolution during speciation in birds. *Pro-  
310 ceedings of the Royal Society B: Biological Sciences* **280**, 20131065. (doi:[10.1098/rspb.2013.1065](https://doi.org/10.1098/rspb.2013.1065))
- 311 29. Cooney CR, Varley ZK, Nouri LO, Moody CJA, Jardine MD, Thomas GH. 2019 Sexual selection pre-  
312 dictes the rate and direction of colour divergence in a large avian radiation. *Nature Communications*  
**10**, 1773. (doi:[10.1038/s41467-019-09859-7](https://doi.org/10.1038/s41467-019-09859-7))
- 313 30. Martin PR, Montgomerie R, Lougheed SC. 2010 Rapid Sympatry Explains Greater Color  
314 Pattern Divergence in High Latitude Birds. *Evolution* **64**, 336–347. (doi:[10.1111/j.1558-5646.2009.00831.x](https://doi.org/10.1111/j.1558-<br/>5646.2009.00831.x))
- 315 31. Clement P, Hathway R. 2000 *Thrushes*. London: A&C Black Publishers Ltd.
- 316
- 317 32. Nagy J, Végvári Z, Varga Z. 2019 Phylogeny, migration and life history: Filling the gaps in  
318 the origin and biogeography of the *Turdus* thrushes. *Journal of Ornithology* **160**, 529–543.  
(doi:[10.1007/s10336-019-01632-3](https://doi.org/10.1007/s10336-019-01632-3))
- 319 33. McCarthy EM. 2006 *Handbook of avian hybrids of the world*. Oxford ; New York: Oxford University  
320 Press.
- 321 34. Andersson S, Prager M. 2006 Quantifying Colors. In *Bird coloration, Volume 1: Mechanisms and  
322 Measurements* (eds GE Hill, KJ McGraw), pp. 76–77. Cambridge, MA: Harvard University Press.
- 323 35. Vorobyev M, Osorio D. 1998 Receptor noise as a determinant of colour thresholds. *Proceedings.  
324 Biological sciences / The Royal Society* **265**, 351–8. (doi:[10.1098/rspb.1998.0302](https://doi.org/10.1098/rspb.1998.0302))
- 325 36. Hart NS, Partridge JC, Cuthill IC, Bennett AT. 2000 Visual pigments, oil droplets, ocular media and  
326 cone photoreceptor distribution in two species of passerine bird: The blue tit (*Parus caeruleus*  
L.) And the blackbird (*Turdus merula* L.). *Journal of comparative physiology. A, Sensory, neural, and  
327 behavioral physiology* **186**, 375–387. (doi:[10.1007/s003590050437](https://doi.org/10.1007/s003590050437))
- 328 37. Maia R, Gruson H, Endler JA, White TE. 2019 Pavo 2: New tools for the spectral and spatial analysis  
329 of colour in r. *Methods in Ecology and Evolution* **10**, 1097–1107. (doi:[10.1111/2041-210X.13174](https://doi.org/10.1111/2041-210X.13174))
- 330 38. R Core Team. 2020 *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R  
331 Foundation for Statistical Computing.
- 332 39. Endler JA. 1993 The Color of Light in Forests and Its Implications. *Ecological Monographs* **63**, 1–27.  
(doi:[10.2307/2937121](https://doi.org/10.2307/2937121))
- 333 40. Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall  
334 J, Whiting MJ. 2015 An Integrative Framework for the Appraisal of Coloration in Nature. *The  
American Naturalist* **185**, 705–724. (doi:[10.1086/681021](https://doi.org/10.1086/681021))

- 335 41. del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E. 2017 *Handbook of the birds of the world*  
336 *alive*.
- 337 42. BirdLife International and Handbook of the Birds of the World. 2018 *Bird species distribution maps*  
338 *of the world. Version 2018.1*.
- 339 43. Vilela B, Villalobos F. 2015 letsR: A new R package for data handling and analysis in macroecology.  
340 *Methods in Ecology and Evolution* **6**, 1229–1234. (doi:[10.1111/2041-210X.12401](https://doi.org/10.1111/2041-210X.12401))
- 341 44. Bürkner PC. 2017 Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **80**, 1–28. (doi:[10.18637/jss.v080.i01](https://doi.org/10.18637/jss.v080.i01))
- 343 45. Nylander JAA, Olsson U, Alström P, Sanmartín I. 2008 Accounting for phylogenetic uncertainty in  
344 biogeography: A bayesian approach to dispersal-vicariance analysis of the thrushes (Aves: Turdus).  
*Systematic Biology* **57**, 257–268. (doi:[10.1080/10635150802044003](https://doi.org/10.1080/10635150802044003))
- 345 46. Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. 2013 *Bayesian data analysis, third*  
346 *edition*. Third. Boca Raton, FL: CRC Press. (doi:[10.1201/b16018](https://doi.org/10.1201/b16018))
- 347 47. Vehtari A, Gelman A, Gabry J. 2017 Practical Bayesian model evaluation using leave-one-out cross-  
348 validation and WAIC. *Statistics and Computing* **27**, 1413–1432. (doi:[10.1007/s11222-016-9696-4](https://doi.org/10.1007/s11222-016-9696-4))
- 349 48. Makowski D, Ben-Shachar MS, Chen SHA, Lüdecke D. 2019 Indices of Effect Existence and Signif-  
350 icance in the Bayesian Framework. *Frontiers in Psychology* **10**. (doi:[10.3389/fpsyg.2019.02767](https://doi.org/10.3389/fpsyg.2019.02767))
- 351 49. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: A practical information-  
352 theoretic approach*. 2nd ed. New York: Springer.
- 353 50. Simpson RK, Wilson DR, Mistakidis AF, Mennill DJ, Doucet SM. 2021 Sympatry drives colour and  
354 song evolution in wood-warblers (Parulidae). *Proceedings of the Royal Society B: Biological Sciences*  
**288**, 20202804. (doi:[10.1098/rspb.2020.2804](https://doi.org/10.1098/rspb.2020.2804))
- 355 51. Miller ET, Leighton GM, Freeman BG, Lees AC, Ligon RA. 2019 Ecological and geographical over-  
356 lap drive plumage evolution and mimicry in woodpeckers. *Nature Communications* **10**, 1602.  
(doi:[10.1038/s41467-019-09721-w](https://doi.org/10.1038/s41467-019-09721-w))
- 357 52. McNaught MK, Owens IPF. 2002 Interspecific variation in plumage colour among birds:  
358 Species recognition or light environment? *Journal of Evolutionary Biology* **15**, 505–514.  
(doi:[10.1046/j.1420-9101.2002.00431.x](https://doi.org/10.1046/j.1420-9101.2002.00431.x))

**Supplementary Material: Rapid mate recognition promotes greater avian-perceived plumage sexual dichromatism in true thrushes (genus: *Turdus*)**

Alec B. Luro<sup>1\*</sup>, Mark E. Hauber<sup>1</sup>

<sup>5</sup> <sup>6</sup> <sup>1</sup> Department of Evolution, Ecology and Behavior, School of Integrative Biology,  
University of Illinois at Urbana-Champaign \*alec.b.luro@mail.com

## 7 Tables and Figures

Characteristic	Achromatic & Chromatic JND > 1, N = 77 <sup>1</sup>	Achromatic & Chromatic JND > 2, N = 77 <sup>1</sup>	Achromatic & Chromatic JND > 3, N = 77 <sup>1</sup>
	Number of Sexually-Dimorphic Plumage Patches		
0	1 (1.3%)	34 (44%)	49 (64%)
1	4 (5.2%)	14 (18%)	10 (13%)
2	11 (14%)	7 (9.1%)	2 (2.6%)
3	10 (13%)	3 (3.9%)	2 (2.6%)
4	10 (13%)	1 (1.3%)	7 (9.1%)
5	12 (16%)	4 (5.2%)	0 (0%)
6	8 (10%)	3 (3.9%)	0 (0%)
7	4 (5.2%)	4 (5.2%)	3 (3.9%)
8	5 (6.5%)	1 (1.3%)	1 (1.3%)
9	5 (6.5%)	1 (1.3%)	1 (1.3%)
10	7 (9.1%)	5 (6.5%)	2 (2.6%)

**Table S1:** Number of sexually-dimorphic plumage patches for combined achromatic and chromatic just noticeable differences (JND) thresholds by number of *Turdus* thrush species (% of species)

Characteristic	Achromatic > 1 JND, N = 77 <sup>1</sup>	Achromatic > 2 JND, N = 77 <sup>1</sup>	Achromatic > 3 JND, N = 77 <sup>1</sup>	Chromatic > 1 JND, N = 77 <sup>1</sup>	Chromatic > 2 JND, N = 77 <sup>1</sup>	Chromatic > 3 JND, N = 77 <sup>1</sup>
Number of Sexually-Dimorphic Plumage Patches						
0	8 (10%)	41 (53%)	51 (66%)	6 (7.8%)	47 (61%)	61 (79%)
1	19 (25%)	10 (13%)	10 (13%)	15 (19%)	11 (14%)	5 (6.5%)
2	14 (18%)	9 (12%)	4 (5.2%)	22 (29%)	5 (6.5%)	3 (3.9%)
3	11 (14%)	5 (6.5%)	7 (9.1%)	11 (14%)	7 (9.1%)	2 (2.6%)
4	11 (14%)	5 (6.5%)	3 (3.9%)	14 (18%)	1 (1.3%)	2 (2.6%)
5	14 (18%)	7 (9.1%)	2 (2.6%)	9 (12%)	6 (7.8%)	4 (5.2%)

<sup>1</sup>Statistics presented: n (%)

Table S2: Number of sexually-dimorphic plumage patches for separate achromatic and chromatic just noticeable differences (JND) thresholds by number of *Turdus* thrush species (% of species).

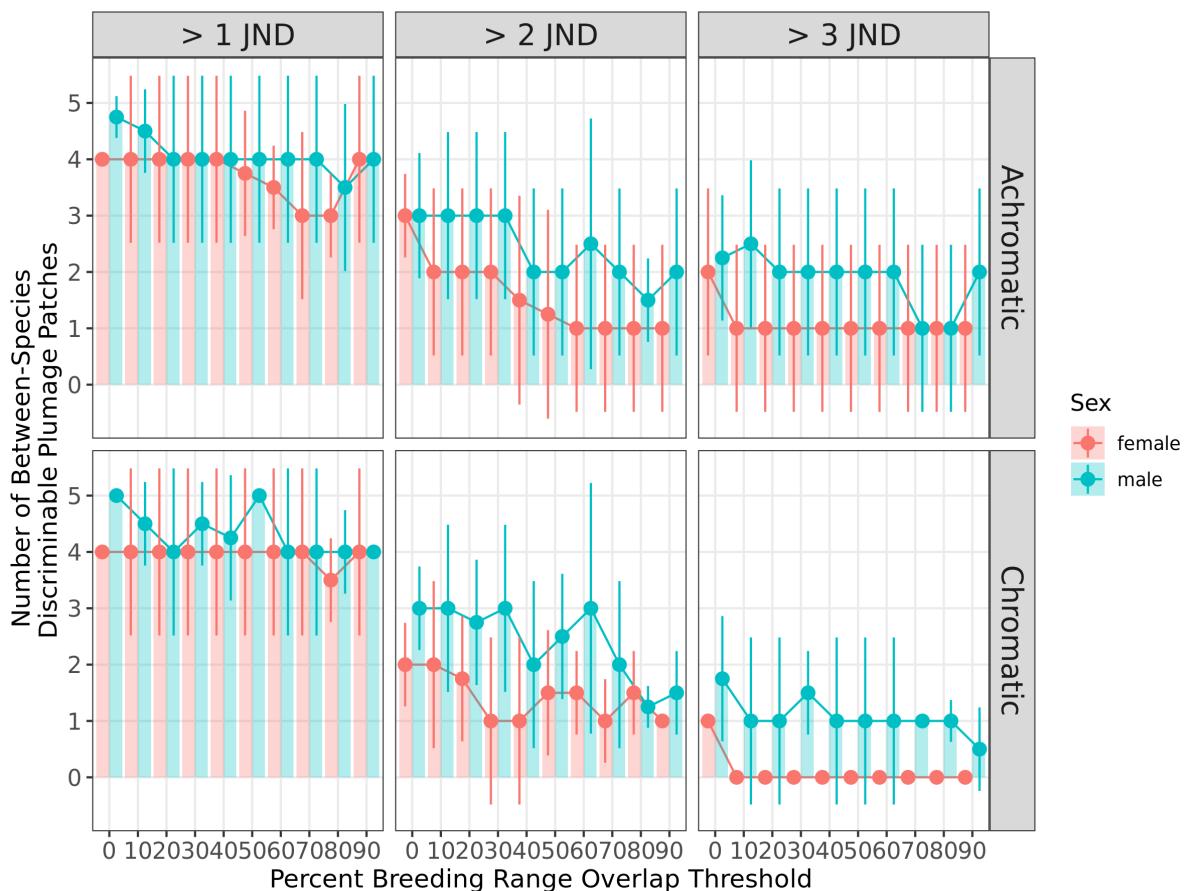


Fig S1: Median  $\pm$  median absolute deviation of number of distinguishable plumage patches by just noticeable differences (JND) thresholds of 1,2 and 3 between male and female *Turdus* thrush species in sympatry at various breeding range overlaps (percent).