

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

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7 **Abstract**

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

20 **Keywords**

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

22 **Introduction**

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

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

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

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

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

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

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

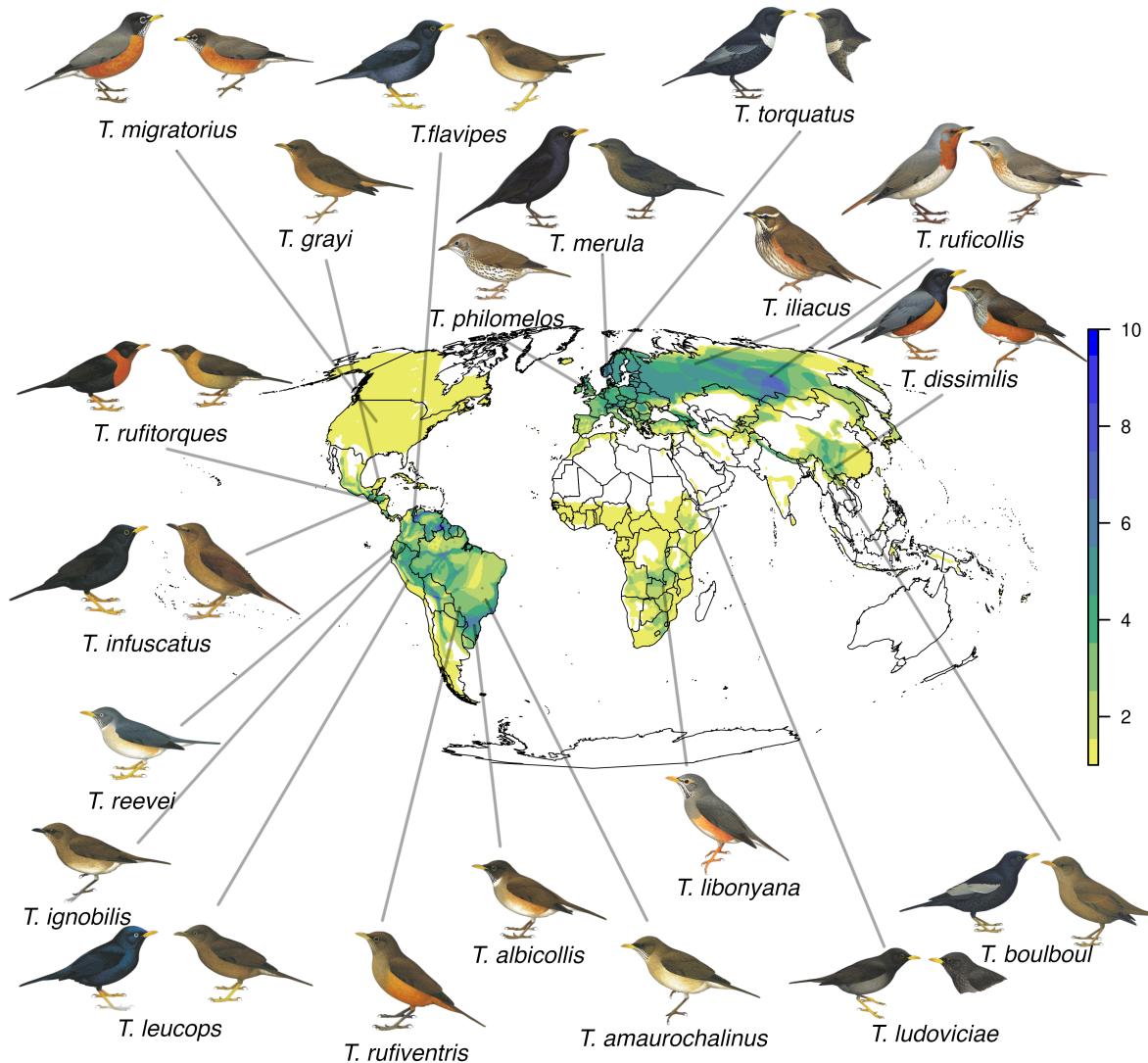


Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International, with representative species' males and females shown for species with sexually dimorphic plumage. The color scale indicates the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations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

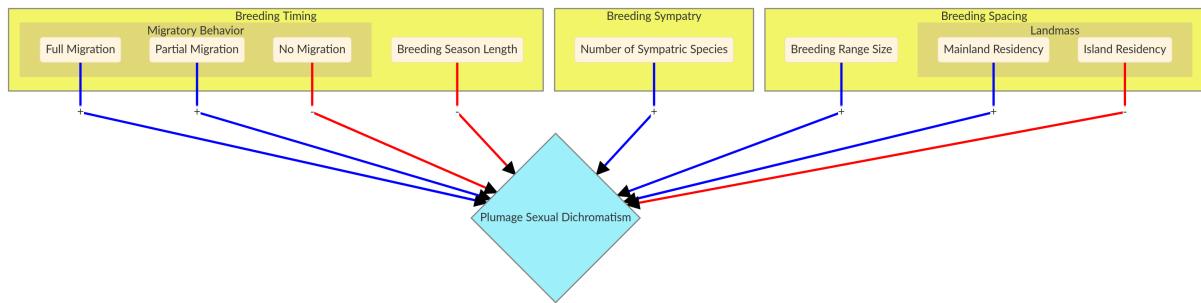


Figure 2: Hypotheses and predictions for each model. Arrow colours indicate predicted correlation, positive (blue) and negative (red)

Methods

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

Plumage sexual dichromatism

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

We applied a receptor-noise limited visual model [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 colours 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

104 between-sex plumage visual contrast [40]. Additionally, we modeled the number of divergent plumage
105 patches (at the three different JND thresholds listed above) within sexes and between different sympatric
106 species under different levels of breeding range overlap (10% increments between 0-90%).

107 **Life History Data**

108 **Breeding Timing Model**

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

115 **Breeding Sympatry Model**

116 Species’ breeding ranges were acquired from *BirdLife International* [42]. We calculated congener breeding
117 range overlaps (as percentages) using the *letsR* package in R [43]. We then calculated the number of sym-
118 patric species as the number of congeners with breeding ranges that overlap >30% with the focal species’
119 breeding range [27]. Comparisons of the number of sexually-dimorphic plumage patches vs. the number
120 of sympatric species among different breeding range overlap thresholds are provided in Supplementary
121 Figure 1.

122 **Breeding Spacing Model**

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

128 **Statistical modeling**

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

137 Our breeding timing models included the following predictors: z-scores of breeding season length
138 (mean-centered by $\mu = 5.4$ months, and scaled by one standard deviation $\sigma = 2.3$ months), migratory
139 behaviour (no migration as the reference category versus partial or full migration), and their interaction.
140 Breeding sympatry models included the number of sympatric species with greater than 30% breeding range
141 overlap as the only predictor of the probability of having a sexually-dichromatic plumage patch. Breeding
142 spacing models included \log_e transformed breeding range size (km²) and breeding landmass (mainland
143 as the reference category versus island). We also ran null models (intercept only) for all responses. All
144 models' intercepts and response standard deviations were assigned a weakly informative prior (Student
145 T: df = 3, location = 0, scale = 10) [46], and predictor coefficients were assigned flat uninformative priors.
146 We ran each model for 6,000 iterations across 6 chains and assessed Markov Chain Monte Carlo (MCMC)
147 convergence using the Gelman-Rubin diagnostic (Rhat) [46]. We then performed k-fold cross-validation
148 [47] to refit each model K=16 times. For each k-fold, the training dataset included a randomly selected set
149 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
150 training dataset. Finally, we compared differences between the models' expected log pointwise predictive
151 densities (ELPD) to assess which model(s) best predicted the probability of having a sexually-dichromatic
152 plumage patch. [47].

153 Models' predictor effects were assessed using 90% highest-density intervals of the posterior distribu-
154 tions and probability of direction, the proportion of the posterior distribution that shares the same sign
155 (positive or negative) as the posterior median [48], to provide estimates of the probability of that a predi-
156 ctor has an entirely positive or negative effect on the presence of sexually-dimorphic plumage patches. We
157 assume predictor estimates with a probability of direction ≥ 0.90 to be indicative of a reliable existence
158 of a predictor's effect on sexually-dimorphic plumage patches [48].

159 Results

160 Avian visual modeling

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

170 **Model comparisons**

171 *Breeding sympathy, breeding timing, and breeding spacing* performed considerably better than *intercept-only*
172 (null models) in predicting the probability of a species having a sexually-dimorphic plumage patch. We
173 obtained $N \geq 4000$ effective posterior samples for each model parameter and all models' Markov Chains
174 (MCMC) successfully converged ($Rhat = 1$ for all models' parameters). All *breeding sympathy, breeding tim-*
175 *ing, and breeding spacing* models performed similarly well and substantially better than *intercept only* mod-
176 els in predicting the probability of having a sexually-dimorphic plumage patch with achromatic JND values
177 $> 1, 2, \text{ or } 3$ (Table 1; all models predicting achromatic plumage patches had ELPD values within 4, follow-
178 ing the convention of [49]). Among models predicting the probability of having a sexually-dichromatic
179 plumage patch with chromatic JND values $> 1, 2, \text{ or } 3$, all *breeding sympathy, breeding timing, and breeding*
180 *spacing* models performed much better than *intercept only* models, and *breeding sympathy* models had the
181 top predictive performance (Table 1; *breeding sympathy* models all have ELPD = 0, only the *breeding spacing*
182 models predicting dichromatic plumage patches had similar predictive performance).

183 **Achromatic plumage sexual dimorphism predictors**

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

202 **Chromatic plumage sexual dimorphism predictors**

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

206 longer breeding season length was associated with lower odds of a species having a plumage patch with
 207 chromatic JND > 2 (OR [90% HDI] = 0.14 [0.01, 1.42], 86% reduction in odds per 2.3 month increase
 208 in breeding season). Both full and partial migratory behaviour rather than no migration are associated
 209 with greater odds of a species having a plumage patch JND > 1 (partial migration, OR [90% HDI] = 2.2
 210 [0.94, 4.9]), JND > 2 (full migration, OR [90% HDI] = 80.51 [2.8, 3432.9]) and JND > 3 (partial migration,
 211 OR [90% HDI] = 71.2 [0.32, 59062.9]; full migration, OR [90% HDI] = 234.7 [0.51, 300382.6]). For
 212 *breeding spacing models*, island residency rather than mainland residency was associated with lower odds
 213 of having a plumage patch > 1 chromatic JND (island, OR [90% HDI] = 0.27 [0.09, 0.89]). Finally, more
 214 *Turdus* species in sympatry was associated with higher odds of a species having a sexually-dimorphic
 215 chromatic plumage patch with JND > 1 (number of sympatric species, OR [90% HDI] = 1.4 [1.18, 1.67],
 216 40% increase in odds per each additional sympatric species), JND > 2 (sympatric species, OR [90% HDI]
 217 = 1.59 [1.01, 2.52], 59% increase in odds per each additional sympatric species), and JND > 3 (sympatric
 218 species, OR [90% HDI] = 2.11 [1.03, 4.46], 111% increase in odds per each additional sympatric species).

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

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

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

Model	Parameter	Achromatic, JND > 1	Achromatic, JND > 2	Achromatic, JND > 3	Chromatic, JND > 1	Chromatic, JND > 2	Chromatic, JND > 3
Breeding Timing							
	Intercept	0 (0, 0.54), pd = 0.98	0 (0, 0.19), pd = 0.99	0 (0, 0.19), pd = 0.99	0.41 (0.05, 2.79), pd = 0.78	0 (0, 1.73), pd = 0.95	0 (0, 1.37), pd = 0.96
	Breeding Season Length	0.1 (0.01, 1.05), pd = 0.97	0.25 (0.03, 1.49), pd = 0.91	0.25 (0.03, 1.49), pd = 0.91	0.89 (0.56, 1.4), pd = 0.66	0.14 (0.01, 1.42), pd = 0.94	0.08 (0, 9.14), pd = 0.83
	Partial Migration vs. No Migration	0.76 (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	4.37 (0.95, 24.41), pd = 0.96	66.52 (3.19, 1802.4), pd = 0.99	22.34 (1.59, 307.9), pd = 0.98	2.29 (0.69, 7.31), pd = 0.88	80.31 (2.81, 343.86), pd = 0.99	234.71 (0.51, 200382.62), pd = 0.95
	Breeding Season Length x Partial Migration	1.34 (0.48, 3.92), pd = 0.68	20.71 (0.87, 589.09), pd = 0.96	8.28 (0.76, 109.11), pd = 0.94	1.39 (0.65, 31.2), pd = 0.76	9.03 (0.44, 251.36), pd = 0.9	34.46 (0.08, 68228.71), pd = 0.85
	Breeding Season Length x Full Migration	4.34 (0.67, 39.63), pd = 0.9	66.3 (0.59, 11415.7), pd = 0.93	16.41 (0.27, 824.69), pd = 0.89	1.68 (0.31, 8.33), pd = 0.7	160.6 (0.84, 67791.13), pd = 0.95	433.67 (0.01, 371945.69), pd = 0.85
	Phylogenetic Signal λ , Median (90% Credible Interval)	0.29 (0.16, 0.43)	0.72 (0.56, 0.86)	0.61 (0.42, 0.8)	0.17 (0.08, 0.28)	0.74 (0.57, 0.88)	0.89 (0.77, 0.97)
Breeding Spacing							
	Intercept	0 (0, 2.44), pd = 0.95	0 (0, 0.14), pd = 0.98	0 (0, 0.14), pd = 0.98	0.51 (0.03, 9.7), pd = 0.65	0 (0, 7.63), pd = 0.92	0 (0, 8.19), pd = 0.91
	Island vs. Mainland	1.08 (0.25, 4.79), pd = 0.54	0.53 (0.01, 17.83), pd = 0.61	0.92 (0.05, 19.32), pd = 0.52	0.27 (0.09, 0.89), pd = 0.97	0.03 (0, 3.99), pd = 0.89	0.04 (0, 67.59), pd = 0.77
	Breeding Range Size	1.08 (0.88, 1.32), pd = 0.75	1.23 (0.76, 2.01), pd = 0.77	1.3 (0.87, 1.93), pd = 0.87	1.02 (0.87, 1.19), pd = 0.58	1.24 (0.75, 2.05), pd = 0.77	1.26 (0.54, 2.99), pd = 0.69
	Phylogenetic Signal λ , Median (90% Credible Interval)	0.27 (0.15, 0.41)	0.71 (0.56, 0.85)	0.6 (0.42, 0.77)	0.15 (0.07, 0.25)	0.72 (0.55, 0.86)	0.85 (0.71, 0.95)
Breeding Sympatry							
	Intercept	0.41 (0.03, 5.83), pd = 0.72	0 (0, 0.98), pd = 0.95	0 (0, 0.34), pd = 0.98	0.25 (0.04, 1.35), pd = 0.91	0 (0, 1.12), pd = 0.95	0 (0, 0.29), pd = 0.98
	Number of Sympatric Species ($\geq 30\%$ Breeding Range Overlap)	1.03 (0.84, 1.27), pd = 0.61	1.15 (0.74, 1.75), pd = 0.71	1.13 (0.76, 1.63), pd = 0.71	1.4 (1.18, 1.67), pd = 0.99	1.59 (1.01, 2.52), pd = 0.96	2.11 (1.03, 4.46), pd = 0.97
	Phylogenetic Signal λ , Median (90% Credible Interval)	0.26 (0.14, 0.39)	0.7 (0.54, 0.83)	0.59 (0.41, 0.77)	0.13 (0.06, 0.23)	0.69 (0.52, 0.83)	0.82 (0.67, 0.94)

219 **Discussion**

220 Our results provide comparative correlative evidence in support of predictions of the recognition hypothesis
221 for plumage sexual dimorphism in true thrushes. We used a receptor-noise limited model of *Turdus*
222 *merula* vision [35,36] to measure avian-perceivable visual contrast of plumage colours and found that the
223 odds of plumage sexual dimorphism are much greater for *Turdus* thrush species that have full or partial
224 migration rather than no migration, have relatively short breeding seasons, and are in sympatry with many
225 other true thrush species (Table 1,2). Our results align with prior comparative studies of avian plumage
226 sexual dimorphism where strong associations of sexual dichromatism with greater migratory behaviour
227 [10] and more sympatric taxa [27] were found among many species of different passerine families.

228 Further, we determined that sympatric *Turdus* species have distinguishable plumage colouration differences
229 from one another when measuring plumage appearance from the avian visual perspective (Fig. S1).
230 Divergent plumage colouration within sexes between closely-related species indicates that plumage sex-
231 ual dichromatism may have evolved to facilitate species and mate recognition in *Turdus* species breeding
232 under higher sympatry with other true thrushes. However, we cannot directly determine if the plumage
233 sexual dimorphism in sympatric *Turdus* species is the result of reproductive character displacement. We
234 do not know if past changes in species' plumage sexual dimorphism occurred before or during periods of
235 sympatry with other *Turdus* species. Regardless, present-day plumage sexual dimorphism and perceivable
236 differences in plumage colouration between sympatric species likely reduces the challenge of finding com-
237 patible mates by signaling an individual's sex, breeding status, and species. For example, the four species
238 *Turdus* hybrid zone in north-central Asia [33] is a particularly striking example where reproductive charac-
239 ter displacement has likely occurred and all four species exhibit strong plumage sexual dimorphism (Fig.
240 S2). Comparing within sexes between sister species pairs of *T.ruficollis* and *T.atrogularis*, and *T.naumanni*
241 and *T.eunomus* [45], plumage patterns of the species pairs are nearly identical except for a divergence
242 in colour. *T.ruficollis* and *T.atrogularis* share similar facial and throat colouring patterns, with the main
243 difference being red colouration in *T.ruficollis* in opposition to the black colouration of *T.atrogularis*. In
244 the second species pair, *T.naumanni* has red ventral plumage colouration and *T.eunomus* has black ventral
245 plumage colouration .

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

255 **Conclusions**

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

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270 **References**

- 271 1. Andersson M. 1994 Species Recognition, Sexual Selection, and Speciation. In *Sexual Selection*, pp.
272 207–226. Princeton University Press. (doi:[10.2307/j.ctvs32s1x.13](https://doi.org/10.2307/j.ctvs32s1x.13))
- 273 2. Gröning J, Hochkirch A. 2008 Reproductive Interference Between Animal Species. *The Quarterly
274 Review of Biology* **83**, 257–282. (doi:[10.1086/590510](https://doi.org/10.1086/590510))
- 275 3. Pfennig KS, Hurlbert AH. 2012 Heterospecific interactions and the proliferation of sexually dimor-
276 phic traits. *Current Zoology* **58**, 453–462. (doi:[10.1093/czoolo/58.3.453](https://doi.org/10.1093/czoolo/58.3.453))
- 277 4. West-Eberhard MJ. 1983 Sexual Selection, Social Competition, and Speciation. *The Quarterly Re-
278 view of Biology* **58**, 155–183. (doi:[10.1086/413215](https://doi.org/10.1086/413215))
- 279 5. Martin PR, Montgomerie R, Lougheed SC. 2015 Color Patterns of Closely Related Bird Species Are
280 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))
- 281 6. Bitton P-P, Doucet SM. 2016 Sympatric black-headed and elegant trogons focus on dif-
282 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))
- 283 7. Martin TE, Badyaev AV. 1996 Sexual Dichromatism in Birds: Importance of Nest Predation and
284 Nest Location for Females Versus Males. *Evolution* **50**, 2454–2460. (doi:[10.2307/2410712](https://doi.org/10.2307/2410712))

- 285 8. Burns KJ. 1998 A Phylogenetic Perspective on the Evolution of Sexual Dichromatism in Tanagers (thraupidae): The Role of Female Versus Male Plumage. *Evolution* **52**, 1219–1224.
286 (doi:[10.1111/j.1558-5646.1998.tb01849.x](https://doi.org/10.1111/j.1558-5646.1998.tb01849.x))
- 287 9. Badyaev AV, Hill GE. 2003 Avian Sexual Dichromatism in Relation to Phylogeny and Ecology. *Annual Review of Ecology, Evolution, and Systematics* **34**, 27–49.
288 (doi:[10.1146/annurev.ecolsys.34.011802.132441](https://doi.org/10.1146/annurev.ecolsys.34.011802.132441))
- 289 10. Dale J, Dey C, Delhey K, Kempenaers B, Valcu M. 2015 The effects of life-history and social selection on male and female plumage coloration. *Nature* **000**, 1–17. (doi:[10.1038/nature15509](https://doi.org/10.1038/nature15509))
- 290 11. Dunn PO, Armenta JK, Whittingham LA. 2015 Natural and sexual selection act on different axes
291 of variation in avian plumage color. *Science Advances* **1**, e1400155. (doi:[10.1126/sciadv.1400155](https://doi.org/10.1126/sciadv.1400155))
- 292 12. Hawkins GL, Hill GE, Mercadante A. 2012 Delayed plumage maturation and delayed reproductive
293 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))
- 294 13. Hamilton TH. 1961 On the Functions and Causes of Sexual Dimorphism in Breeding Plumage
295 Characters of North American Species of Warblers and Orioles. *The American Naturalist* **45**, 64–
296 73. (doi:[10.1086/282167](https://doi.org/10.1086/282167))
- 297 14. Saetre G-P, Slagsvold T. 1992 Evidence for sex recognition from plumage colour by the pied fly-
298 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))
- 299 15. Friedman NR, Hofmann CM, Kondo B, Omland KE. 2009 Correlated evolution of migration
300 and sexual dichromatism in the new world orioles (*Icterus*). *Evolution* **63**, 3269–3274.
300 (doi:[10.1111/j.1558-5646.2009.00792.x](https://doi.org/10.1111/j.1558-5646.2009.00792.x))
- 301 16. Simpson RK, Johnson MA, Murphy TG. 2015 Migration and the evolution of sexual dichromatism:
302 Evolutionary loss of female coloration with migration among wood-warblers. *Proceedings of the
303 Royal Society B: Biological Sciences* **282**, 20150375. (doi:[10.1098/rspb.2015.0375](https://doi.org/10.1098/rspb.2015.0375))
- 304 17. Matysioková B, Remeš V, Cockburn A. 2017 Broad-scale variation in sexual dichromatism in song-
305 birds is not explained by sex differences in exposure to predators during incubation. *Journal of
306 Avian Biology* **48**, 1322–1330. (doi:[10.1111/jav.01144](https://doi.org/10.1111/jav.01144))
- 307 18. Badyaev AV, Ghalambor CK. 1998 Does a Trade-Off Exist between Sexual Ornamentation and
308 Ecological Plasticity? Sexual Dichromatism and Occupied Elevational Range in Finches. *Oikos* **82**,
319–324. (doi:[10.2307/3546972](https://doi.org/10.2307/3546972))
- 309 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.
310 (doi:[10.1046/j.1365-2435.2000.00474.x](https://doi.org/10.1046/j.1365-2435.2000.00474.x))
- 311 20. Tobias JA, Seddon N. 2009 Sexual selection and ecological generalism are correlated in antbirds.
312 *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))

- 311 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))
- 312 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))
- 313 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))
- 314 316 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))
- 317 319 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))
- 320 321 26. Laaksonen T et al. 2015 Sympatric divergence and clinal variation in multiple coloration traits of
Ficedula flycatchers. *Journal of Evolutionary Biology* **28**, 779–790. (doi:[10.1111/jeb.12604](https://doi.org/10.1111/jeb.12604))
- 322 323 27. Cooney CR, Tobias JA, Weir JT, Botero CA, Seddon N. 2017 Sexual selection, specia-
tion and constraints on geographical range overlap in birds. *Ecology Letters* **20**, 863–871.
(doi:[10.1111/ele.12780](https://doi.org/10.1111/ele.12780))
- 324 325 28. Seddon N et al. 2013 Sexual selection accelerates signal evolution during speciation in birds. *Pro-
ceedings of the Royal Society B: Biological Sciences* **280**, 20131065. (doi:[10.1098/rspb.2013.1065](https://doi.org/10.1098/rspb.2013.1065))
- 326 327 29. Cooney CR, Varley ZK, Nouri LO, Moody CJA, Jardine MD, Thomas GH. 2019 Sexual selection pre-
dicts the rate and direction of colour divergence in a large avian radiation. *Nature Communications*
10, 1773. (doi:[10.1038/s41467-019-09859-7](https://doi.org/10.1038/s41467-019-09859-7))
- 328 329 30. Martin PR, Montgomerie R, Lougheed SC. 2010 Rapid Sympatry Explains Greater Color
Pattern Divergence in High Latitude Birds. *Evolution* **64**, 336–347. (doi:[10.1111/j.1558-5646.2009.00831.x](https://doi.org/10.1111/j.1558-
5646.2009.00831.x))
- 330 331 31. Clement P, Hathway R. 2000 *Thrushes*. London: A&C Black Publishers Ltd.
- 332 333 32. Nagy J, Végvári Z, Varga Z. 2019 Phylogeny, migration and life history: Filling the gaps in
the origin and biogeography of the Turdus thrushes. *Journal of Ornithology* **160**, 529–543.
(doi:[10.1007/s10336-019-01632-3](https://doi.org/10.1007/s10336-019-01632-3))
- 334 335 33. McCarthy EM. 2006 *Handbook of avian hybrids of the world*. Oxford ; New York: Oxford University
Press.
- 336 337 34. Andersson S, Prager M. 2006 Quantifying Colors. In *Bird coloration, Volume 1: Mechanisms and
Measurements* (eds GE Hill, KJ McGraw), pp. 76–77. Cambridge, MA: Harvard University Press.
- 338

- 339 35. Vorobyev M, Osorio D. 1998 Receptor noise as a determinant of colour thresholds. *Proceedings.*
340 *Biological sciences / The Royal Society* **265**, 351–8. (doi:[10.1098/rspb.1998.0302](https://doi.org/10.1098/rspb.1998.0302))
- 341 36. Hart NS, Partridge JC, Cuthill IC, Bennett AT. 2000 Visual pigments, oil droplets, ocular media and
cone photoreceptor distribution in two species of passerine bird: The blue tit (*Parus caeruleus*
L.) And the blackbird (*Turdus merula* L.). *Journal of comparative physiology. A, Sensory, neural, and*
behavioral physiology **186**, 375–387. (doi:[10.1007/s003590050437](https://doi.org/10.1007/s003590050437))
- 342 37. Maia R, Gruson H, Endler JA, White TE. 2019 Pavo 2: New tools for the spectral and spatial analysis
343 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))
- 344 38. R Core Team. 2020 R: *A Language and Environment for Statistical Computing*. Vienna, Austria: R
345 Foundation for Statistical Computing.
- 346 39. Endler JA. 1993 The Color of Light in Forests and Its Implications. *Ecological Monographs* **63**, 1–27.
347 (doi:[10.2307/2937121](https://doi.org/10.2307/2937121))
- 348 40. Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall
349 J, Whiting MJ. 2015 An Integrative Framework for the Appraisal of Coloration in Nature. *The*
350 *American Naturalist* **185**, 705–724. (doi:[10.1086/681021](https://doi.org/10.1086/681021))
- 351 41. del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E. 2017 *Handbook of the birds of the world*
352 *alive*.
- 353 42. BirdLife International and Handbook of the Birds of the World. 2018 *Bird species distribution maps*
354 *of the world. Version 2018.1*.
- 355 43. Vilela B, Villalobos F. 2015 letsR: A new R package for data handling and analysis in macroecology.
356 *Methods in Ecology and Evolution* **6**, 1229–1234. (doi:[10.1111/2041-210X.12401](https://doi.org/10.1111/2041-210X.12401))
- 357 44. Bürkner PC. 2017 Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statis-*
358 *tical Software* **80**, 1–28. (doi:[10.18637/jss.v080.i01](https://doi.org/10.18637/jss.v080.i01))
- 359 45. Nylander JAA, Olsson U, Alström P, Sanmartín I. 2008 Accounting for phylogenetic uncertainty in
biogeography: A bayesian approach to dispersal-vicariance analysis of the thrushes (Aves: *Turdus*).
360 *Systematic Biology* **57**, 257–268. (doi:[10.1080/10635150802044003](https://doi.org/10.1080/10635150802044003))
- 361 46. Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. 2013 *Bayesian data analysis, third*
362 *edition*. Third. Boca Raton, FL: CRC Press. (doi:[10.1201/b16018](https://doi.org/10.1201/b16018))
- 363 47. Vehtari A, Gelman A, Gabry J. 2017 Practical Bayesian model evaluation using leave-one-out cross-
364 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))
- 365 48. Makowski D, Ben-Shachar MS, Chen SHA, Lüdecke D. 2019 Indices of Effect Existence and Signif-
366 icance in the Bayesian Framework. *Frontiers in Psychology* **10**. (doi:[10.3389/fpsyg.2019.02767](https://doi.org/10.3389/fpsyg.2019.02767))
- 367 49. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: A practical information-*
368 *theoretic approach*. 2nd ed. New York: Springer.
- 369 50. Simpson RK, Wilson DR, Mistakidis AF, Mennill DJ, Doucet SM. 2021 Sympatry drives colour and
song evolution in wood-warblers (Parulidae). *Proceedings of the Royal Society B: Biological Sciences*
370 **288**, 20202804. (doi:[10.1098/rspb.2020.2804](https://doi.org/10.1098/rspb.2020.2804))

- 371 51. Miller ET, Leighton GM, Freeman BG, Lees AC, Ligon RA. 2019 Ecological and geographical over-
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))
- 372 52. McNaught MK, Owens IPF. 2002 Interspecific variation in plumage colour among birds:
Species recognition or light environment? *Journal of Evolutionary Biology* **15**, 505–514.
(doi:[10.1046/j.1420-9101.2002.00431.x](https://doi.org/10.1046/j.1420-9101.2002.00431.x))
- 374

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

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7 Tables and Figures

Characteristic	Achromatic & Chromatic JND > 1, N = 77 ¹	Achromatic & Chromatic JND > 2, N = 77 ¹	Achromatic & Chromatic JND > 3, N = 77 ¹
	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)

- ⁸ 1. McCarthy EM. 2006 *Handbook of avian hybrids of the world*. Oxford ; New York: Oxford University Press.

Characteristic	Achromatic > 1 JND, N = 77 ¹	Achromatic > 2 JND, N = 77 ¹	Achromatic > 3 JND, N = 77 ¹	Chromatic > 1 JND, N = 77 ¹	Chromatic > 2 JND, N = 77 ¹	Chromatic > 3 JND, N = 77 ¹
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%)

¹Statistics 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).

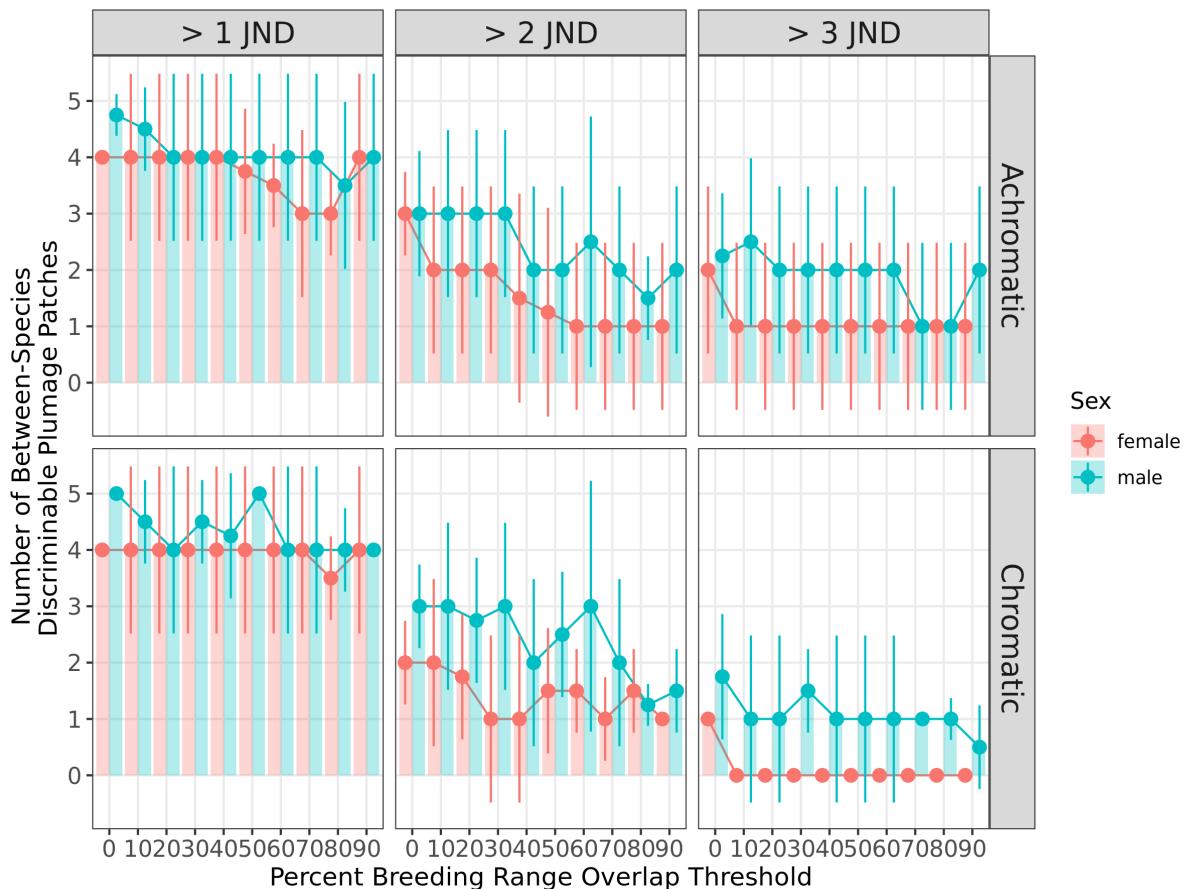


Fig S1: Median \pm median absolute deviation of number of distinguishable plumage patches by just noticeable differences (JND) thresholds of 1,2 and 3 between male and female *Turdus* thrush species in sympatry at various breeding range overlaps (percent).

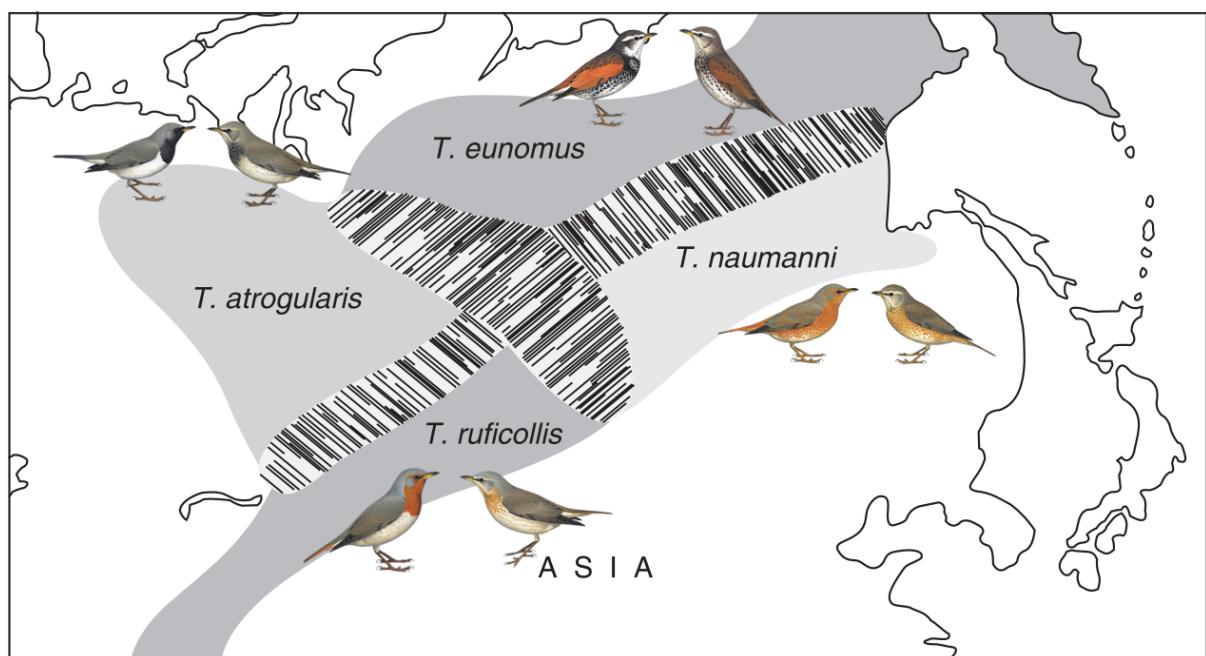


Fig S2: Four species hybrid zone in north-central Asia (*T. atrogularis*, *T. ruficollis*, *T. eunomus*, and *T. naumannii*). Map is from [1]. Illustrations © HBW Alive/Lynx Edicions.