

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

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7 Abstract

8 Keywords

dichromatism, plumage, species recognition

10 Introduction

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

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

30 plumage colour elaboration and sexual dichromatism than species living on islands with limited breeding
31 ranges [18–23].

32 Moreover, plumage sexual dichromatism likely plays a role in hybridization avoidance via reproductive
33 character displacement to facilitate species and mate recognition. For example, in European *Ficedula* fly-
34 catchers, female choice selects for divergent male plumage colouration, leading to character displacement
35 between species and populations and reduced rates of hybridization [24–26]. More broadly and across
36 taxa, greater plumage dichromatism is positively correlated with transitions from allopatry to parapatry
37 and increases in geographic range overlaps among passerine sister species pairs [27]. Plumage sexual
38 dichromatism has also been found to be positively associated with species richness among sister species
39 pairs, and dichromatism mainly increases through changes in male plumage [28], suggesting that female
40 choice and male-male competition lead to concurrent changes in male plumage and speciation events.
41 Further, plumage sexual dichromatism is positively associated with greater interspecific plumage colour
42 evolution rate and divergence in *Tyrannida* suboscines [29]. Therefore, plumage sexual dichromatism may
43 be an especially favourable trait to facilitate species and mate recognition when closely-related species
44 have sympatric breeding ranges [5,30].

45 True thrushes (genus: *Turdus*) are an exceptionally diverse genus of passerine birds consisting of about
46 ~86 species distributed across the globe (Fig. 1). Plumage sexual dimorphism and migratory behaviors
47 vary substantially between species and have evolved multiple times in thrushes across the world [31,32].
48 Interestingly, there have been several documented cases of hybridization in *Turdus* thrushes, and there
49 is a large hybrid zone between four *Turdus* species (*T. atrogularis*, *T. eunomus*, *T. naumanni*, *T. ruficollis*)
50 in north-central Asia [33], indicating that some sympatric *Turdus* species interbreed. Therefore, the true
51 thrushes are an ideal passerine clade for examining the species recognition hypothesis for plumage sexual
52 dimorphism.

53 Overall, ecological conditions that increase the time and degree of difficulty in finding a suitable con-
54 specific mate should select for phenotypic traits that reliably signal species and sex identity. Taken to-
55 gether, repeated findings across various bird lineages of greater plumage dichromatism in species that
56 are i) migratory rather than nonmigratory, ii) have shorter breeding seasons, ii) live on mainlands rather
57 than islands, iv) have larger breeding ranges, and v) breed in sympatry with closely-related species sug-
58 gests that circumstances where rapid species recognition is challenging strongly favour the evolution and
59 maintenance of prominent plumage sexual dichromatism in birds. Here, we test predictions of the species
60 recognition hypothesis for sexually-dimorphic traits. To this end, we evaluate the potential influences of
61 breeding timing, spacing, and sympatry on plumage dichromatism in the *Turdus* thrushes .

62 Methods

63 *Plumage sexual dichromatism*

64 A total of N=77 *Turdus* thrush species (approximately ~89% of all known true thrush species) were sam-
65 pled for plumage spectral reflectance using prepared bird skin specimens at the American Museum of

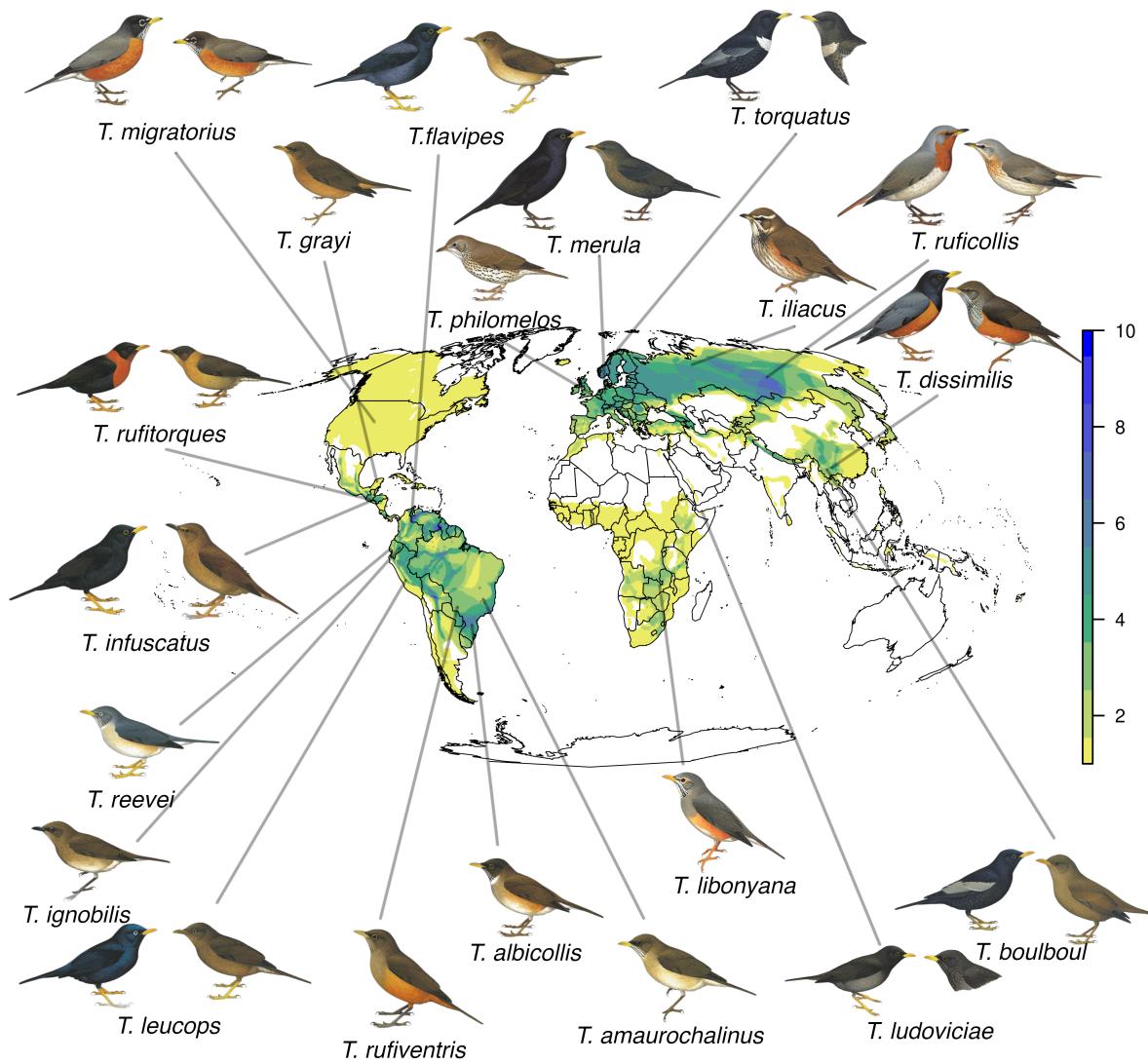


Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International. Colors indicate the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations © HBW Alive/Lynx Edicions

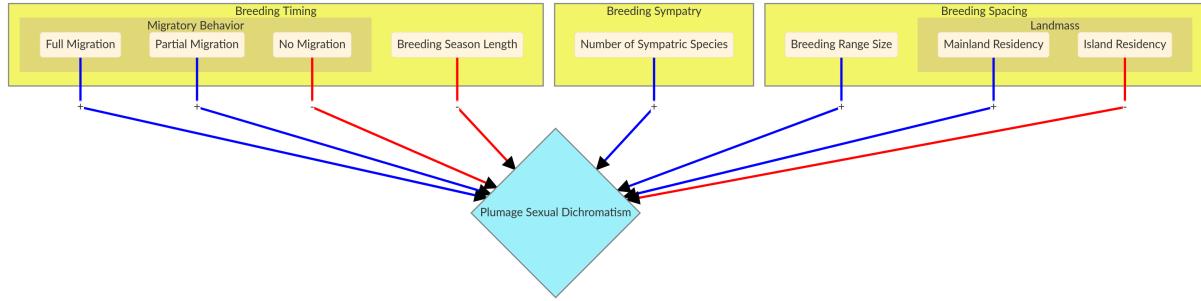


Figure 2: Hypotheses and predictions for each model. Arrow colours indicate predicted correlation, positive (blue) and negative (red).

Natural History in New York City and the Field Museum in Chicago. 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 mm^2 at a 90° angle to the surface of the feather patch. Measurements were taken using a JAZ spectrometer with a pulsed-xenon light source (Ocean Optics, Dunedin, USA) and we used a diffuse 99% reflectance white standard (Spectralon WS-1-SL, Labsphere, North Sutton NH, USA).

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

91 **Life History Data**

92 **Breeding Timing Model**

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

99 **Breeding Sympathy Model**

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

106 **Breeding Spacing Model**

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

112 **Statistical modeling**

113 We used phylogenetically-corrected Bayesian multilevel logistic regression models using the *brms* v2.13.0
114 package [44] in R v4.0.0 [38] where responses, the number of sexually-dichromatic patches >1, 2, and
115 3 chromatic and achromatic JNDs, were modelled as binomial trials (N=5 plumage patch “trials”) to test
116 for associations with breeding timing, breeding sympathy and breeding spacing. For all phylogenetically-
117 corrected models, we used the *Turdus* phylogeny from Nylander et al. (2008) [45] to create a covariance
118 matrix of species’ phylogenetic relationships. All models used a dataset of N=67 out of the *Turdus* species
119 for which all the types of data (see above) were available.

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

125 *spacing* models included \log_e transformed breeding range size (km²) and breeding landmass (mainland as
126 the reference category versus island). We also ran null models (intercept only) for all responses. All models'
127 intercepts and response standard deviations were assigned a weak prior (Student T: df = 3, location = 0,
128 scale = 10), and predictor coefficients were assigned flat priors. We ran each model for 6,000 iterations
129 across 6 chains and assessed Markov Chain Monte Carlo (MCMC) convergence using the Gelman-Rubin
130 diagnostic (Rhat) [46]. We then performed k-fold cross-validation [47] to refit each model K=16 times.
131 For each k-fold, the training dataset included a randomly selected set of $N - N \frac{1}{K}$ or N≈63 species,
132 and the testing dataset included $N \frac{1}{K}$ or N≈4 species not included in the training dataset. Finally, we
133 compared differences between the models' expected log pointwise predictive densities (ELPD) to assess
134 which model(s) best predicted the probability of having a sexually-dichromatic plumage patch. [47].

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

141 Results

142 Avian visual modeling

143 Among N=77 *Turdus* species, the following proportion have sexually monomorphic plumage (both achro-
144 matic and chromatic metrics): 1.3% (n=1 species) have no sexually-dimorphic patches > 1 JND , 44%
145 (n=34 species) have no dimorphic patches > 2 JND, and 63% (n=49 species) have no dimorphic patches
146 > 3 JND. Conversely,

147 Model comparisons

148 We obtained N ≥ 4000 effective posterior samples for each model parameter and all models' Markov
149 Chains (MCMC) successfully converged (Rhat = 1 for all models' parameters) (Supplementary Figure 3, 4).
150 All *breeding sympathy*, *breeding timing*, and *breeding spacing* models performed similarly well and substan-
151 tially better than *intercept only* models in predicting the probability of having a sexually dimorphic plumage
152 patch with achromatic JND values > 1, 2, or 3 (Table 1; all models predicting achromatic plumage patches
153 had ELPD values within 4, following the convention of Burnham and Anderson (2002)[49]). Among mod-
154 els predicting the probability of having a sexually-dichromatic plumage patch with chromatic JND values
155 >1, 2, or 3, all *breeding sympathy*, *breeding timing*, and *breeding spacing* models performed much better than
156 *intercept only* models, and *breeding sympathy* models had the top predictive performance (Table 1; *breed-*
157 *ing sympathy* models all have ELPD =0, only the *breeding spacing* models predicting dichromatic plumage
158 patches with had similar predictive performance).

159 **Achromatic plumage sexual dimorphism predictors**

160 All model predictors' effect estimates are provided as the posterior median odds-ratio (OR) and 90%
161 highest-density interval (HDI) in Table 2. Among predictors of achromatic sexually-dimorphic plumage
162 patches, only predictors included in the *breeding timing* model have predictors with probability of direction
163 (*pd*) values ≥ 0.90 (Table 2). Specifically, longer breeding season length was associated with lower odds of
164 a species having a sexually-dimorphic plumage patch with achromatic JND > 2 (breeding season length,
165 OR [90% HDI] = 0.10 [0.01, 1.1], 89.5% decrease in odds per 2.3-month increase in breeding season) and
166 JND > 3 (breeding season length, OR [90% HDI] = 0.25 [0.03, 1.5], 75% decrease in odds per 2.3-month
167 increase in breeding season). Additionally, full migratory behaviour, rather than no migratory behaviour,
168 was associated with greater odds of a species having a sexually-dimorphic plumage patch with achromatic
169 JND > 1 (full migration, OR [90% HDI] = 4.97 [0.95, 24.4]), JND > 2 (full migration, OR [90% HDI] = 66.5
170 [3.2, 1802.4]) and JND > 3 (OR [90% HDI] = 22.3 [1.6, 307.9]). Finally, both full and partial migratory
171 behaviour, rather than no migration behaviour, in conjunction with longer breeding season lengths are
172 associated with greater odds of a species having a sexually-dimorphic plumage patch with achromatic
173 JND > 1 (breeding season length x full migration, OR [90% HDI] = 4.84 [0.67, 39.6]), JND > 2 (breeding
174 season length x full migration, OR = 66.3 [0.59, 11415.7]; breeding season length x partial migration, OR
175 [90% HDI] = 20.7 [0.9, 589.1]) and JND > 3 (breeding season length x partial migration, OR [90% HDI] =
176 8.28 [0.76, 109.1]).

177 **Chromatic plumage sexual dimorphism predictors**

178 Among predictors of *breeding timing* models predicting chromatic sexually-dimorphic plumage patches,
179 longer breeding season length was associated with lower odds of a species having a plumage patch with
180 chromatic JND > 2 (OR [90% HDI] = 0.14 [0.01, 1.42], 86% reduction in odds per 2.3 month increase in
181 breeding season), and both full and partial migratory behaviour rather than no migration are associated
182 with greater odds of a species having a plumage patch JND > 1 (partial migration, OR [90% HDI] = 2.2
183 [0.94, 4.9]), JND > 2 (full migration, OR [90% HDI] = 80.51 [2.8, 3432.9]) and JND > 3 (partial migration,
184 OR [90% HDI] = 71.2 [0.32, 59062.9]; full migration, OR [90% HDI] = 234.7 [0.51, 300382.6]). For
185 *breeding spacing models*, island residency rather than mainland residency was associated with lower odds
186 of having a plumage patch > 1 chromatic JND (island, OR [90% HDI] = 0.27 [0.09, 0.89]). Finally, more
187 *Turdus* species in sympatry was associated with higher odds of a species having a chromatic plumage
188 patch with JND > 1 (number of sympatric species, OR [90% HDI] = 1.4 [1.18, 1.67], 40% increase in odds
189 per each additional sympatric species), JND > 2 (sympatric species, OR [90% HDI] = 1.59 [1.01, 2.52], 59%
190 increase in odds per each additional sympatric species), and JND > 3 (sympatric species, OR [90% HDI]
191 = 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
Achromatic					
1 JND	0 \pm 0 (-122.17 \pm 0.67)	-2.51 \pm 2.49 (-124.68 \pm 2.38)	-2.59 \pm 1.01 (-124.76 \pm 1.04)	-21.69 \pm 7.36 (-143.87 \pm 7.51)	
2 JND	0 \pm 0 (-98.94 \pm 7.56)	-1.19 \pm 3.95 (-100.13 \pm 9.22)	-0.7 \pm 1.34 (-99.64 \pm 7.92)	-52.42 \pm 12.67 (-151.36 \pm 13.4)	
3 JND	-0.04 \pm 1.4 (-85.4 \pm 8.91)	-1.7 \pm 4.41 (-87.07 \pm 10.71)	0 \pm 0 (-85.37 \pm 8.76)	-28.54 \pm 10.02 (-113.91 \pm 13.65)	
Chromatic					
1 JND	0 \pm 0 (-115.75 \pm 2.95)	-5.67 \pm 3.55 (-121.42 \pm 2.28)	-2.73 \pm 3.4 (-118.49 \pm 2.67)	-14.8 \pm 7.22 (-130.55 \pm 7.05)	
2 JND	0 \pm 0 (-88.47 \pm 8.77)	-3.8 \pm 4.46 (-92.27 \pm 10.01)	-3.32 \pm 5.29 (-91.79 \pm 10.91)	-50.53 \pm 14.49 (-139 \pm 16.77)	
3 JND	0 \pm 0 (-62.77 \pm 10.41)	-8 \pm 4.32 (-70.77 \pm 12.29)	-4.43 \pm 3.9 (-67.2 \pm 11.72)	-47.63 \pm 15.34 (-110.4 \pm 20.01)	

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

Model	Parameter	Achromatic, JND > 1	Achromatic, JND > 2	Achromatic, JND > 3	Chromatic, JND > 1	Chromatic, JND > 2	Chromatic, JND > 3
Breeding Timing							
	Intercept	0 (0, 0.54), pd = 0.98	0 (0, 0.19), pd = 0.99	0 (0, 0.19), pd = 0.99	0.41 (0.05, 2.79), pd = 0.78	0 (0, 1.73), pd = 0.95	0 (0, 1.37), pd = 0.96
	Breeding Season Length	0.1 (0.01, 1.05), pd = 0.97	0.25 (0.03, 1.49), pd = 0.91	0.25 (0.03, 1.49), pd = 0.91	0.89 (0.56, 1.4), pd = 0.66	0.14 (0.01, 1.42), pd = 0.94	0.08 (0, 9.14), pd = 0.83
	Partial Migration vs. No Migration	0.56 (0.31, 2.75), pd = 0.53	4.11 (0.3, 61.54), pd = 0.83	3.65 (0.44, 33.64), pd = 0.85	2.2 (0.24, 4.89), pd = 0.94	6.7 (0.42, 134.8), pd = 0.88	71.16 (0.32, 59062.92), pd = 0.92
	Full Migration vs. No Migration	4.37 (0.95, 24.41), pd = 0.96	66.52 (3.19, 1802.4), pd = 0.99	22.34 (1.59, 307.9), pd = 0.98	2.29 (0.69, 7.31), pd = 0.88	80.31 (2.81, 343.86), pd = 0.99	234.71 (0.51, 200382.62), pd = 0.95
	Breeding Season Length x Partial Migration	1.34 (0.48, 3.92), pd = 0.68	20.71 (0.87, 589.09), pd = 0.96	8.28 (0.76, 109.11), pd = 0.94	1.39 (0.65, 31.2), pd = 0.76	9.03 (0.44, 251.36), pd = 0.9	34.46 (0.08, 68228.71), pd = 0.85
	Breeding Season Length x Full Migration	4.34 (0.67, 39.63), pd = 0.9	66.3 (0.59, 11415.7), pd = 0.93	16.41 (0.27, 824.69), pd = 0.89	1.68 (0.31, 8.33), pd = 0.7	160.6 (0.84, 67791.13), pd = 0.95	433.67 (0.01, 371945.69), pd = 0.85
	Phylogenetic Signal λ , Median (90% Credible Interval)	0.29 (0.16, 0.43)	0.72 (0.56, 0.86)	0.61 (0.42, 0.8)	0.17 (0.08, 0.28)	0.74 (0.57, 0.88)	0.89 (0.77, 0.97)
Breeding Spacing							
	Intercept	0 (0, 2.44), pd = 0.95	0 (0, 0.14), pd = 0.98	0 (0, 0.14), pd = 0.98	0.51 (0.03, 9.7), pd = 0.65	0 (0, 7.63), pd = 0.92	0 (0, 8.19), pd = 0.91
	Island vs. Mainland	1.08 (0.25, 4.79), pd = 0.54	0.53 (0.01, 17.83), pd = 0.61	0.92 (0.05, 19.32), pd = 0.52	0.27 (0.09, 0.89), pd = 0.97	0.03 (0, 3.99), pd = 0.89	0.04 (0, 67.59), pd = 0.77
	Breeding Range Size	1.08 (0.88, 1.32), pd = 0.75	1.23 (0.76, 2.01), pd = 0.77	1.3 (0.87, 1.93), pd = 0.87	1.02 (0.87, 1.19), pd = 0.58	1.24 (0.75, 2.05), pd = 0.77	1.26 (0.54, 2.99), pd = 0.69
	Phylogenetic Signal λ , Median (90% Credible Interval)	0.27 (0.15, 0.41)	0.71 (0.56, 0.85)	0.6 (0.42, 0.77)	0.15 (0.07, 0.25)	0.72 (0.55, 0.86)	0.85 (0.71, 0.95)
Breeding Sympatry							
	Intercept	0.41 (0.03, 5.83), pd = 0.72	0 (0, 0.98), pd = 0.95	0 (0, 0.34), pd = 0.98	0.25 (0.04, 1.35), pd = 0.91	0 (0, 1.12), pd = 0.95	0 (0, 0.29), pd = 0.98
	Number of Sympatric Species ($\geq 30\%$ Breeding Range Overlap)	1.03 (0.84, 1.27), pd = 0.61	1.15 (0.74, 1.75), pd = 0.71	1.13 (0.76, 1.63), pd = 0.71	1.4 (1.18, 1.67), pd = 0.99	1.59 (1.01, 2.52), pd = 0.96	2.11 (1.03, 4.46), pd = 0.97
	Phylogenetic Signal λ , Median (90% Credible Interval)	0.26 (0.14, 0.39)	0.7 (0.54, 0.83)	0.59 (0.41, 0.77)	0.13 (0.06, 0.23)	0.69 (0.52, 0.83)	0.82 (0.67, 0.94)

192 **Discussion**

193 Our results yield observational evidence in support the species recognition hypothesis for plumage sexual
194 dimorphism in true thrushes. We found that the odds of plumage sexual dimorphism are much greater
195 for *Turdus* thrush species that have full or partial migration rather than no migration, have relatively short
196 breeding seasons, and are in sympatry with many other congeneric species (Table 1,2). Further, we deter-
197 mined that sympatric species have distinguishable plumage coloration differences from one when mea-
198 suring plumage appearance from the avian visual perspective (Supplementary Figure 1). Our results align
199 with broader comparative studies of plumage sexual dimorphism where strong associations between mi-
200 gratory behavior [10] and sympatry [27] were found among many species of different passerine families.

201 Our study does not consider differences in song, an important behavioral trait also used in avian mate
202 choice and recognition [50,51]. However, because plumage coloration is more static than song, it is likely
203 a more reliable signal for species recognition under many circumstances, especially in breeding range
204 locations where closely-related heterospecifics are in high sympatry [52–54].

205 Other studies have found that closely-related species tend to have more similar plumage appearance
206 than expected if plumage coloration had evolved to facilitate species recognition via reproductive charac-
207 ter displacement [55,56], and attribute the lack of major plumage color divergence in sympatric species
208 to constraints of a shared light environment [57]. Greater similarity in appearance between highly sym-
209 patric closely-related heterospecifics versus allopatric heterospecifics is expected assuming sympatric
210 species share similar light environment constraints and natural selection pressures (e.g., predators, para-
211 sites, and weather). Despite greater similarity in plumage appearance in comparison to allopatric species,
212 closely-related sympatric species can still have substantially different achromatic or chromatic plumage
213 appearances when measuring plumage coloration differences from the avian visual perspective as we
214 have in our analyses.

215 accounting for avian vision and differences in achromatic and chromatic differences in plumage ap-
216 pearance

217 **Conclusions**

218 **Acknowledgements**

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