

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

Alec B. Luro^{1*}, Mark E. Hauber¹

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

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

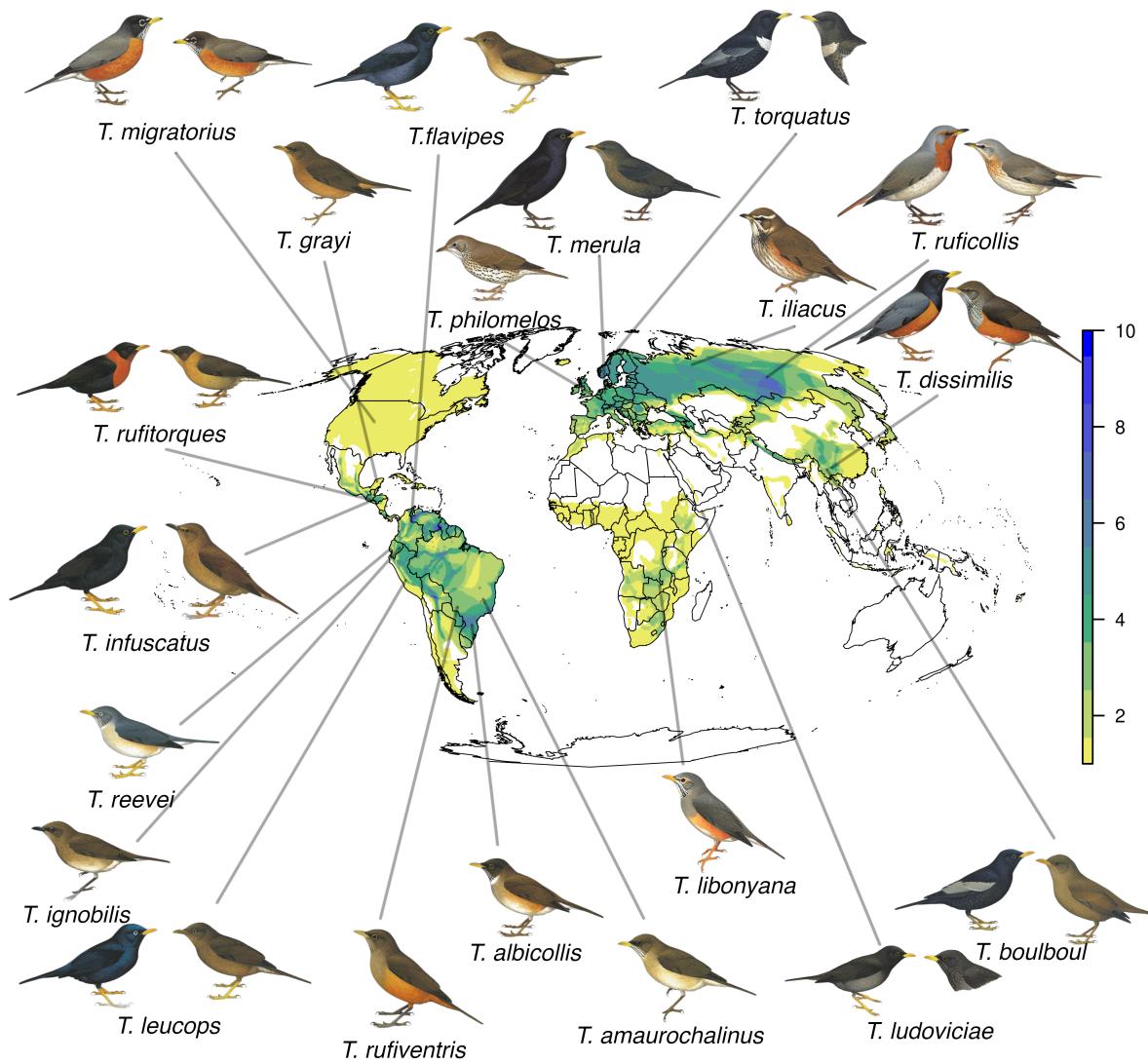


Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International. Colors indicate the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations © HBW Alive/Lynx Edicions

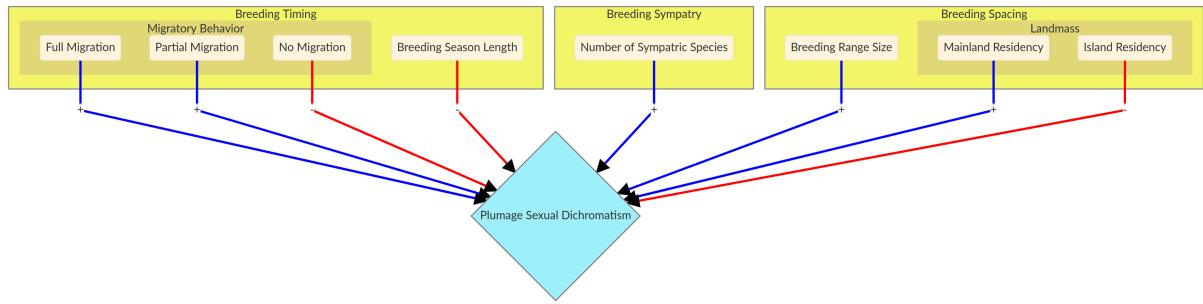


Figure 2: Hypotheses and predictions for each model. Arrow colours indicate predicted correlation, positive (blue) and negative (red).

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%).

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

154 Model comparisons

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

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

166 **Achromatic plumage sexual dimorphism predictors**

167 All model predictors' effect estimates are provided as the posterior median odds-ratio (OR) and 90%
168 highest-density interval (HDI) in Table 2. Among predictors of achromatic sexually-dimorphic plumage
169 patches, only predictors included in the *breeding timing* model have predictors with probability of direction
170 (*pd*) values ≥ 0.90 (Table 2). Specifically, longer breeding season length was associated with lower odds of
171 a species having a sexually-dimorphic plumage patch with achromatic JND > 2 (breeding season length,
172 OR [90% HDI] = 0.10 [0.01, 1.1], 89.5% decrease in odds per 2.3-month increase in breeding season) and
173 JND > 3 (breeding season length, OR [90% HDI] = 0.25 [0.03, 1.5], 75% decrease in odds per 2.3-month
174 increase in breeding season). Additionally, full migratory behaviour, rather than no migratory behaviour,
175 was associated with greater odds of a species having a sexually-dimorphic plumage patch with achromatic
176 JND > 1 (full migration, OR [90% HDI] = 4.97 [0.95, 24.4]), JND > 2 (full migration, OR [90% HDI] = 66.5
177 [3.2, 1802.4]) and JND > 3 (OR [90% HDI] = 22.3 [1.6, 307.9]). Finally, both full and partial migratory
178 behaviour, rather than no migration behaviour, in conjunction with longer breeding season lengths are
179 associated with greater odds of a species having a sexually-dimorphic plumage patch with achromatic
180 JND > 1 (breeding season length x full migration, OR [90% HDI] = 4.84 [0.67, 39.6]), JND > 2 (breeding
181 season length x full migration, OR = 66.3 [0.59, 11415.7]; breeding season length x partial migration, OR
182 [90% HDI] = 20.7 [0.9, 589.1]) and JND > 3 (breeding season length x partial migration, OR [90% HDI] =
183 8.28 [0.76, 109.1]).

184 **Chromatic plumage sexual dimorphism predictors**

185 Among predictors of *breeding timing* models predicting chromatic sexually-dimorphic plumage patches,
186 longer breeding season length was associated with lower odds of a species having a plumage patch with
187 chromatic JND > 2 (OR [90% HDI] = 0.14 [0.01, 1.42], 86% reduction in odds per 2.3 month increase in
188 breeding season), and both full and partial migratory behaviour rather than no migration are associated
189 with greater odds of a species having a plumage patch JND > 1 (partial migration, OR [90% HDI] = 2.2
190 [0.94, 4.9]), JND > 2 (full migration, OR [90% HDI] = 80.51 [2.8, 3432.9]) and JND > 3 (partial migration,
191 OR [90% HDI] = 71.2 [0.32, 59062.9]; full migration, OR [90% HDI] = 234.7 [0.51, 300382.6]). For
192 *breeding spacing models*, island residency rather than mainland residency was associated with lower odds
193 of having a plumage patch > 1 chromatic JND (island, OR [90% HDI] = 0.27 [0.09, 0.89]). Finally, more
194 *Turdus* species in sympatry was associated with higher odds of a species having a chromatic plumage
195 patch with JND > 1 (number of sympatric species, OR [90% HDI] = 1.4 [1.18, 1.67], 40% increase in odds

196 per each additional sympatric species), JND > 2 (sympatric species, OR [90% HDI] = 1.59 [1.01, 2.52], 59%
 197 increase in odds per each additional sympatric species), and JND > 3 (sympatric species, OR [90% HDI]
 198 = 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	0.76 (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)

199 **Discussion**

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

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

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

222 accounting for avian vision and differences in achromatic and chromatic differences in plumage ap-
223 pearance

224 **Conclusions**

225 **Acknowledgements**

226 **References**

- 227 1. Andersson M. 1994 Species Recognition, Sexual Selection, and Speciation. In *Sexual Selection*, pp.
228 207–226. Princeton University Press. (doi:[10.2307/j.ctvs32s1x.13](https://doi.org/10.2307/j.ctvs32s1x.13))
- 229 2. Grönig J, Hochkirch A. 2008 Reproductive Interference Between Animal Species. *The Quarterly
230 Review of Biology* **83**, 257–282. (doi:[10.1086/590510](https://doi.org/10.1086/590510))
- 231 3. Pfennig KS, Hurlbert AH. 2012 Heterospecific interactions and the proliferation of sexually dimor-
phic traits. *Current Zoology* **58**, 453–462. (doi:[10.1093/czoolo/58.3.453](https://doi.org/10.1093/czoolo/58.3.453))

- 232
- 233 4. West-Eberhard MJ. 1983 Sexual Selection, Social Competition, and Speciation. *The Quarterly Re-*
234 *view of Biology* **58**, 155–183. (doi:[10.1086/413215](https://doi.org/10.1086/413215))
- 235 5. Martin PR, Montgomerie R, Lougheed SC. 2015 Color Patterns of Closely Related Bird Species Are
236 More Divergent at Intermediate Levels of Breeding-Range Sympatry. *The American Naturalist* **185**,
237 443–451. (doi:[10.1086/680206](https://doi.org/10.1086/680206))
- 238 6. Bitton P-P, Doucet SM. 2016 Sympatric black-headed and elegant trogons focus on dif-
239 ferent plumage characteristics for species recognition. *Animal Behaviour* **116**, 213–221.
240 (doi:[10.1016/j.anbehav.2016.03.035](https://doi.org/10.1016/j.anbehav.2016.03.035))
- 241 7. Martin TE, Badyaev AV. 1996 Sexual Dichromatism in Birds: Importance of Nest Predation and
242 Nest Location for Females Versus Males. *Evolution* **50**, 2454–2460. (doi:[10.2307/2410712](https://doi.org/10.2307/2410712))
- 243 8. Burns KJ. 1998 A Phylogenetic Perspective on the Evolution of Sexual Dichromatism in Tan-
244 agers (thraupidae): The Role of Female Versus Male Plumage. *Evolution* **52**, 1219–1224.
245 (doi:[10.1111/j.1558-5646.1998.tb01849.x](https://doi.org/10.1111/j.1558-5646.1998.tb01849.x))
- 246 9. Badyaev AV, Hill GE. 2003 Avian Sexual Dichromatism in Relation to Phylogeny
247 and Ecology. *Annual Review of Ecology, Evolution, and Systematics* **34**, 27–49.
248 (doi:[10.1146/annurev.ecolsys.34.011802.132441](https://doi.org/10.1146/annurev.ecolsys.34.011802.132441))
- 249 10. Dale J, Dey C, Delhey K, Kempenaers B, Valcu M. 2015 The effects of life-history and social selec-
250 tion on male and female plumage coloration. *Nature* **000**, 1–17. (doi:[10.1038/nature15509](https://doi.org/10.1038/nature15509))
- 251 11. Dunn PO, Armenta JK, Whittingham LA. 2015 Natural and sexual selection act on different axes
252 of variation in avian plumage color. *Science Advances* **1**, e1400155. (doi:[10.1126/sciadv.1400155](https://doi.org/10.1126/sciadv.1400155))
- 253 12. Hawkins GL, Hill GE, Mercadante A. 2012 Delayed plumage maturation and delayed reproductive
254 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))
- 255 13. Hamilton TH. 1961 On the Functions and Causes of Sexual Dimorphism in Breeding Plumage
256 Characters of North American Species of Warblers and Orioles. *The American Naturalist* **45**, 64–
257 73. (doi:[10.1086/282167](https://doi.org/10.1086/282167))
- 258 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))
- 259 15. Friedman NR, Hofmann CM, Kondo B, Omland KE. 2009 Correlated evolution of migra-
260 tion and sexual dichromatism in the new world orioles (*Icterus*). *Evolution* **63**, 3269–3274.
261 (doi:[10.1111/j.1558-5646.2009.00792.x](https://doi.org/10.1111/j.1558-5646.2009.00792.x))
- 262 16. Simpson RK, Johnson MA, Murphy TG. 2015 Migration and the evolution of sexual dichromatism:
263 Evolutionary loss of female coloration with migration among wood-warblers. *Proceedings of the
264 Royal Society B: Biological Sciences* **282**, 20150375. (doi:[10.1098/rspb.2015.0375](https://doi.org/10.1098/rspb.2015.0375))

- 259 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))
- 260
- 261 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))
- 262
- 263 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))
- 264
- 265 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))
- 266
- 267 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))
- 268
- 269 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))
- 270
- 271 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))
- 272
- 273 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))
- 274
- 275 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))
- 276
- 277 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))
- 278
- 279 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))
- 280
- 281 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))
- 282
- 283 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))
- 284

- 285 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))
- 286
- 287 31. Clement P, Hathway R. 2000 *Thrushes*. London: A&C Black Publishers Ltd.
- 288
- 289 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))
- 290
- 291 33. McCarthy EM. 2006 *Handbook of avian hybrids of the world*. Oxford ; New York: Oxford University
Press.
- 292
- 293 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.
- 294
- 295 35. Vorobyev M, Osorio D. 1998 Receptor noise as a determinant of colour thresholds. *Proceedings.
Biological sciences / The Royal Society* **265**, 351–8. (doi:[10.1098/rspb.1998.0302](https://doi.org/10.1098/rspb.1998.0302))
- 296
- 297 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))
- 298
- 299 37. Maia R, Gruson H, Endler JA, White TE. 2019 Pavo 2: New tools for the spectral and spatial analysis
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))
- 300
- 301 38. R Core Team. 2020 R: A Language and Environment for Statistical Computing. Vienna, Austria: R
Foundation for Statistical Computing.
- 302
- 303 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))
- 304
- 305 40. Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall
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))
- 306
- 307 41. del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E. 2017 *Handbook of the birds of the world
alive*.
- 308
- 309 42. BirdLife International and Handbook of the Birds of the World. 2018 *Bird species distribution maps
of the world. Version 2018.1*.
- 310
- 311 43. Vilela B, Villalobos F. 2015 letsR: A new R package for data handling and analysis in macroecology.
Methods in Ecology and Evolution **6**, 1229–1234. (doi:[10.1111/2041-210X.12401](https://doi.org/10.1111/2041-210X.12401))
- 312
- 313 44. Bürkner PC. 2017 Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statis-
tical Software* **80**, 1–28. (doi:[10.18637/jss.v080.i01](https://doi.org/10.18637/jss.v080.i01))
- 314

- 315 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).
Systematic Biology **57**, 257–268. (doi:[10.1080/10635150802044003](https://doi.org/10.1080/10635150802044003))
- 316
- 317 46. Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. 2013 *Bayesian data analysis, third*
edition. Third. Boca Raton, FL: CRC Press. (doi:[10.1201/b16018](https://doi.org/10.1201/b16018))
- 318
- 319 47. Vehtari A, Gelman A, Gabry J. 2017 Practical Bayesian model evaluation using leave-one-out cross-
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))
- 320
- 321 48. Makowski D, Ben-Shachar MS, Chen SHA, Lüdecke D. 2019 Indices of Effect Existence and Signif-
icance in the Bayesian Framework. *Frontiers in Psychology* **10**. (doi:[10.3389/fpsyg.2019.02767](https://doi.org/10.3389/fpsyg.2019.02767))
- 322
- 323 49. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: A practical information-
theoretic approach*. 2nd ed. New York: Springer.
- 324
- 325 50. Qvarnström A, Haavie J, Sæther SA, Eriksson D, Pärt T. 2006 Song similarity predicts hy-
bridization in flycatchers. *Journal of Evolutionary Biology* **19**, 1202–1209. (doi:[10.1111/j.1420-9101.2006.01140.x](https://doi.org/10.1111/j.1420-9101.2006.01140.x))
- 326
- 327 51. Freeman BG, Montgomery GA. 2017 Using song playback experiments to measure species recogni-
tion between geographically isolated populations: A comparison with acoustic trait analyses. *The
Auk* **134**, 857–870. (doi:[10.1642/AUK-17-63.1](https://doi.org/10.1642/AUK-17-63.1))
- 328
- 329 52. Emlen ST, Rising JD, Thompson WL. 1975 A BEHAVIORAL AND MORPHOLOGICAL STUDY OF
SYMPATRY IN THE INDIGO AND LAZULI BUNTINGS OF THE GREAT PLAINS. *THE WILSON BUL-
LETIN* **87**, 36.
- 330
- 331 53. Baker MC, Baker AEM. 1990 Reproductive Behavior of Female Buntings: Isolating Mechanisms in
a Hybridizing Pair of Species. *Evolution* **44**, 332–338. (doi:[10.1111/j.1558-5646.1990.tb05202.x](https://doi.org/10.1111/j.1558-5646.1990.tb05202.x))
- 332
- 333 54. Uy JAC, Moyle RG, Filardi CE, Chevron ZA. 2009 Difference in plumage color used in species recog-
nition between incipient species is linked to a single amino acid substitution in the melanocortin-1
receptor. *American Naturalist* **174**, 244–254. (doi:[10.1086/600084](https://doi.org/10.1086/600084))
- 334
- 335 55. Simpson RK, Mistakidis AF, Doucet SM. 2020 Natural and sexual selection shape the evolution of
colour and conspicuousness in North American wood-warblers (Parulidae). *Biological Journal of the
Linnean Society* **130**, 89–100. (doi:[10.1093/biolinnean/blaa015](https://doi.org/10.1093/biolinnean/blaa015))
- 336
- 337 56. 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))
- 338
- 339 57. 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))
- 340