

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

4 Alec B. Luro^{1*}, Mark E. Hauber¹

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

7 **Abstract**

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

19 **Keywords**

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

21 **Introduction**

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

30 closely-related species. Conditions likely to favour traits signaling individuals' species and breeding status
31 include high sympatry with many closely-related species, limited time to find a compatible breeding mates,
32 and low rates of encounter with potential breeding mates [1].

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

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

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

65 Overall, ecological conditions that increase the time and degree of difficulty in finding a suitable con-
66 specific mate should select for phenotypic traits that reliably signal species and sex identity. Across
67 various bird lineages, greater plumage dichromatism is present in species that are i) migratory rather than
68 nonmigratory, ii) have shorter breeding seasons, iii) live on mainlands rather than islands, iv) have larger

69 breeding ranges (distributions), and v) breed in sympatry with more closely-related species. These pat-
 70 terns suggest that circumstances where rapid species recognition is challenging strongly favour the evolu-
 71 tion and maintenance of prominent plumage sexual dichromatism in birds. Here, we test these predictions
 72 of the species recognition hypothesis for sexually-dimorphic avian plumage by evaluating the potential
 73 influences of breeding timing, spacing, and sympatry on plumage dichromatism in the *Turdus* thrushes.

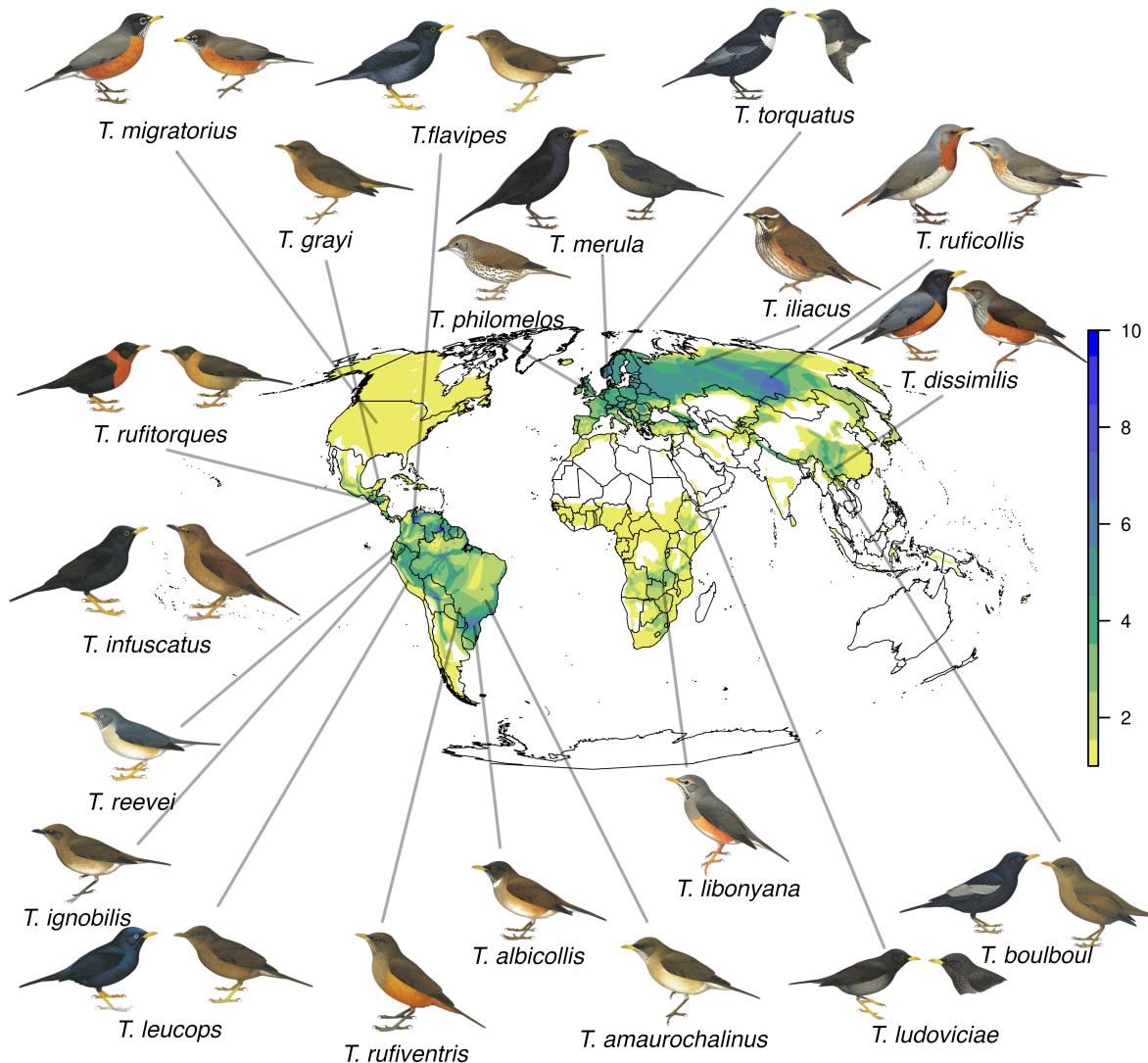


Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International. Colors indicate the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations © HBW Alive/Lynx Edicions

74 Methods

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

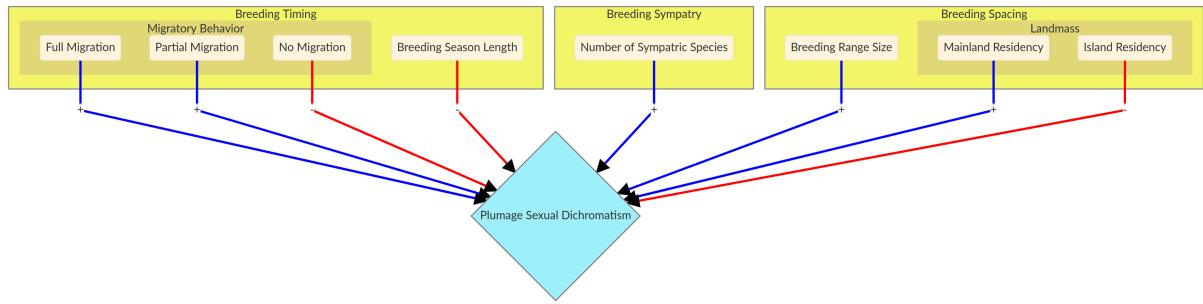


Figure 2: Hypotheses and predictions for each model. Arrow colours indicate predicted correlation, positive (blue) and negative (red)

76 **Plumage sexual dichromatism**

77 A total of N=77 *Turdus* thrush species (approximately ~89% of all known true thrush species) were sam-
 78 pled for plumage spectral reflectance using prepared bird skin specimens at the American Museum of
 79 Natural History in New York City and the Field Museum in Chicago. Reflectance measurements spanning
 80 300-700nm were taken in triplicate from the belly, breast, throat, crown, and mantle plumage patches
 81 [34] of each individual. N=3 male and N=3 female individuals were measured for most species (excep-
 82 tions: *T. lawrencii*, N=2 males and N=2 females; *T. swalesi*, N=1 male and N=1 female). Reflectance spectra
 83 were measured using a 400 µm fiber optic reflection probe fitted with a rubber stopper to maintain a con-
 84 sistent measuring distance of 3 mm and area of 2 mm² at a 90° angle to the surface of the feather patch.
 85 Measurements were taken using a JAZ spectrometer with a pulsed-xenon light source (Ocean Optics,
 86 Dunedin, USA) and we used a diffuse 99% reflectance white standard (Spectralon WS-1-SL, Labsphere,
 87 North Sutton NH, USA).

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

104 **Life History Data**

105 **Breeding Timing Model**

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

112 **Breeding Sympatry Model**

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

119 **Breeding Spacing Model**

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

125 **Statistical modeling**

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

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

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

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

Results

Avian visual modeling

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

Model comparisons

Breeding sympathy, breeding timing, and breeding spacing performed considerably better than *intercept-only* (null models) in predicting the probability of a species having a sexually-dimorphic plumage patch. We obtained N ≥ 4000 effective posterior samples for each model parameter and all models' Markov Chains (MCMC) successfully converged (Rhat = 1 for all models' parameters) (Supplementary Figure 3, 4). All *breeding sympathy, breeding timing, and breeding spacing* models performed similarly well and substantially

better than *intercept only* models in predicting the probability of having a sexually-dimorphic plumage patch with achromatic JND values > 1, 2, or 3 (Table 1; all models predicting achromatic plumage patches had ELPD values within 4, following the convention of [49]). Among models predicting the probability of having a sexually-dichromatic plumage patch with chromatic JND values >1, 2, or 3, all *breeding sympathy*, *breeding timing*, and *breeding spacing* models performed much better than *intercept only* models, and *breeding sympathy* models had the top predictive performance (Table 1; *breeding sympathy* models all have ELPD =0, only the *breeding spacing* models predicting dichromatic plumage patches had similar predictive performance).

Achromatic plumage sexual dimorphism predictors

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

Chromatic plumage sexual dimorphism predictors

Migratory behaviour, shorter breeding season lengths, and a high number of sympatric *Turdus* species were strongly associated with greater odds of a species having chromatic plumage sexual dimorphism. Among predictors of *breeding timing* models predicting chromatic sexually-dimorphic plumage patches, longer breeding season length was associated with lower odds of a species having a plumage patch with chromatic JND > 2 (OR [90% HDI] = 0.14 [0.01, 1.42], 86% reduction in odds per 2.3 month increase in breeding season). Both full and partial migratory behaviour rather than no migration are associated with greater odds of a species having a plumage patch JND > 1 (partial migration, OR [90% HDI] = 2.2 [0.94, 4.9]), JND > 2 (full migration, OR [90% HDI] = 80.51 [2.8, 3432.9]) and JND > 3 (partial migration,

209 OR [90% HDI] = 71.2 [0.32, 59062.9]; full migration, OR [90% HDI] = 234.7 [0.51, 300382.6]). For
 210 *breeding spacing models*, island residency rather than mainland residency was associated with lower odds
 211 of having a plumage patch > 1 chromatic JND (island, OR [90% HDI] = 0.27 [0.09, 0.89]). Finally, more
 212 *Turdus* species in sympatry was associated with higher odds of a species having a sexually-dimorphic
 213 chromatic plumage patch with JND > 1 (number of sympatric species, OR [90% HDI] = 1.4 [1.18, 1.67],
 214 40% increase in odds per each additional sympatric species), JND > 2 (sympatric species, OR [90% HDI]
 215 = 1.59 [1.01, 2.52], 59% increase in odds per each additional sympatric species), and JND > 3 (sympatric
 216 species, OR [90% HDI] = 2.11 [1.03, 4.46], 111% increase in odds per each additional sympatric species).

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

Plumage Metric	JND Threshold	Model			
		Breeding Sympatry	Breeding Timing	Breeding Spacing	Intercept Only
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)

217 **Discussion**

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

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

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

254 **Conclusions**

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

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

⁴ Alec B. Luro^{1*}, Mark E. Hauber¹

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

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%)

¹ Statistics presented: n (%)

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
⁹ 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).

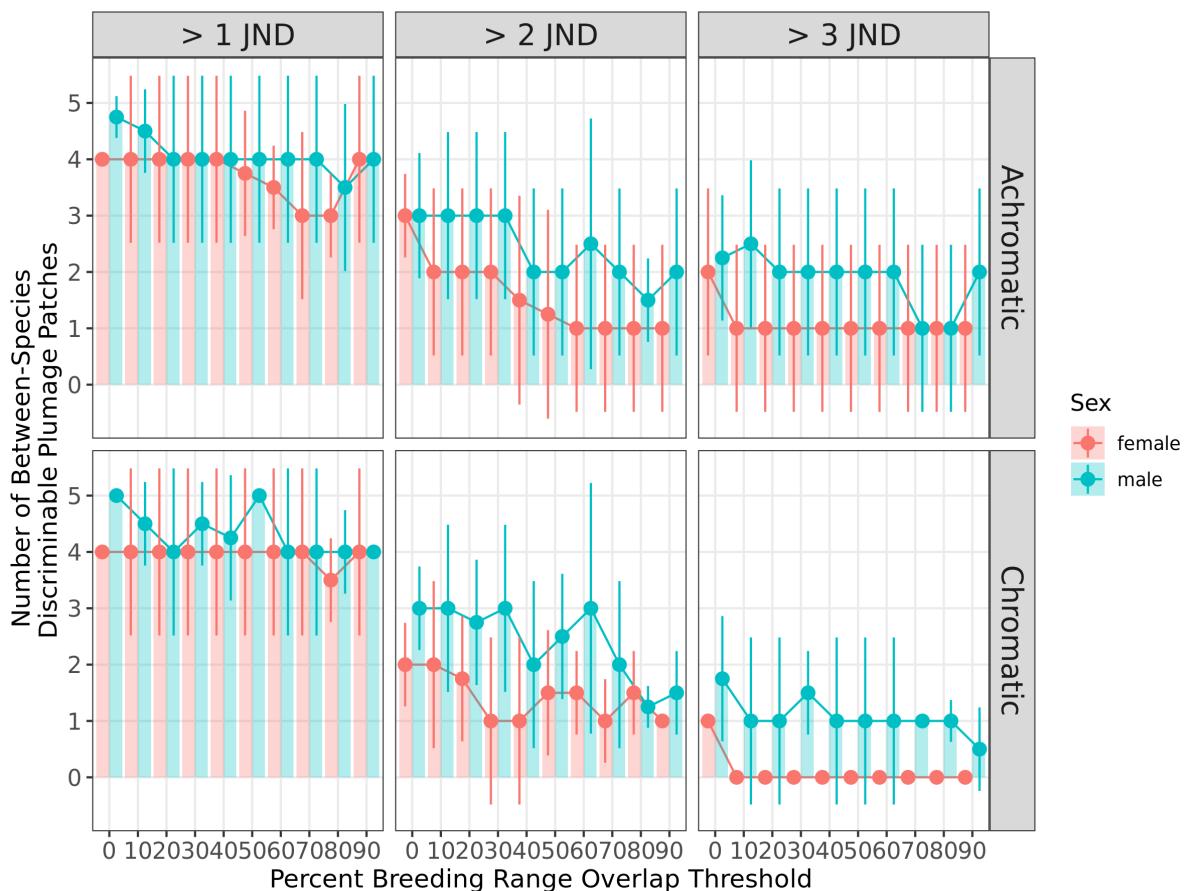


Fig S1: Median \pm median absolute deviation of number of distinguishable plumage patches by just noticeable differences (JND) thresholds of 1,2 and 3 between male and female *Turdus* thrush species in sympatry at various breeding range overlaps (percent).

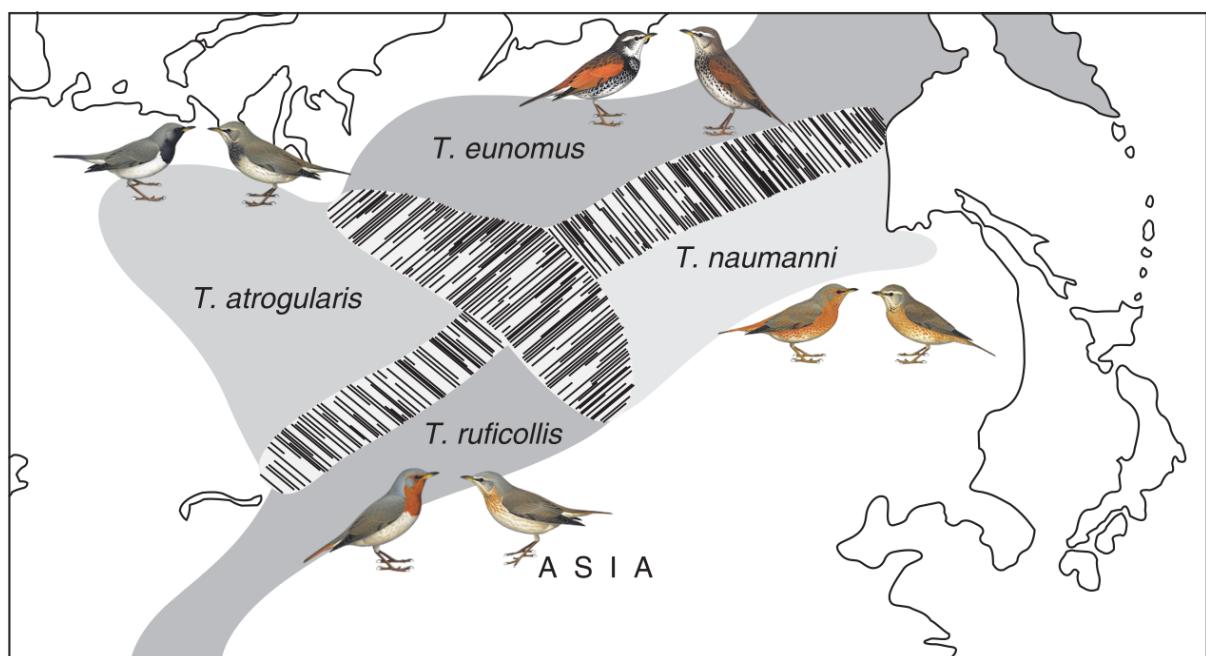


Fig S2: Four species hybrid zone in north-central Asia (*T. atrogularis*, *T. ruficollis*, *T. eunomus*, and *T. naumannii*). Map is from [1]. Illustrations © HBW Alive/Lynx Edicions.