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

Alec B. Luro[1]*, Mark E. Hauber[1]

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

Abstract

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

Keywords

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

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 and speed of mate recognition by reducing the effort, error, and time involved when searching for compatible mates and lessen the likelihood of mating with heterospecifics [3]. 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 mate recognition should be more likely to arise and be maintained under conditions that increase both the difficulty of finding a compatible mate

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

In birds, plumage colour is a highly conspicuous trait signaling species and (often) sex identity [5,6]. Plumage sexual dichromatism, or the distinct set of differences in the appearance of male and female feather colours and patterns, is common in birds and is usually attributed to different natural and sexual selection pressures on males and females [7–11]. Plumage sexual dichromatism results in a visibly perceivable trait useful for recognizing an individual's species, sex, and (sometimes) age (e.g., in species with sex-specific delayed plumage maturation, see [12]), reducing the time and effort necessary to identify a suitable mate [13,14]. Evidence in favour of this recognition hypothesis for sexual dichromatism includes a positive association of greater plumage sexual dichromatism with migratory behaviour and shorter breeding seasons [9]. Additional support for the recognition hypothesis includes a consistent pattern of greater plumage sexual dichromatism and plumage colour elaboration in avian species that reside on mainland continents and have large geographic ranges in comparison to species that do not migrate, reside on islands, and have limited breeding ranges [10,15–23].

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

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

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

various bird lineages, greater plumage dichromatism is present in species that are i) migratory rather than nonmigratory, ii) have shorter breeding seasons, iii) live on mainlands rather than islands, iv) have larger breeding ranges (distributions), and v) breed in sympatry with more closely-related species. These patterns suggest that ecological circumstances where rapid and accurate mate recognition is challenging strongly favour the evolution and maintenance of prominent plumage sexual dichromatism in birds. Here, we test these predictions of the recognition hypothesis for sexually-dimorphic avian plumage by evaluating the potential influences of breeding timing, spacing, and sympatry on plumage dichromatism in *Turdus* thrushes (Fig. 2).

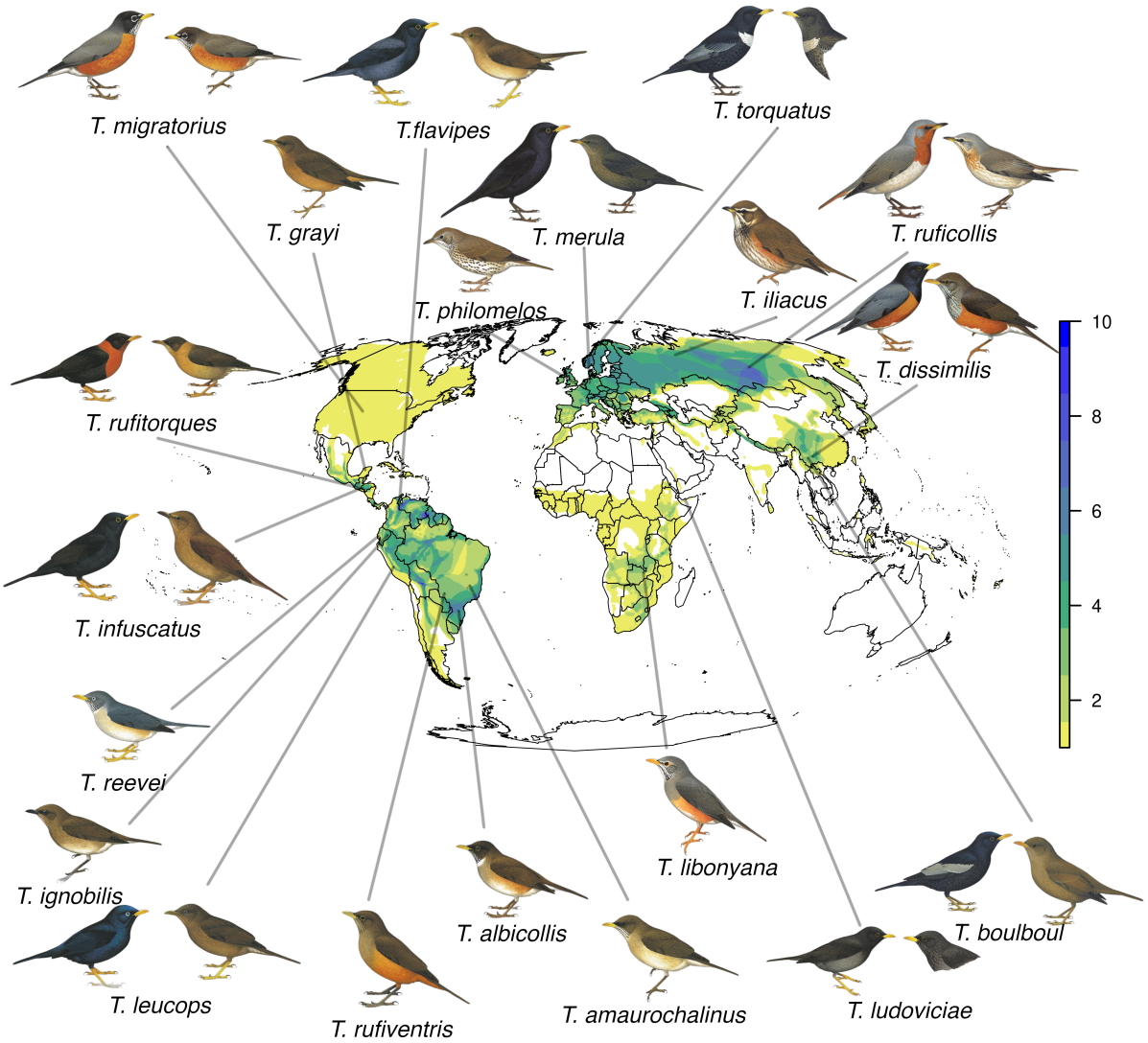

Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International, with representative species' males and females shown for species with sexually dimorphic plumage. The color scale indicates the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations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

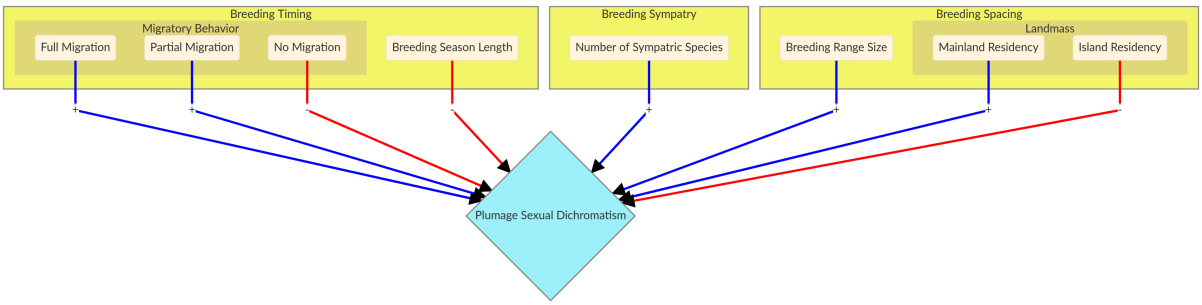

Figure 2: Hypotheses and predictions for each model (large yellow boxes). Arrow colours indicate predicted correlation, positive (blue) and negative (red)

Methods

Initial pre-registration of the study's methods and analyses are available on Open Science Framework [34].

Plumage sexual dichromatism

A total of N=77 *Turdus* thrush species (approximately ~89% of all known true thrush species) were sampled for plumage spectral reflectance using prepared bird skin specimens at the American Museum of Natural History in New York City and the Field Museum in Chicago, USA. Reflectance measurements spanning 300-700nm were taken in triplicate from the belly, breast, throat, crown, and mantle plumage patches [35] of each individual. N=3 male and N=3 female individuals were measured for most species (exceptions: *T. lawrencii*, N=2 males and N=2 females; *T. swalesi*, N=1 male and N=1 female). Reflectance spectra were measured using a 400 µm fiber optic reflection probe fitted with a rubber stopper to maintain a consistent measuring distance of 3 mm and area of 2 mm2 at a 90° angle to the surface of the feather patch. Measurements were taken using a JAZ spectrometer with a pulsed-xenon light source (Ocean Optics, Dunedin, USA) and we used a diffuse 99% reflectance white standard (Spectralon WS-1-SL, Labsphere, North Sutton NH, USA).

We applied a receptor-noise limited visual model [36] of the European Blackbird (*T. merula*) visual system [37] in the *pavo* [38] package in R v4.0.0 [39] to calculate avian-perceived chromatic and achromatic visual contrast (in units of "Just-Noticeable Differences",or JNDs) of male vs. female plumage patches for all sampled *Turdus* species. Chromatic and achromatic JNDs were calculated for male-female pairs within each species (i.e., N=9 JND values calculated per patch for each species where N=3 males and N=3 females sampled), and then JND values were averaged for each species' respective plumage patches. Under ideal laboratory conditions, 1 JND is generally considered to be the discriminable threshold past which an observer is predicted to be able to perceive the two colours as different. However, natural light environments vary both spatially and temporally [40], 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 [41]. Additionally, we modeled the number of divergent plumage patches (at the three different JND thresholds listed above) within sexes and between different sympatric species under different levels of breeding range overlap (10% increments between 0-90%).

Life History Data

Breeding Timing Model

We collected data on migration behaviour and breeding season length from *Thrushes* [31] and the *Handbook of the Birds of the World* [42]. We assigned three different kinds of migratory behaviour: 1) *full migration* when a species description clearly stated that a species "migrates", 2) *partial migration* when a species was described to have "altitudinal migration", "latitudinal migration" or "movement during non-breeding season", or 3) *sedentary* when a species was described as "resident" or "sedentary". Breeding season length was defined as the number of months the species breeds each year.

Breeding Sympatry Model

Species' breeding ranges were acquired from *BirdLife International* [43]. We calculated congener breeding range overlaps (as percentages) using the *letsR* package in R [44]. We then calculated the number of sympatric species as the number of congeners with breeding ranges that overlap >30% with the focal species' breeding range [27]. Comparisons of the number of sexually-dimorphic plumage patches vs. the number of sympatric species among different breeding range overlap thresholds are provided in Supplementary Figure 1.

Breeding Spacing Model

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

Statistical modeling

We used phylogenetically-corrected Bayesian multilevel logistic regression models using the *brms* v2.13.0 package [45] in R v4.0.0 [39]. We modeled plumage sexual dichromatism responses as the number of sexually-dichromatic patches > 1, 2, or 3 chromatic and achromatic JNDs. Plumage dichromatism responses were modeled as binomial trials (N=5 plumage patch "trials") to test for associations with breeding timing, breeding sympatry and breeding spacing. For all phylogenetically-corrected models, we used the *Turdus* molecular phylogeny from Nylander et al. (2008) [46] to create a covariance matrix of species'

phylogenetic relationships. All models used a dataset of N=67 out of the *Turdus* species for which all the types of data (see above) were available.

Our *breeding timing* models included the following predictors: z-scores of breeding season length (mean-centered by μ = 5.4 months, and scaled by one standard deviation σ = 2.3 months), migratory behaviour (no migration as the reference category versus partial or full migration), and their interaction. *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) [47], 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) [47]. We then performed k-fold cross-validation [48] 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≈63 species, and the testing dataset included $N\frac{1}{K}$ or N≈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. [48].

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 [49], 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 reliable existence of a predictor's effect on sexually-dimorphic plumage patches [49].

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., following [27] 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 three achromatic and chromatic JND thresholds except for sympatric females at a chromatic JND threshold > 3 (Fig. S1).

Model comparisons

Breeding sympatry, *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). All *breeding sympatry*, *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 [50]). Among models predicting the probability of having a sexually-dichromatic plumage patch with chromatic JND values >1, 2, or 3, all *breeding sympatry*, *breeding timing*, and *breeding spacing* models performed much better than *intercept only* models, and *breeding sympatry* models had the top predictive performance (Table 1; *breeding sympatry* models all have ELPD =0, only the *breeding spacing* models predicting dichromatic plumage patches had similar predictive performance).

Achromatic plumage sexual dichromatism predictors

Migratory behaviour and shorter breeding season lengths were strongly associated with greater odds of a species having achromatic plumage sexual dichromatism. 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 dichromatism predictors

Migratory behaviour, shorter breeding season lengths, and larger numbers of sympatric *Turdus* species were strongly associated with greater odds of a species having chromatic plumage sexual dichromatism. 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, OR [90% HDI] = 71.2 [0.32, 59062.9]; full migration, OR [90% HDI] = 234.7 [0.51, 300382.6]). For *breeding spacing models*, island residency rather than mainland residency was associated with lower odds of having a plumage patch > 1 chromatic JND (island, OR [90% HDI] = 0.27 [0.09, 0.89]). Finally, more *Turdus* species in sympatry was associated with higher odds of a species having a sexually-dimorphic chromatic plumage patch with JND > 1 (number of sympatric species, OR [90% HDI] = 1.4 [1.18, 1.67], 40% increase in odds per each additional sympatric species), JND > 2 (sympatric species, OR [90% HDI] = 1.59 [1.01, 2.52], 59% increase in odds per each additional sympatric species), and JND > 3 (sympatric species, OR [90% HDI] = 2.11 [1.03, 4.46], 111% increase in odds per each additional sympatric species).

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

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

Table 2: Model predictor effect estimates (posterior median odds ratio and 90% highest-density interval) on the presence of a plumage patch with achromatic or chromatic visual contrast values $>$ 1, 2, and 3 JND. Model effects with a probability of direction (pd) value $\geq$ 0.90 are bolded in **red** for a negative effect and **blue** for a positive effect on plumage dichromatism. Phylogenetic signal (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	0.31 (0.02, 5.29), pd = 0.76	**0 (0, 0.54), pd = 0.98**	**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	0.94 (0.54, 1.75), pd = 0.57	**0.1 (0.01, 1.05), pd = 0.97**	**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	0.96 (0.31, 2.75), pd = 0.53	4.11 (0.3, 61.54), pd = 0.83	3.65 (0.44, 35.64), pd = 0.85	**2.2 (0.94, 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	**4.97 (0.95, 24.41), pd = 0.96**	**66.52 (3.19, 1802.4), pd = 0.99**	**22.34 (1.59, 307.91), pd = 0.98**	2.29 (0.69, 7.31), pd = 0.88	**80.51 (2.81, 3432.88), pd = 0.99**	**234.71 (0.51, 300382.62), 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, 3.12), 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	**4.84 (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, 37194569.46), 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	0.14 (0, 7.49), pd = 0.8	**0 (0, 2.44), pd = 0.95**	**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, 81.95), 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 (≥ 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)

Discussion

Our results provide comparative correlative evidence in support of predictions of the recognition hypothesis for plumage sexual dichromatism in true thrushes. We used a receptor-noise limited model of *Turdus merula* vision [36,37] to measure avian-perceivable visual contrast of plumage colours and found that the odds of plumage sexual dichromatism are much greater for *Turdus* thrush species that have full or partial migration rather than no migration, have relatively short breeding seasons, and are in sympatry with many other true thrush species (Table 1,2). Our results align with prior comparative studies of avian plumage sexual dichromatism where strong associations of sexual dichromatism with greater migratory behaviour [10] and more sympatric taxa [27] were found among many species of different passerine families.

Further, we determined that sympatric *Turdus* species have distinguishable plumage colouration differences from one another when measuring plumage appearance from the avian visual perspective (Fig. S1). Divergent plumage colouration within sexes between closely-related species indicates that plumage sexual dichromatism may have evolved to facilitate species and mate recognition in *Turdus* species breeding under higher sympatry with other true thrushes. However, we cannot directly determine if the plumage sexual dichromatism in sympatric *Turdus* species is the result of reproductive character displacement. We do not know if past changes in species' plumage sexual dichromatism occurred before or during periods of sympatry with other *Turdus* species. Regardless, present-day plumage sexual dichromatism and perceivable differences in plumage colouration between sympatric species likely reduces the challenge of finding compatible mates by signaling an individual's sex, breeding status, and species. For example, the four species *Turdus* hybrid zone in north-central Asia [33] is a particularly striking example where reproductive character displacement has likely occurred and all four species exhibit strong plumage sexual dichromatism (Fig. S2). Comparing within sexes between sister species pairs of *T.ruficollis* and *T.atrogularis*, and *T.naumanni* and *T.eunomus* [46], plumage patterns of the species pairs are nearly identical except for a divergence in colour. *T.ruficollis* and *T.atrogularis* share similar facial and throat colouring patterns, with the main difference being red colouration in *T.ruficollis* in opposition to the black colouration of *T.atrogularis*. In the second species pair, *T.naumanni* has red ventral plumage colouration and *T.eunomus* has black ventral plumage colouration.

Previous studies have found that closely-related sympatric species tend to have more similar plumage appearance than expected if plumage colouration patterns had evolved to facilitate species recognition via reproductive character displacement [51,52]. The potential lack of major plumage colour divergence among closely-related sympatric species may be attributable to constraints imposed by a shared light environment on colour signal efficiency [53], or similar natural selection pressures (e.g., predators, parasites, and weather). Generally, despite greater similarity in plumage appearance in comparison to allopatric species, closely-related sympatric species can still have substantially different and biologically-relevant differences in achromatic or chromatic interspecific visual contrast of plumage patches when measuring plumage colouration differences from the avian visual perspective (as we have found in our analyses).

Conclusions

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

Acknowledgements

We thank the American Museum of Natural History in New York City and Field Museum of Chicago for access to museum specimens used in this study. We also thank the Department of Evolution, Ecology, and Behavior at the University of Illinois for funding and support. MEH was funded by the University of Illinois Harley Jones Van Cleave Professorship. We are grateful for the extensive feedback and comments from Becky Fuller, Jeffrey Hoover, and Al Roca that greatly improved the manuscript.

Data Accessibility

Data and code used for the analyses can be found at https://github.com/aluro2/Turdus-Dichromatism.

Author Contributions

Alec Luro: Conceptualization, Investigation, Methodology, Software, Formal Analysis, Data Curation, Visualization, Writing-Original Draft, Writing-Review & Editing. **Mark Hauber**: Conceptualization, Resources, Supervision, Project administration, Funding acquisition, Writing-Review & Editing.

References

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

4. West-Eberhard MJ. 1983 Sexual Selection, Social Competition, and Speciation. *The Quarterly Review of Biology* **58**, 155–183. (doi:10.1086/413215)

5. Martin PR, Montgomerie R, Lougheed SC. 2015 Color Patterns of Closely Related Bird Species Are More Divergent at Intermediate Levels of Breeding-Range Sympatry. *The American Naturalist* **185**, 443–451. (doi:10.1086/680206)

6. Bitton P-P, Doucet SM. 2016 Sympatric black-headed and elegant trogons focus on different plumage characteristics for species recognition. *Animal Behaviour* **116**, 213–221. (doi:10.1016/j.anbehav.2016.03.035)

7. Martin TE, Badyaev AV. 1996 Sexual Dichromatism in Birds: Importance of Nest Predation and Nest Location for Females Versus Males. *Evolution* **50**, 2454–2460. (doi:10.2307/2410712)

8. Burns KJ. 1998 A Phylogenetic Perspective on the Evolution of Sexual Dichromatism in Tanagers (thraupidae): The Role of Female Versus Male Plumage. *Evolution* **52**, 1219–1224. (doi:10.1111/j.1558-5646.1998.tb01849.x)

9. Badyaev AV, Hill GE. 2003 Avian Sexual Dichromatism in Relation to Phylogeny and Ecology. *Annual Review of Ecology, Evolution, and Systematics* **34**, 27–49. (doi:10.1146/annurev.ecolsys.34.011802.132441)

10. Dale J, Dey C, Delhey K, Kempenaers B, Valcu M. 2015 The effects of life-history and social selection on male and female plumage coloration. *Nature* **000**, 1–17. (doi:10.1038/nature15509)

11. Dunn PO, Armenta JK, Whittingham LA. 2015 Natural and sexual selection act on different axes of variation in avian plumage color. *Science Advances* **1**, e1400155. (doi:10.1126/sciadv.1400155)

12. Hawkins GL, Hill GE, Mercadante A. 2012 Delayed plumage maturation and delayed reproductive investment in birds. *Biological Reviews* **87**, 257–274. (doi:10.1111/j.1469-185X.2011.00193.x)

13. Hamilton TH. 1961 On the Functions and Causes of Sexual Dimorphism in Breeding Plumage Characters of North American Species of Warblers and Orioles. *The American Naturalist* **45**, 64–73. (doi:10.1086/282167)

14. Saetre G-P, Slagsvold T. 1992 Evidence for sex recognition from plumage colour by the pied flycatcher, Ficedula hypoleuca. *Animal Behaviour* **44**, 293–299. (doi:10.1016/0003-3472(92)90035-8)

15. Friedman NR, Hofmann CM, Kondo B, Omland KE. 2009 Correlated evolution of migration and sexual dichromatism in the new world orioles (Icterus). *Evolution* **63**, 3269–3274. (doi:10.1111/j.1558-5646.2009.00792.x)

16. Simpson RK, Johnson MA, Murphy TG. 2015 Migration and the evolution of sexual dichromatism: Evolutionary loss of female coloration with migration among wood-warblers. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20150375. (doi:10.1098/rspb.2015.0375)

17. Matysioková B, Remeš V, Cockburn A. 2017 Broad-scale variation in sexual dichromatism in songbirds is not explained by sex differences in exposure to predators during incubation. *Journal of Avian Biology* **48**, 1322–1330. (doi:10.1111/jav.01144)

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)

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)

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)

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)

22. Doutrelant C, Paquet M, Renoult 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)

23. Kearns AM, Joseph L, Austin JJ, Driskell AC, Omland KE. 2020 Complex mosaic of sexual dichromatism and monochromatism in Pacific robins results from both gains and losses of elaborate coloration. *Journal of Avian Biology* **51**. (doi:10.1111/jav.02404)

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)

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)

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)

27. Cooney CR, Tobias JA, Weir JT, Botero CA, Seddon N. 2017 Sexual selection, speciation and constraints on geographical range overlap in birds. *Ecology Letters* **20**, 863–871. (doi:10.1111/ele.12780)

28. Seddon N *et al.* 2013 Sexual selection accelerates signal evolution during speciation in birds. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20131065. (doi:10.1098/rspb.2013.1065)

29. Cooney CR, Varley ZK, Nouri LO, Moody CJA, Jardine MD, Thomas GH. 2019 Sexual selection predicts the rate and direction of colour divergence in a large avian radiation. *Nature Communications* **10**, 1773. (doi:10.1038/s41467-019-09859-7)

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)

31. Clement P, Hathway R. 2000 *Thrushes*. London: A&C Black Publishers Ltd.

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)

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

34. Luro A, Hauber ME. 2019 Plumage dichromatism in Turdus thrushes. (doi:10.17605/OSF.IO/ZUM6D)

35. 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.

36. 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)

37. 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)

38. 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)

39. R Core Team. 2020 *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

40. Endler JA. 1993 The Color of Light in Forests and Its Implications. *Ecological Monographs* **63**, 1–27. (doi:10.2307/2937121)

41. 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)

42. del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E. 2017 *Handbook of the birds of the world alive*.

43. BirdLife International and Handbook of the Birds of the World. 2018 *Bird species distribution maps of the world. Version 2018.1*.

44. 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)

45. Bürkner PC. 2017 Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **80**, 1–28. (doi:10.18637/jss.v080.i01)

46. 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)

47. 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)

48. 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)

49. Makowski D, Ben-Shachar MS, Chen SHA, Lüdecke D. 2019 Indices of Effect Existence and Significance in the Bayesian Framework. *Frontiers in Psychology* **10**. (doi:10.3389/fpsyg.2019.02767)

50. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: A practical information-theoretic approach*. 2nd ed. New York: Springer.

51. Simpson RK, Wilson DR, Mistakidis AF, Mennill DJ, Doucet SM. 2021 Sympatry drives colour and song evolution in wood-warblers (Parulidae). *Proceedings of the Royal Society B: Biological Sciences* **288**, 20202804. (doi:10.1098/rspb.2020.2804)

52. Miller ET, Leighton GM, Freeman BG, Lees AC, Ligon RA. 2019 Ecological and geographical overlap drive plumage evolution and mimicry in woodpeckers. *Nature Communications* **10**, 1602. (doi:10.1038/s41467-019-09721-w)

53. 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)

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

Alec B. Luro[1]*, Mark E. Hauber[1]

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

Supplementary 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).

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%)

[1] Statistics presented: n (%)

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

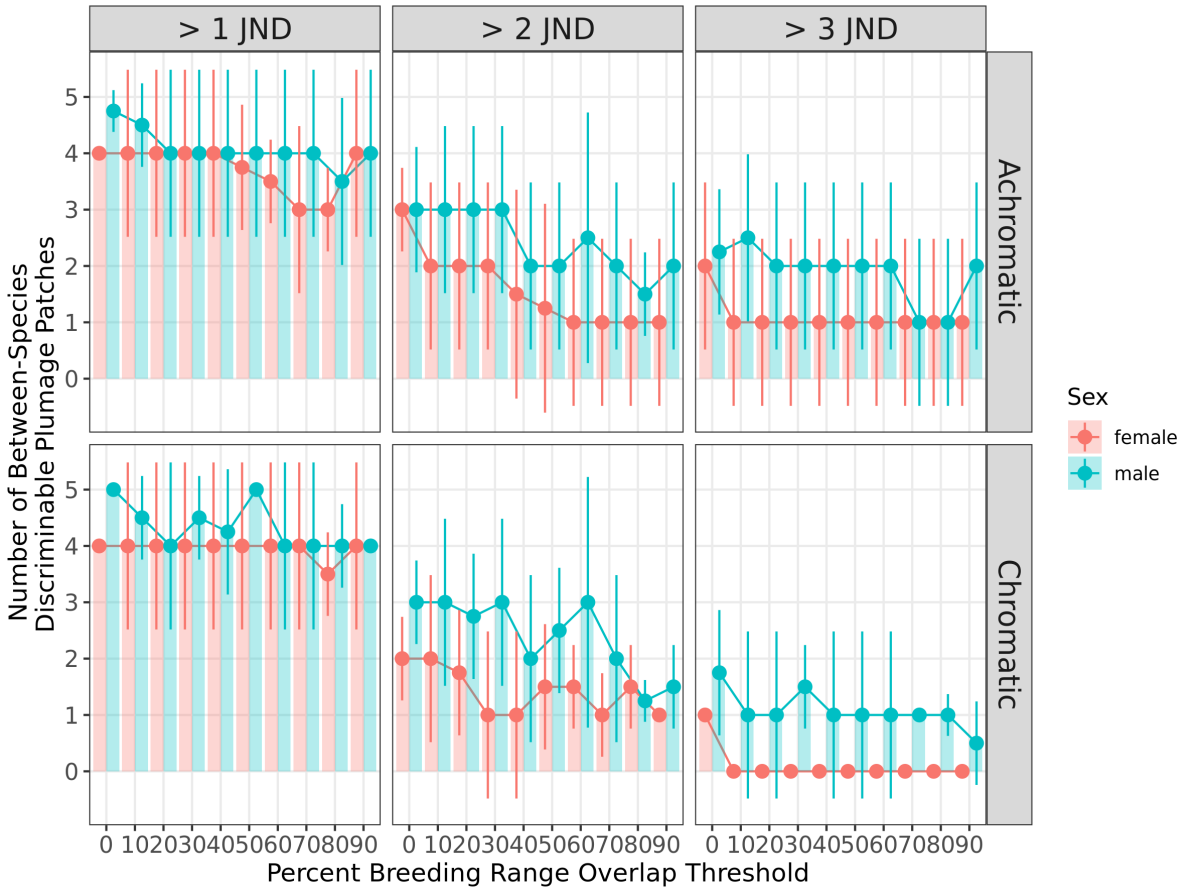

Fig S1: Median ± median absolute deviation of number of distinguishable plumage patches by just noticeable differences (JND) thresholds of 1, 2, and 3 between male and female *Turdus* thrush species in sympatry at various breeding range overlaps (percent).

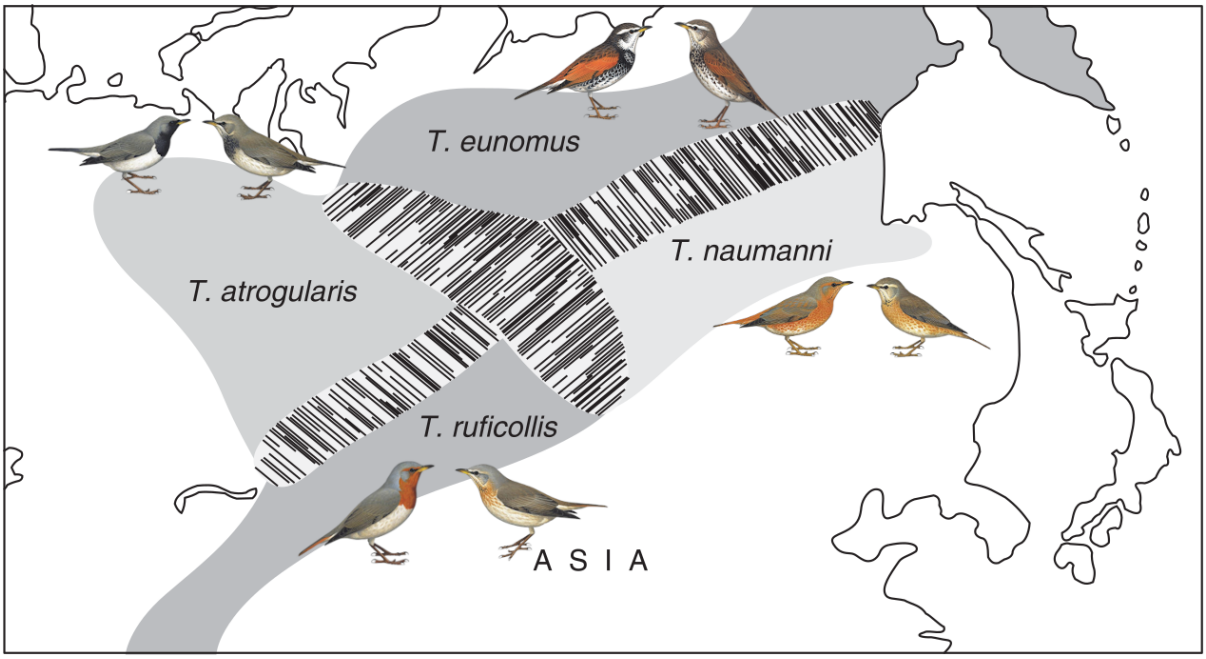

Fig S2: Four species hybrid zone in north-central Asia (*T.atrogularis*, *T.ruficollis*,*T.eunomus*, and *T.naumanni*). Map is from [1]. Illustrations © HBW Alive/Lynx Edicions.

References

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