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

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# 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 the species recognition hypothesis for plumage sexual dimorphism 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 contrast between male and female plumage patches and tested the influence of breeding timing, spacing, and *Turdus* species sympatry on plumage sexual dimorphism. Time and opportunities for mate sampling are more limited in migratory rather than non-migratory species, and we found that true thrush species with migratory behaviour have greater plumage sexual dimorphism than non-migratory species. Additionally, we found that plumage sexual dimorphism is positively correlated with the number of *Turdus* thrush species breeding in sympatry. Our results suggest that species recognition plays a prominent role in the evolution of plumage sexual dimorphism.

## Keywords

*dichromatism*, *plumage*, *species recognition*

# Introduction

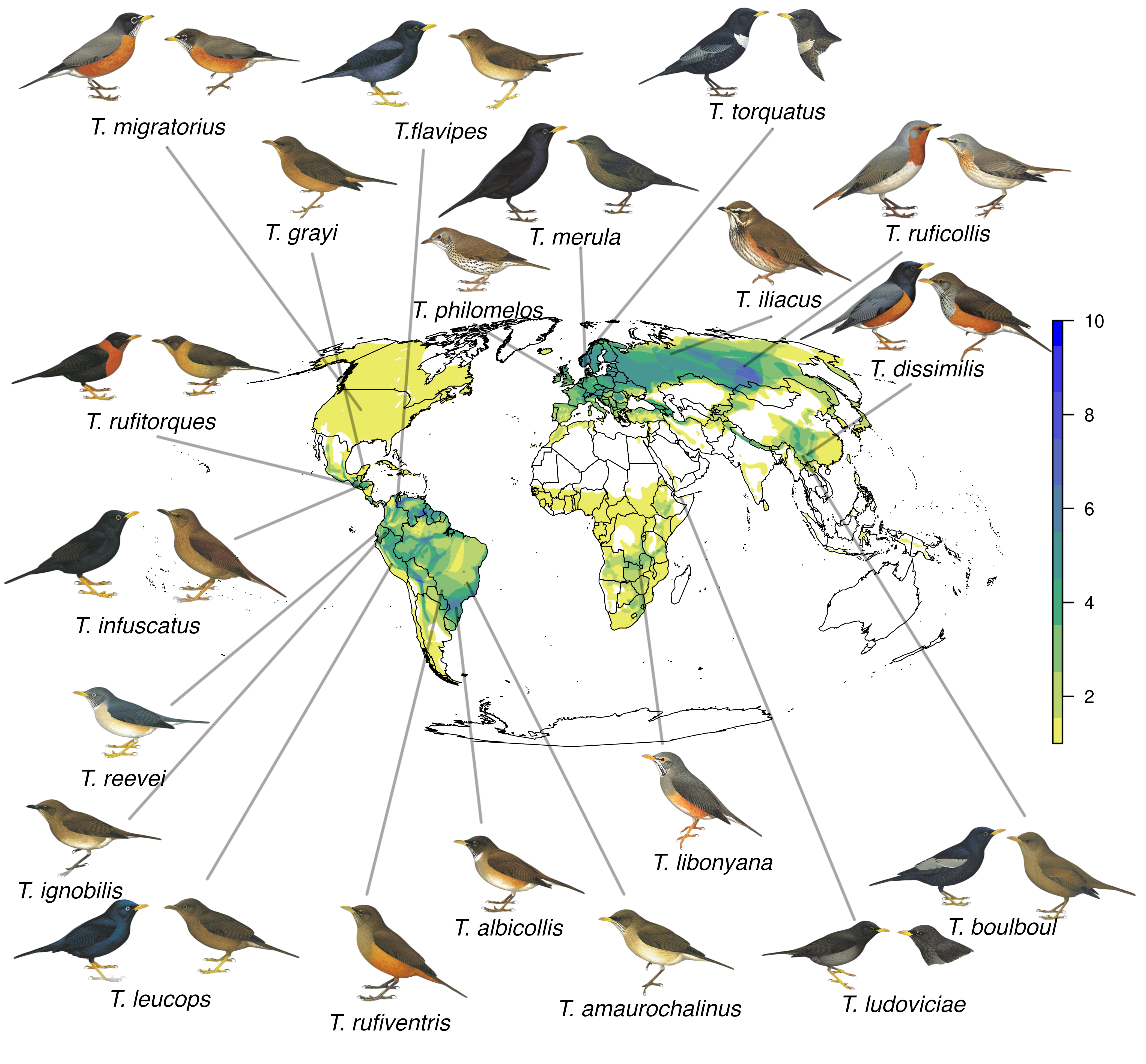
Species recognition is necessary in sexually reproducing lineages for individuals to find compatible mates and produce viable offspring [[1](#ref-andersson1994),[2](#ref-groning2008)]. Conspicuous traits signaling species and sex identity increase the ease of species recognition by reducing the time and effort expended when searching for compatible mates and lessen the likelihood of mating with heterospecifics [[3](#ref-pfennig2012)]. 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](#ref-west-eberhard1983)]. 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](#ref-andersson1994)].

In birds, plumage colour is a highly conspicuous trait signaling species and (often) sex identity [[5](#ref-martin2015a),[6](#ref-bitton2016)] . 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](#ref-martin1996)–[11](#ref-dunn2015)]. 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](#ref-hawkins2012)]), reducing the time and effort necessary to identify a suitable mate [[13](#ref-hamilton1961),[14](#ref-saetre1992)]. 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](#ref-badyaev2003)]. 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](#ref-dale2015),[15](#ref-friedman2009)–[17](#ref-matysiokova2017)]. Additionally, bird species that reside on mainland continents and have larger breeding ranges often have greater plumage colour elaboration and sexual dichromatism than species living on islands with limited breeding ranges [[18](#ref-badyaev1998)–[23](#ref-kearns2020)].

Moreover, plumage sexual dichromatism likely plays a role in hybridization avoidance via reproductive character displacement to facilitate species and mate recognition. For example, in European *Ficedula* flycatchers, female choice selects for divergent male plumage colouration, leading to character displacement between species and populations and reduced rates of hybridization [[24](#ref-alatalo1994)–[26](#ref-laaksonen2015)]. 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](#ref-cooney2017)]. Plumage sexual dichromatism has also been found to be positively associated with species richness among sister species pairs, and dichromatism mainly increases through changes in male plumage [[28](#ref-seddon2013)], suggesting that female choice and male-male competition lead to concurrent changes in male plumage colour and speciation events. Further, plumage sexual dichromatism is positively associated with greater interspecific plumage colour evolution rate and divergence in *Tyrannida* suboscines [[29](#ref-cooney2019)]. Therefore, plumage sexual dichromatism may be an especially favourable trait for facilitating species and mate recognition when closely-related species have sympatric breeding ranges [[5](#ref-martin2015a),[30](#ref-martin2010)].

True thrushes (genus: *Turdus*) are an exceptionally diverse genus of passerine birds consisting of about ~86 species distributed across the globe (Fig. 1). Plumage sexual dimorphism and migratory behaviors vary substantially between species and have evolved multiple times in thrushes across the world [[31](#ref-clement2000),[32](#ref-nagy2019)]. Interestingly, there have been several documented cases of hybridization in *Turdus* thrushes, and there is a large hybird zone between four *Turdus* species (*T. atrogularis*, *T. eunomus*, *T. naumanni*, *T. ruficollis*) in north-central Asia [[33](#ref-mccarthy2006)], indicating that some sympatric *Turdus* species interbreed. Therefore, the true thrushes are an ideal passerine clade for examining the species recognition hypothesis for plumage sexual dimorphism.

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. Taken together, repeated findings across various bird lineages of greater plumage dichromatism in species that are i) migratory rather than nonmigratory, ii) have shorter breeding seasons, ii) live on mainlands rather than islands, iv) have larger breeding ranges, and v) breed in sympatry with closely-related species suggests that circumstances where rapid species recognition is challenging strongly favour the evolution and maintenance of prominent plumage sexual dichromatism in birds. Here, we test predictions of the species recognition hypothesis for sexually-dimorphic traits. To this end, we evaluate the potential influences of breeding timing, spacing, and sympatry on plumage dichromatism in the *Turdus* thrushes.



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

# Methods

## *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. Reflectance measurements spanning 300-700nm were taken in triplicate from the belly, breast, throat, crown and mantle plumage patches [[34](#ref-andersson2006)] of each individual. N=3 male and N=3 female individuals were measured for most species (exceptions: *T. lawrencii*, N=2 males and N=2 females; *T. swalesi*, N=1 male and N=1 female). Reflectance spectra were measured using a 400 μm fiber optic reflection probe fitted with a rubber stopper to maintain a consistent measuring distance of 3 mm and area of 2 mm2 at a 90° angle to the surface of the feather patch. Measurements were taken using a JAZ spectrometer with a pulsed-xenon light source (Ocean Optics, Dunedin, USA) and we used a diffuse 99% reflectance white standard (Spectralon WS-1-SL, Labsphere, North Sutton NH, USA).

We applied a receptor-noise limited visual model [[35](#ref-vorobyev1998)] of the European Blackbird (*T. merula*) visual system [[36](#ref-hart2000)] in the *pavo* [[37](#ref-maia2019)]⁠ package in R v4.0.0 [[38](#ref-rcoreteam2020)]⁠ 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](#ref-endler1993)]⁠, 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](#ref-kemp2015)]⁠. 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%).

## *Life History Data*

### *Breeding Timing Model*

We collected data on migration behaviour and breeding season length from *Thrushes* [[31](#ref-clement2000)] and the *Handbook of the Birds of the World* [[41](#ref-delhoyo2017)]⁠. 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* [[42](#X6c896e2b80dd0fca0e8ee32fce3f4251147131f)]⁠. We calculated congener breeding range overlaps (as percentages) using the *letsR* package in R [[43](#ref-vilela2015)]⁠. 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](#ref-cooney2017)]. 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 2.

### *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 an oceanic body of water.

## *Statistical modeling*

We used phylogenetically-corrected Bayesian multilevel logistic regression models using the *brms* v2.13.0 package [[44](#ref-burkner2017)] in R v4.0.0 [[38](#ref-rcoreteam2020)]⁠ where responses, the number of sexually-dichromatic patches >1, 2, and 3 chromatic and achromatic JNDs, were modelled 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* phylogeny from Nylander et al. (2008) [[45](#ref-nylander2008)] 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 = 5.4 months, and scaled by one standard deviation = 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 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 weak prior (Student T: df = 3, location = 0, scale = 10), and predictor coefficients were assigned flat 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](#ref-gelman2013)]. We then performed k-fold cross-validation [[47](#ref-vehtari2017)] to refit each model *K*=16 times. For each k-fold, the training dataset included a randomly selected set of or N≈63 species, and the testing dataset included 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. [[47](#ref-vehtari2017)]⁠.

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](#ref-makowski2019)], 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](#ref-makowski2019)].

# 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). Conversely, 98.7% (n=78 species) have at least one sexually-dimorphic plumage patch > 1 JND, 56% (n=43 species) have at least one plumage patch > 2 JND, and 37% (n=28 species) have at least one patch > 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 except for sympatric females at a chromatic JND threshold > 3 (Fig. S1).

## *Model comparisons*

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 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 Burnham and Anderson (2002)[[49](#ref-burnham2002)]). 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 with had similar predictive performance).

## *Achromatic plumage sexual dimorphism predictors*

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*

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), and 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 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 sympatic 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).

# Discussion

Our results provide correlative evidence in support of the species recognition hypothesis for plumage sexual dimorphism in true thrushes. We used a receptor-noise limited model of *Turdus merula* vision [[35](#ref-vorobyev1998),[36](#ref-hart2000)] to measure avian-perceivable visual contrast of plumage colours and found that the odds of plumage sexual dimorphism 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 broader comparative studies of plumage sexual dimorphism where strong associations between migratory behavior [[10](#ref-dale2015)] and sympatry [[27](#ref-cooney2017)] 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). Therefore, plumage sexual dichromatism may have evolved to facilitate species recognition in species breeding under high sympatry with other true thrushes. However, we cannot directly determine if plumage sexual dimorphism in sympatric *Turdus* species is the result of reproductive character displacement. Namely, we do not know if past changes in species’ plumage sexual dimorphism occurred before or during periods of sympatry with other *Turdus* species. Regardless, present-day plumage sexual dimorphism and perceivable differences in plumage colouration between sympatric species likely reduces the challenge of finding compatible mates.

Previous studies have found that closely-related sympatric species tend to have more similar plumage appearance than expected if plumage colouration had evolved to facilitate species recognition via reproductive character displacement [[50](#ref-simpson2021),[51](#ref-miller2019)]. 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 [[52](#ref-mcnaught2002)], 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 dimorphism in true thrushes (*Turdus*) are consistent with predictions of the species recognition hypothesis for plumage sexual dimorphism. Migratory behaviour and limited breeding seasons reduce the amount of time available to find a mate, and greater plumage sexual dimorphism may help migratory species find compatible mates more rapidly. Greater plumage sexual dimorphism 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 dimorphism likely reduces species recognition errors and hybridization.

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