

# Rapid species recognition favors greater avian-perceived plumage dichromatism in true thrushes (genus: *Turdus*)

Alec B. Luro<sup>1\*</sup>, Mark E. Hauber<sup>1</sup>

<sup>1</sup> Department of Evolution, Ecology and Behavior, School of Integrative Biology,  
University of Illinois at Urbana-Champaign \*alec.b.luro@mail.com

## Abstract

## Keywords

*dichromatism, plumage, species recognition*

## Background

Species recognition is necessary for individuals to find compatible conspecific mates and produce viable offspring [1,2]. Specifically, conspicuous traits signaling species and sex identity are predicted to reduce the time and effort expended when searching for mates and likelihood of mating with heterospecifics [2]. Accordingly, traits which facilitate species and mate recognition should be favored when congeneric species are highly sympatric, when the time to find a mate is limited, and when conspecifics are not encountered often [1]. 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 [3]. In birds, plumage colouration is a highly conspicuous trait which signals species [4,5] and (often) sex identity.

Plumage sexual dichromatism, distinct differences in the appearance of male versus female feather colouration, is common in birds and is often attributed to differing selection pressures on males and females [6–10]. Fundamentally, plumage sexual dichromatism results in a visible trait useful for recognizing an individual's species, sex, and age (in species with delayed plumage maturation, see [11]), reducing the time and effort necessary to find a suitable mate. 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 ranges [8,9,12–14].

Further, plumage sexual dichromatism likely plays a role in hybridization avoidance via character displacement for species and mate recognition [15]. For example, in European *Ficedula* flycatchers, female choice selects for divergent male plumage colouration, leading to character displacement and reduced rates of hybridization [16]. More broadly, greater plumage dichromatism is positively correlated with transitions from allopatry to parapatry and an increase in geographic range overlap among a large sample of passerine sister species pairs [17]. In addition, plumage sexual dichromatism is positively associated with

species richness among 84 sister species pairs, and dichromatism is increased mainly by changes in male plumage [15], suggesting that female choice and male-male competition lead to concurrent changes in male plumage and speciation events. Further, plumage sexual dichromatism is positively associated with greater interspecific plumage color evolution rate and divergence in *Tyrannida* suboscines [18]. Therefore, plumage sexual dichromatism may be an especially favorable trait to facilitate species and mate recognition when closely-related species have overlapping breeding ranges.

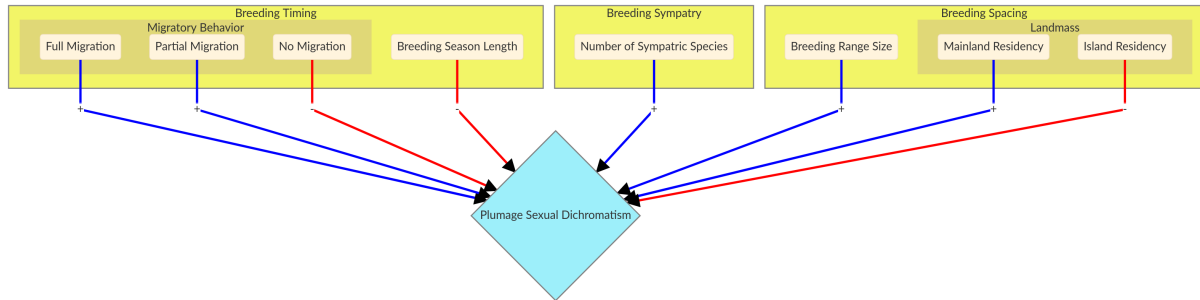


Figure 1: Hypotheses and predictions by model. Arrow colors indicate predicted correlation, positive (blue) and negative (red).

## 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 [19] 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  $\mu$ m fiber optic reflection probe fitted with a rubber stopper to maintain a consistent measuring distance of 3 mm and area of 2 mm<sup>2</sup> 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 [20] of the European Blackbird (*T. merula*) visual system [21] in the *pavo* [22] package in R v4.0.0 [23] 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 envi-

ronments vary both spatially and temporally [24], 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 [25].

## **Life History Data**

### **Breeding Timing Model**

We collected data on migration behavior and breeding season length from *Thrushes* [26] and the *Handbook of the Birds of the World* [27]. We assigned three different kinds of migratory behavior: 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* [28]. We calculated congener breeding range overlaps (as percentages) using the *letsR* package in R [29]. 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 [17].

### **Breeding Spacing Model**

Species’ breeding range sizes (in km<sup>2</sup>) 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 [30] in R v4.0.0 [23] where responses, the number of sexually-dichromatic patches >1, 2, and 3 chromatic and achromatic JNDs, 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* phylogeny from Nylander et al. (2008) [31] 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  $\mu = 5.4$  months, and scaled by one standard deviation  $\sigma = 2.3$  months), migratory behavior (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 (km<sup>2</sup>) 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) [32]. We then performed k-fold cross-validation [33] 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. [33].

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 [34], 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  $\geq 0.90$  to be indicative of a true existence of a predictor's effect on sexually-dimorphic plumage patches [34].

## Results

### Model comparisons

We obtained  $N \geq 4000$  effective samples for each model parameter and all models' Markov Chains (MCMC) successfully converged (Rhat = 1 for all models' parameters) (Supplementary Figure). 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)[35]). 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 best 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  $\geq 0.90$  (Table 2). Specifically, longer breeding season length is 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 behavior, rather than no migratory behavior, is 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 behavior, rather than no migration behavior, 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 is 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 behavior 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 is 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 is 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 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  $\pm$  standard error (kfold IC  $\pm$  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 ( $\lambda$ ) 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 $> 3$
<b>Breeding Timing</b>	Intercept	0.31 (0.02, 5.29), pd = 0.76	<b>0.0 (0.54), pd = 0.98</b>	<b>0.0 (0.19), pd = 0.99</b>	0.41 (0.05, 2.79), pd = 0.78	<b>0.0 (0.173), pd = 0.95</b>	<b>0.0 (0.137), pd = 0.96</b>
	Breeding Season Length	0.94 (0.54, 1.75), pd = 0.57	<b>0.1 (0.01, 1.05), pd = 0.97</b>	<b>0.25 (0.03, 1.49), pd = 0.91</b>	0.89 (0.56, 1.4), pd = 0.66	<b>0.14 (0.01, 1.42), pd = 0.94</b>	0.08 (0.9, 1.4), 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	<b>2.2 (0.94, 4.89), pd = 0.94</b>	6.7 (0.42, 134.8), pd = 0.88	<b>71.16 (0.32, 5906.292), pd = 0.92</b>
	Full Migration vs. No Migration	<b>4.97 (0.95, 24.41), pd = 0.96</b>	<b>66.52 (3.19, 1802.4), pd = 0.99</b>	<b>22.34 (1.59, 307.91), pd = 0.98</b>	2.29 (0.69, 7.31), pd = 0.88	<b>80.51 (2.81, 3432.88), pd = 0.99</b>	<b>234.71 (0.51, 300382.62), pd = 0.95</b>
	Breeding Season Length x Partial Migration	1.34 (0.48, 3.92), pd = 0.68	<b>20.71 (0.87, 589.09), pd = 0.96</b>	<b>8.28 (0.76, 109.11), pd = 0.94</b>	1.39 (0.65, 3.12), pd = 0.76	<b>9.03 (0.44, 251.36), pd = 0.9</b>	34.46 (0.08, 68228.71), pd = 0.85
	Breeding Season Length x Full Migration	<b>4.84 (0.67, 39.63), pd = 0.9</b>	<b>66.3 (0.59, 11415.7), pd = 0.93</b>	16.41 (0.27, 824.69), pd = 0.89	1.68 (0.31, 8.33), pd = 0.7	<b>160.6 (0.84, 67791.13), pd = 0.95</b>	433.67 (0.01, 37194569.46), pd = 0.85
	Phylogenetic Signal $\lambda$ , 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)
<b>Breeding Spacing</b>	Intercept	0.14 (0.7, 7.49), pd = 0.8	<b>0.0 (2.44), pd = 0.95</b>	<b>0.0 (0.14), pd = 0.98</b>	0.51 (0.03, 9.7), pd = 0.65	<b>0.0 (7.63), pd = 0.92</b>	<b>0.0 (8.195), pd = 0.91</b>
	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	<b>0.27 (0.09, 0.89), pd = 0.97</b>	0.03 (0.3, 9.99), pd = 0.89	0.04 (0.6759), 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 $\lambda$ , 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)
<b>Breeding Sympatry</b>	Intercept	0.41 (0.03, 5.83), pd = 0.72	<b>0.0 (0.98), pd = 0.95</b>	<b>0.0 (0.34), pd = 0.98</b>	<b>0.25 (0.04, 1.35), pd = 0.91</b>	<b>0.0 (1.12), pd = 0.95</b>	<b>0.0 (0.29), pd = 0.98</b>
	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	<b>1.4 (1.18, 1.67), pd = 0.99</b>	<b>1.59 (1.01, 2.52), pd = 0.96</b>	<b>2.11 (1.03, 4.46), pd = 0.97</b>
	Phylogenetic Signal $\lambda$ , 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

## Conclusions

## Acknowledgements

## 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](https://doi.org/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](https://doi.org/10.1086/590510))
3. West-Eberhard MJ. 1983 Sexual Selection, Social Competition, and Speciation. *The Quarterly Review of Biology* **58**, 155–183. (doi:[10.1086/413215](https://doi.org/10.1086/413215))
4. Martin PR, Montgomerie R, Loughheed 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](https://doi.org/10.1086/680206))
5. 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](https://doi.org/10.1016/j.anbehav.2016.03.035))
6. 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](https://doi.org/10.2307/2410712))
7. 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](https://doi.org/10.1111/j.1558-5646.1998.tb01849.x))
8. 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](https://doi.org/10.1146/annurev.ecolsys.34.011802.132441))
9. 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](https://doi.org/10.1038/nature15509))
10. 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](https://doi.org/10.1126/sciadv.1400155))
11. 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](https://doi.org/10.1111/j.1469-185X.2011.00193.x))
12. 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](https://doi.org/10.1111/j.1558-5646.2009.00792.x))



13. 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](https://doi.org/10.1098/rspb.2015.0375))
14. Matysioková B, Remeš V, Cockburn A. 2017 Broad-scale variation in sexual dichromatism in song-birds is not explained by sex differences in exposure to predators during incubation. *Journal of Avian Biology* **48**, 1322–1330. (doi:[10.1111/jav.01144](https://doi.org/10.1111/jav.01144))
15. 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](https://doi.org/10.1098/rspb.2013.1065))
16. Stre G-P, Moum T, Bureš S, Král M, Adamjan M, Moreno J. 1997 A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* **387**, 589–592. (doi:[10.1038/42451](https://doi.org/10.1038/42451))
17. 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](https://doi.org/10.1111/ele.12780))
18. 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](https://doi.org/10.1038/s41467-019-09859-7))
19. 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.
20. Vorobyev M, Osorio D. 1998 Receptor noise as a determinant of colour thresholds. *Proceedings. Biological sciences / The Royal Society* **265**, 351–8. (doi:[10.1098/rspb.1998.0302](https://doi.org/10.1098/rspb.1998.0302))
21. Hart NS, Partridge JC, Cuthill IC, Bennett AT. 2000 Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: The blue tit (*Parus caeruleus* L.) And the blackbird (*Turdus merula* L.). *Journal of comparative physiology. A, Sensory, neural, and behavioral physiology* **186**, 375–387. (doi:[10.1007/s003590050437](https://doi.org/10.1007/s003590050437))
22. Maia R, Gruson H, Endler JA, White TE. 2019 Pavo 2: New tools for the spectral and spatial analysis of colour in r. *Methods in Ecology and Evolution* **10**, 1097–1107. (doi:[10.1111/2041-210X.13174](https://doi.org/10.1111/2041-210X.13174))
23. R Core Team. 2020 *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
24. Endler JA. 1993 The Color of Light in Forests and Its Implications. *Ecological Monographs* **63**, 1–27. (doi:[10.2307/2937121](https://doi.org/10.2307/2937121))
25. Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall J, Whiting MJ. 2015 An Integrative Framework for the Appraisal of Coloration in Nature. *The American Naturalist* **185**, 705–724. (doi:[10.1086/681021](https://doi.org/10.1086/681021))
26. Clement P, Hathway R. 2000 *Thrushes*. London: A&C Black Publishers Ltd.

- 214 27. del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E. 2017 *Handbook of the birds of the world*  
215 *alive*.
- 216 28. BirdLife International and Handbook of the Birds of the World. 2018 *Bird species distribution maps*  
217 *of the world. Version 2018.1*.
- 218 29. Vilela B, Villalobos F. 2015 letsR: A new R package for data handling and analysis in macroecology.  
219 *Methods in Ecology and Evolution* **6**, 1229–1234. (doi:[10.1111/2041-210X.12401](https://doi.org/10.1111/2041-210X.12401))
- 220 30. Bürkner PC. 2017 Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statis-*  
221 *tistical Software* **80**, 1–28. (doi:[10.18637/jss.v080.i01](https://doi.org/10.18637/jss.v080.i01))
- 222 31. 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).  
223 *Systematic Biology* **57**, 257–268. (doi:[10.1080/10635150802044003](https://doi.org/10.1080/10635150802044003))
- 224 32. Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. 2013 *Bayesian data analysis, third*  
225 *edition*. Third. Boca Raton, FL: CRC Press. (doi:[10.1201/b16018](https://doi.org/10.1201/b16018))
- 226 33. Vehtari A, Gelman A, Gabry J. 2017 Practical Bayesian model evaluation using leave-one-out cross-  
227 validation and WAIC. *Statistics and Computing* **27**, 1413–1432. (doi:[10.1007/s11222-016-9696-4](https://doi.org/10.1007/s11222-016-9696-4))
- 228 34. Makowski D, Ben-Shachar MS, Chen SHA, Lüdtke D. 2019 Indices of Effect Existence and Signif-  
229 icance in the Bayesian Framework. *Frontiers in Psychology* **10**. (doi:[10.3389/fpsyg.2019.02767](https://doi.org/10.3389/fpsyg.2019.02767))
- 230 35. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: A practical information-*  
231 *theoretic approach*. 2nd ed. New York: Springer.