

# 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

## 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 [1] of each individual. N=3 male and N=3 female individuals were measured for most species (exceptions: *T. lawrencii*, N=2 males and N=2 females; *T. swalesi*, N=1 male and N=1 female). Reflectance spectra were measured using a 400 µm fiber optic reflection probe fitted with a rubber stopper to maintain a consistent measuring distance of 3 mm and area of 2 mm<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 [2] of the European Blackbird (*T. merula*) visual system [3] in the *pavo* [4] package in R v4.0.0 [5] 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 [6], 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 [7].

## **Life History Data**

### **Breeding Timing Model**

We collected data on migration behavior and breeding season length from *Thrushes* [8] and the *Handbook of the Birds of the World* [9]. 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* [10]. We calculated congener breeding range overlaps (as percentages) using the *letsR* package in R [11]. 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 [12].

### **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 [13] in R v4.0.0 [5] 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) [14] 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) [15]. We then performed k-fold cross-validation [16] 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. [16].

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 [17], 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 [17].

## 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)[18]). 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 patch 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 patch 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 (0.244), 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 (0.7, 63), pd = 0.92</b>          | <b>0.0 (0.8195), 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 (0.112), 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 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.
2. 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))
3. 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))
4. 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))
5. R Core Team. 2020 *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
6. 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))
7. 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))
8. Clement P, Hathway R. 2000 *Thrushes*. London: A&C Black Publishers Ltd.
9. del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E. 2017 *Handbook of the birds of the world alive*.
10. BirdLife International and Handbook of the Birds of the World. 2018 *Bird species distribution maps of the world. Version 2018.1*.
11. Vilela B, Villalobos F. 2015 letsR: A new R package for data handling and analysis in macroecology. *Methods in Ecology and Evolution* **6**, 1229–1234. (doi:[10.1111/2041-210X.12401](https://doi.org/10.1111/2041-210X.12401))
12. 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))

- 159 13. Bürkner PC. 2017 Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statis-*  
160 *tistical Software* **80**, 1–28. (doi:[10.18637/jss.v080.i01](https://doi.org/10.18637/jss.v080.i01))
- 161 14. 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).  
162 *Systematic Biology* **57**, 257–268. (doi:[10.1080/10635150802044003](https://doi.org/10.1080/10635150802044003))
- 163 15. Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. 2013 *Bayesian data analysis, third*  
164 *edition*. Third. Boca Raton, FL: CRC Press. (doi:[10.1201/b16018](https://doi.org/10.1201/b16018))
- 165 16. Vehtari A, Gelman A, Gabry J. 2017 Practical Bayesian model evaluation using leave-one-out cross-  
166 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))
- 167 17. Makowski D, Ben-Shachar MS, Chen SHA, Lüdtke D. 2019 Indices of Effect Existence and Signif-  
168 icance in the Bayesian Framework. *Frontiers in Psychology* **10**. (doi:[10.3389/fpsyg.2019.02767](https://doi.org/10.3389/fpsyg.2019.02767))
- 169 18. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: A practical information-*  
170 *theoretic approach*. 2nd ed. New York: Springer.