

1 Ecological conditions favoring species
2 recognition and rapid mate pairing are
3 associated with greater plumage sexual
4 dichromatism in true thrushes (genus: *Turdus*)

5 Alec B. Luro^{1*}, Mark E. Hauber¹

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

9 **Abstract**

10 **Keywords**

11 **Background**

12 **Methods**

13 ***Plumage sexual dichromatism***

14 A total of N=77 *Turdus* thrush species were sampled for plumage spectral re-
15 flectance using from bird skins at the American Museum of Natural History in
16 New York City and the Field Museum in Chicago. Reflectance measurements
17 from 300-700nm were taken in triplicate for the belly, breast, throat, crown and
18 mantle plumage patches [1] of each individual bird skin. N=3 male and N=3 fe-
19 male individuals were measured for most species (exceptions: *Turdus lawrencii*,
20 N=2 males and N=2 females; *Turdus swalesi*, N=1 male and N=1 female). Re-
21 flectance spectra were measured using a 400 µm fiber optic reflection probe fit-
22 ted with a rubber stopper to maintain a consistent measuring distance of 3 mm
23 and area of 2 mm² at a 90° angle to the surface of the feather patch. Measure-
24 ments were taken using a JAZ spectrometer with a pulsed-xenon light source
25 (Ocean Optics, Dunedin, USA) and all measurements were made relative to a
26 diffuse reflectance white standard (Spectralon WS-1-SL, Labsphere, North Sut-
27 ton NH, USA).

28 We used a receptor-noise limited visual model [2] of the European Blackbird
 29 (*Turdus merula*) visual system [3] in the *pavo* [4] package in R v4.0.0 [5] to calcu-
 30 late avian-perceived chromatic and achromatic visual contrast (in units of “Just-
 31 Noticeable Differences”, or JNDs) of male vs. female plumage patches for all sam-
 32 pled *Turdus* species. Chromatic and achromatic JNDs were calculated for male-
 33 female pairs within each species (i.e., N=9 JND values calculated per patch for
 34 each species where N=3 males and N=3 females sampled), and then JND val-
 35 ues were averaged for each species’ respective plumage patches. Under ideal
 36 laboratory conditions, a JND value of 1 is generally considered to be the discrim-
 37 inable threshold past which an observer is predicted to be able to perceive the
 38 two colors as different. However, natural light environments vary both spatially
 39 and temporally [6], bringing into question the accuracy of a JND=1 threshold for
 40 generalizing visual contrast under natural conditions. Therefore, we calculated
 41 the total number of sexually-dichromatic plumage patches per species (out of
 42 N=5 measured patches) as the number of plumage patches with average JND
 43 values > 1, 2, or 3 to account for uncertainty in visual discrimination thresholds
 44 due to variation in psychophysical and ambient lighting conditions affecting the
 45 strength of between-sex plumage visual contrast [7].

46 **Life History Data**

47 **Breeding Timing Model**

48 We collected data on migration behavior and breeding season length from
 49 *Thrushes* [8] and the *Handbook of the Birds of the World* [9]. We assigned
 50 three different kinds of migratory behavior: 1) *full migration* when a species
 51 description clearly stated that a species “migrates”, 2) *partial migration* when a
 52 species was described to have “altitudinal migration”, “latitudinal migration” or
 53 “movement during non-breeding season”, or 3) *sedentary* when when a species
 54 was described as “resident” or “sedentary”. Breeding season length was defined
 55 as the number of months the species breeds.

56 **Breeding Sympatry Model**

57 Species’ breeding ranges were acquired from *BirdLife International* [10]. We cal-
 58 culated congener breeding range overlaps (as percentages) using the *letsR* pack-
 59 age in R [11]. We then calculated the number of sympatric species as the num-
 60 ber of congeners with breeding ranges that overlap >30% with the focal species’
 61 breeding range [12].

62 **Breeding Spacing Model**

63 Species’ breeding range sizes (in km²) were acquired using the *BirdLife Interna-*
 64 *tional* breeding range maps. Species’ island vs. mainland residence was also de-
 65 termined using breeding ranges from *BirdLife International*. Mainland residence
 66 was assigned if the species had a breeding range on any continent and Japan.

67 Island residence was assigned to species having a breeding range limited to a
68 non-continental landmass entirely surrounded by an oceanic body of water.

69 **Statistical Modeling**

70 We used phylogenetically-corrected Bayesian multilevel logistic regression mod-
71 els using the *brms* v2.13.0 package [13] in R v4.0.0 [5] where responses, the
72 number of sexually-dichromatic patches >1, 2, and 3 chromatic and achromatic
73 JNDs, were modeled as binomial trials ($N=5$ plumage patch “trials”) to test for
74 associations with breeding timing, breeding sympatry and breeding spacing. For
75 all phylogenetically-corrected models, we used the *Turdus* phylogeny from Ny-
76 lander et al. (2008) [14] to create a covariance matrix of species’ phylogenetic
77 relationships. All models used a dataset of $N=67$ *Turdus* species for which all
78 data were available.

79 Our *breeding timing* models included the following predictors: z-scores of breed-
80 ing season length (mean centered and divided by one standard deviation), migra-
81 tory behavior (full migration as the reference category versus partial migration
82 or sedentary), and their interaction. *Breeding sympatry* models included the num-
83 ber of sympatric species with greater than 30% breeding range overlap as the
84 only predictor of the number of sexually-dichromatic plumage patches. *Breeding*
85 *spacing* models included loge transformed breeding range size (km²) and breed-
86 ing landmass (mainland as the reference category versus island). We also ran null
87 models (intercept only) for all responses. All models’ intercepts and response
88 standard deviations were assigned a weak prior (Student T: $df = 3$, location = 0,
89 scale = 10), and predictor coefficients were assigned flat priors. We ran each
90 model for 6,000 iterations across 6 chains and assessed Markov Chain Monte
91 Carlo (MCMC) convergence using the Gelman-Rubin diagnostic (Rhat) [15]. We
92 then performed k-fold cross-validation [16] to refit each model $K=16$ times. For
93 each k-fold, the training dataset included a randomly selected set of $(N - N \cdot \frac{1}{K})$
94 or $N \approx 63$ species, and the testing dataset included $(N \cdot \frac{1}{K})$ or $N \approx 4$ species not included in the training dataset. Finally, we com-
95 pared differences between the models’ expected log pointwise predictive den-
96 sities (ELPD) to assess which model(s) best predicted the number of sexually-
97 dichromatic plumage patches [16].
98

99 **Results**

100 We obtained $N \geq 4000$ effective samples for each model parameter and all mod-
101 els’ Markov Chains (MCMC) successfully converged (Rhat = 1 for all models’ pa-
102 rameters).

103 *Table 1: Expected log pointwise predictive densities (ELPD) differences and kfold in-*
104 *formation criterion values of models.*

105 *Table 2: Model predictor effect estimates (posterior median log-odds) on the number*

		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)

of achromatic and chromatic plumage patches with visual contrast values > 1, 2, and
3 JND. Model effects with a probability of direction (pd) value ≥
0.90 are bolded in red for a negative effect and blue for a positive effect on plumage
dichromatism.

Discussion

Conclusions

Acknowledgements

References

- 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.
- 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))
- 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))
- 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))
- R Core Team. 2020 *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Endler JA, Monographs E, Feb N. 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))

- 126 7. Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer
AG, Hart NS, Marshall J, Whiting MJ. 2015 An Integrative Framework for
127 the Appraisal of Coloration in Nature. *The American Naturalist* **185**, 705–
724. (doi:[10.1086/681021](https://doi.org/10.1086/681021))
- 128 8. Clement P, Hathway R. 2000 *Thrushes*. London: A&C Black Publishers
129 Ltd.
- 130 9. del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E. 2017 *Handbook*
131 *of the birds of the world alive*.
- 132 10. BirdLife International and Handbook of the Birds of the World. 2018 *Bird*
133 *species distribution maps of the world*. Version 2018.1.
- 134 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.
135 (doi:[10.1111/2041-210X.12401](https://doi.org/10.1111/2041-210X.12401))
- 136 12. Cooney CR, Tobias JA, Weir JT, Botero CA, Seddon N. 2017 Sexual se-
lection, speciation and constraints on geographical range overlap in birds.
137 *Ecology Letters* **20**, 863–871. (doi:[10.1111/ele.12780](https://doi.org/10.1111/ele.12780))
- 138 13. Bürkner PC. 2017 Brms: An R package for Bayesian multi-
level models using Stan. *Journal of Statistical Software* **80**, 1–28.
139 (doi:[10.18637/jss.v080.i01](https://doi.org/10.18637/jss.v080.i01))
- 140 14. Nylander JAA, Olsson U, Alström P, Sanmartín I. 2008 Accounting for phy-
logenetic uncertainty in biogeography: A bayesian approach to dispersal-
vicariance analysis of the thrushes (Aves: Turdus). *Systematic Biology* **57**,
141 257–268. (doi:[10.1080/10635150802044003](https://doi.org/10.1080/10635150802044003))
- 142 15. Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. 2013
Bayesian data analysis, third edition. Third. Boca Raton, FL: CRC Press.
143 (doi:[10.1201/b16018](https://doi.org/10.1201/b16018))
- 144 16. Vehtari A, Gelman A, Gabry J. 2017 Practical Bayesian model evaluation
using leave-one-out cross-validation and WAIC. *Statistics and Computing*
145 **27**, 1413–1432. (doi:[10.1007/s11222-016-9696-4](https://doi.org/10.1007/s11222-016-9696-4))