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

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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 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 [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

30 an observer is predicted to be able to perceive the two colors as different. However, natural light envi-

31 ronments vary both spatially and temporally [6], bringing into question the accuracy of a 1 JND thresh-

32 old for generalizing visual contrast under natural conditions. Therefore, we calculated the total number

33 of sexually-dichromatic plumage patches per species (out of N=5 measured patches) as the number of

34 plumage patches with average JND values > 1, 2, or 3 to account for uncertainty in visual discrimination

35 thresholds due to variation in psychophysical and ambient lighting conditions affecting the strength of

36 between-sex plumage visual contrast [7].

Life History Data

Breeding Timing Model

39 We collected data on migration behavior and breeding season length from *Thrushes* [8] and the *Handbook*

40 *of the Birds of the World* [9]. We assigned three different kinds of migratory behavior: 1) *full migration*

41 when a species description clearly stated that a species "migrates", 2) *partial migration* when a species

42 was described to have "altitudinal migration", "latitudinal migration" or "movement during non-breeding

43 season", or 3) *sedentary* when when a species was described as "resident" or "sedentary". Breeding season

44 length was defined as the number of months the species breeds each year.

Breeding Sympatry Model

46 Species' breeding ranges were acquired from *BirdLife International* [10]. We calculated congener breeding

47 range overlaps (as percentages) using the *letsR* package in R [11]. We then calculated the number of

48 sympatric species as the number of congeners with breeding ranges that overlap >30% with the focal

49 species' breeding range [12].

Breeding Spacing Model

51 Species' breeding range sizes (in km2) were acquired using the *BirdLife International* breeding range maps.

52 Species' island vs. mainland residence was also determined using breeding ranges from *BirdLife Interna-*

53 *tional*. Mainland residence was assigned if the species had a breeding range on any continent and Japan.

54 Island residence was assigned to species having a breeding range limited to a non-continental landmass

55 entirely surrounded by an oceanic body of water.

Statistical Modeling

57 We used phylogenetically-corrected Bayesian multilevel logistic regression models using the *brms* v2.13.0

58 package [13] in R v4.0.0 [5] where responses, the number of sexually-dichromatic patches >1, 2, and 3

59 chromatic and achromatic JNDs, were modeled as binomial trials (N=5 plumage patch "trials") to test

60 for associations with breeding timing, breeding sympatry and breeding spacing. For all phylogenetically-

61 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 and divided by one standard deviation), migratory behavior (full migration as the reference category versus partial migration or sedentary), 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 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.

Results

We obtained N ≥ 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 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).

All model predictors' effect estimates are provided as the posterior median log-odds and 90% highest-density interval in Table 2. Among predictors of achromatically sexually-dimorphic plumage patches, only predictors included in the *breeding timing* model have predictors with probability of direction (*pd*) values > 0.9 (Table 2). Specifically, greater breeding season length is associated with lower odds of a species

having a sexually-dimorphic plumage patch with achromatic JND > 2 and lower odds of having a plumage patch with achromatic JND > 3. 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, JND > 2 and JND > 3. Finally, both partial and full 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), JND > 2 (breeding season length x both full and partial migration) and JND > 3 (breeding season length x partial migration).

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

Plumage Metric	JND Threshold	Model			
		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 log-odds 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 ≥ 0.90 are bolded in **red** for a negative effect and **blue** for a positive effect on plumage dichromatism.

Model	Parameter	Achromatic, 1 JND	Achromatic, 2 JND	Achromatic, 3 JND	Chromatic, 1 JND	Chromatic, 2 JND	Chromatic, 3 JND
Breeding Timing							
	Intercept	-1.16 (-3.87, 1.67), pd = 0.76	**-8.36 (-16.28, -0.62), pd = 0.98**	**-7.81 (-14.83, -1.66), pd = 0.99**	-0.88 (-2.98, 1.03), pd = 0.78	**-7.21 (-15.29, 0.55), pd = 0.95**	**-12.71 (-28.03, 0.31), pd = 0.96**
	Breeding Season Length	-0.06 (-0.62, 0.56), pd = 0.57	**-2.26 (-4.72, 0.05), pd = 0.97**	**-1.39 (-3.56, 0.4), pd = 0.91**	-0.12 (-0.59, 0.34), pd = 0.66	**-1.99 (-4.64, 0.35), pd = 0.94**	-2.5 (-8.12, 2.21), pd = 0.83
	Partial Migration vs. No Migration	-0.04 (-1.16, 1.01), pd = 0.53	1.41 (-1.2, 4.12), pd = 0.83	1.29 (-0.82, 3.57), pd = 0.85	**0.79 (-0.06, 1.59), pd = 0.94**	1.9 (-0.87, 4.9), pd = 0.88	**4.26 (-1.13, 10.99), pd = 0.92**
	Full Migration vs. No Migration	**1.6 (-0.05, 3.19), pd = 0.96**	**4.2 (1.16, 7.5), pd = 0.99**	**3.11 (0.46, 5.73), pd = 0.98**	0.83 (-0.37, 1.99), pd = 0.88	**4.39 (1.03, 8.14), pd = 0.99**	**5.46 (-0.68, 12.61), pd = 0.95**
	Breeding Season Length x Partial Migration	0.29 (-0.73, 1.37), pd = 0.68	**3.03 (-0.14, 6.38), pd = 0.96**	**2.11 (-0.27, 4.69), pd = 0.94**	0.33 (-0.43, 1.14), pd = 0.76	**2.2 (-0.82, 5.53), pd = 0.9**	3.54 (-2.58, 11.13), pd = 0.85
	Breeding Season Length x Full Migration	**1.58 (-0.4, 3.68), pd = 0.9**	**4.19 (-0.53, 9.34), pd = 0.93**	2.8 (-1.3, 6.72), pd = 0.89	0.52 (-1.16, 2.12), pd = 0.7	**5.08 (-0.18, 11.12), pd = 0.95**	6.07 (-4.27, 17.43), 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	-1.94 (-6.01, 2.01), pd = 0.8	**-9.77 (-20.11, 0.89), pd = 0.95**	**-10.31 (-19.2, -1.98), pd = 0.98**	-0.67 (-3.63, 2.27), pd = 0.65	**-8.32 (-18.86, 2.03), pd = 0.92**	**-12.87 (-30.57, 4.41), pd = 0.91**
	Island vs. Mainland	0.08 (-1.38, 1.57), pd = 0.54	-0.64 (-4.43, 2.88), pd = 0.61	-0.09 (-3.02, 2.96), pd = 0.52	**-1.3 (-2.45, -0.12), pd = 0.97**	-3.39 (-8.67, 1.38), pd = 0.89	-3.26 (-12.57, 4.21), pd = 0.77
	Breeding Range Size	0.08 (-0.13, 0.28), pd = 0.75	0.21 (-0.27, 0.7), pd = 0.77	0.26 (-0.14, 0.66), pd = 0.87	0.02 (-0.14, 0.18), pd = 0.58	0.21 (-0.29, 0.72), pd = 0.77	0.23 (-0.62, 1.1), 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	-0.9 (-3.45, 1.76), pd = 0.72	**-6.89 (-14.7, -0.02), pd = 0.95**	**-6.74 (-13.39, -1.09), pd = 0.98**	**-1.38 (-3.25, 0.3), pd = 0.91**	**-6.34 (-13.61, 0.11), pd = 0.95**	**-11.29 (-22.79, -1.24), pd = 0.98**
	Number of Sympatric Species (≥ 30% Breeding Range Overlap)	0.03 (-0.18, 0.24), pd = 0.61	0.14 (-0.31, 0.56), pd = 0.71	0.12 (-0.27, 0.49), pd = 0.71	**0.34 (0.17, 0.51), pd = 0.99**	**0.46 (0.01, 0.92), pd = 0.96**	**0.75 (0.03, 1.5), 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

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)

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)

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)

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)

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)

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)

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)

13. 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)

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). *Systematic Biology* **57**, 257–268. (doi:10.1080/10635150802044003)

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. (doi:10.1201/b16018)

16. 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)

17. 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)

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