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

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Abstract

Keywords

plumage, *dichromatism*, *species recognition*

Background

Methods

Plumage sexual dichromatism

A total of N=77 *Turdus* thrush species were sampled for plumage spectral reflectance using from bird skins at the American Museum of Natural History in New York City and the Field Museum in Chicago. Reflectance measurements from 300-700nm were taken in triplicate for the belly, breast, throat, crown and mantle plumage patches [1] of each individual bird skin. N=3 male and N=3 female individuals were measured for most species (exceptions: *Turdus lawrencii*, N=2 males and N=2 females; *Turdus 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 all measurements were made relative to a diffuse reflectance white standard (Spectralon WS-1-SL, Labsphere, North Sutton NH, USA).

We used a receptor-noise limited visual model [2] of the European Blackbird (*Turdus 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

28 females sampled), and then JND values were averaged for each species' respective plumage patches. Un-
29 der ideal laboratory conditions, a JND value of 1 is generally considered to be the discriminable threshold
30 past which an observer is predicted to be able to perceive the two colors as different. However, nat-
31 ural light environments vary both spatially and temporally [6], bringing into question the accuracy of a
32 JND=1 threshold for generalizing visual contrast under natural conditions. Therefore, we calculated the
33 total number of sexually-dichromatic plumage patches per species (out of N=5 measured patches) as the
34 number of plumage patches with average JND values > 1, 2, or 3 to account for uncertainty in visual dis-
35 crimination thresholds due to variation in psychophysical and ambient lighting conditions affecting the
36 strength of between-sex plumage visual contrast [7].

Life History Data
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Breeding Timing Model
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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.

Breeding Sympatry Model
45

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
50

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
56

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

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 *Turdus* species for which all data 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 number of sexually-dichromatic plumage patches. *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 number of sexually-dichromatic plumage patches [16].

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).

Table 1: Expected log pointwise predictive densities (ELPD) differences and kfold information criterion values of models.

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% credible 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

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