

¹ Rapid species recognition favors greater avian-perceived
² plumage dichromatism in true thrushes (genus: *Turdus*)

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⁶ **Abstract**

⁷ **Keywords**

⁸ *dichromatism, plumage, species recognition*

⁹ **Introduction**

¹⁰ Species recognition is necessary in sexually reproducing lineages for individuals to find compatible con-
¹¹ specific mates and produce viable offspring [1,2]. Specifically, conspicuous traits signaling species and sex
¹² identity reduce the time and effort expended when searching for compatible mates and lessen the likeli-
¹³ hood of mating with heterospecifics [3]. Accordingly, traits which facilitate species and mate recognition
¹⁴ should be favored when closely-related species are highly sympatric, when the time to find a mate is lim-
¹⁵ ited, and when conspecifics are not encountered often [1]. Alternatively, traits used in species and mate
¹⁶ recognition may also serve as signals of status to conspecifics and reduce costly conflicts over resources
¹⁷ and mates [4].

¹⁸ In birds, plumage colouration is a highly conspicuous trait which signals species and (often) sex iden-
¹⁹ tity [5,6] . Plumage sexual dichromatism, a distinct set of differences in the appearance of male versus
²⁰ female feather colouration, is common in birds and is often attributed to differing selection pressures on
²¹ males and females [7–11]. Fundamentally, plumage sexual dichromatism results in a visible trait useful
²² for recognizing an individual's species, sex, and age (e.g., in species with delayed plumage maturation,
²³ see [12]), reducing the time and effort necessary to identify a suitable mate [13,14]. Evidence in favor
²⁴ of the species recognition hypothesis for sexual dichromatism includes a positive association between
²⁵ migratory behaviour, shorter breeding seasons, and plumage sexual dichromatism [9]. Specifically, bird
²⁶ species that migrate to and from their breeding territories and have large geographic ranges tend to have
²⁷ greater plumage sexual dichromatism than species that do not migrate and have limited breeding ranges
²⁸ [10,15–17]. Additionally, bird species that reside on mainland continents and have larger breeding ranges
²⁹ often have greater plumage colour elaboration and sexual dichromatism than species living on islands with
³⁰ limited breeding ranges [18–23].

Moreover, plumage sexual dichromatism likely plays a role in hybridization avoidance via character displacement to facilitate species and mate recognition. For example, in European *Ficedula* flycatchers, female choice selects for divergent male plumage colouration, leading to character displacement between species and populations and reduced rates of hybridization [24]. More broadly and across taxa, greater plumage dichromatism is positively correlated with transitions from allopatry to parapatry and increases in geographic range overlaps among passerine sister species pairs [25]. Plumage sexual dichromatism has also been found to be positively associated with species richness among sister species pairs, and dichromatism mainly increases through changes in male plumage [26], 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 colour evolution rate and divergence in *Tyrannida* suboscines [27]. Therefore, plumage sexual dichromatism may be an especially favourable trait to facilitate species and mate recognition when closely-related species have sympatric breeding ranges.

True thrushes (genus: *Turdus*) are an exceptionally diverse genus of passerine birds consisting of about ~86 species distributed across the globe (Fig. 1). Plumage sexual dimorphism and migratory behaviors vary substantially between species and have evolved multiple times in thrushes across the world [28,29]. Interestingly, there have been several documented cases of hybridization in *Turdus* thrushes, and there is a large hybrid zone between four *Turdus* species (*T. atrogularis*, *T. eunomus*, *T. naumanni*, *T. ruficollis*) in north-central Asia [30], indicating that some sympatric *Turdus* species interbreed. Therefore, the true thrushes are an ideal passerine clade for examining the species recognition hypothesis for plumage sexual dimorphism.

Overall, ecological conditions that increase the time and degree of difficulty in finding a suitable conspecific mate should select for phenotypic traits that reliably signal species and sex identity. Taken together, repeated findings across various bird lineages of greater plumage dichromatism in species that are i) migratory rather than nonmigratory, ii) have shorter breeding seasons, ii) live on mainlands rather than islands, iv) have larger breeding ranges, and v) breed in sympatry with closely-related species suggests that circumstances where rapid species recognition is challenging strongly favour the evolution and maintenance of prominent plumage sexual dichromatism in birds. Here, we test predictions of the species recognition hypothesis for sexually-dimorphic traits. To this end, we evaluate the potential influences of breeding timing, spacing, and sympatry on plumage dichromatism in the *Turdus* thrushes .

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 [31]

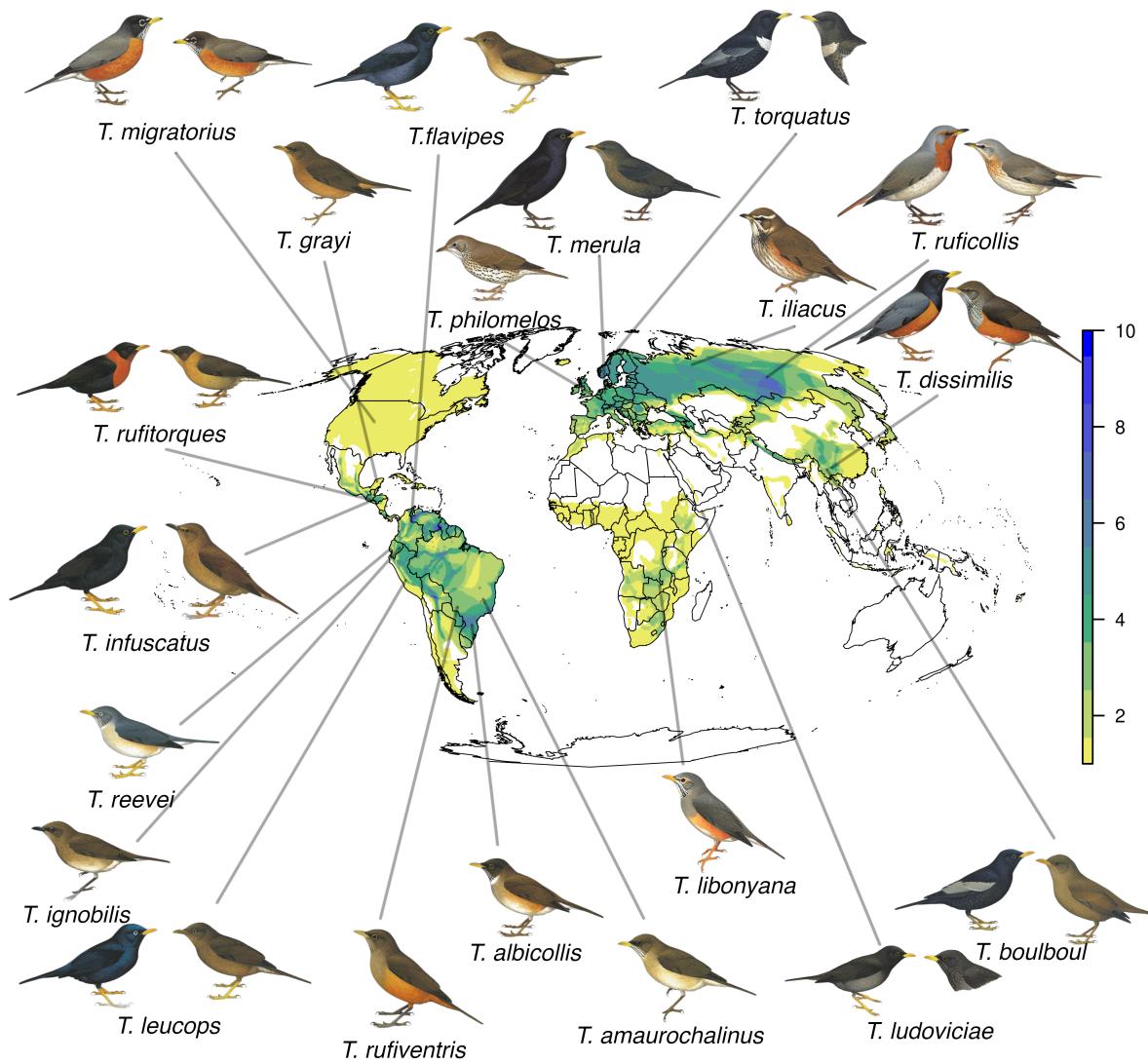


Figure 1: Breeding ranges of all recognized *Turdus* species from BirdLife International. Colors indicate the number of *Turdus* thrush species in sympatry with overlapping breeding ranges. Illustrations © HBW Alive/Lynx Edicions

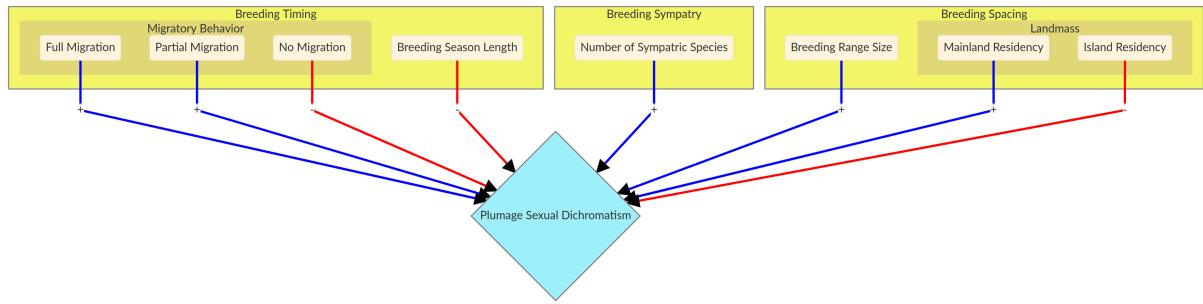


Figure 2: Hypotheses and predictions for each model. Arrow colours indicate predicted correlation, positive (blue) and negative (red).

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^2 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 [32] of the European Blackbird (*T. merula*) visual system [33] in the *pavo* [34] package in R v4.0.0 [35] 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 [36], 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 [37]. Additionally, we modeled the number of divergent plumage patches (JND >1, 2, and 3) within sexes and between different sympatric species under different levels of breeding range overlap (10% increments between 0-90%, Supplementary Figure 1).

90 Life History Data

91 Breeding Timing Model

We collected data on migration behaviour and breeding season length from *Thrushes* [28] and the *Handbook of the Birds of the World* [38]. We assigned three different kinds of migratory behaviour: 1) full migration when a species description clearly stated that a species “migrates”, 2) partial migration when a

95 species was described to have “altitudinal migration”, “latitudinal migration” or “movement during non-
96 breeding season”, or 3) sedentary when a species was described as “resident” or “sedentary”. Breeding
97 season length was defined as the number of months the species breeds each year.

98 **Breeding Sympathy Model**

99 Species’ breeding ranges were acquired from *BirdLife International* [39]. We calculated congener breeding
100 range overlaps (as percentages) using the *letsR* package in R [40]. We then calculated the number of sym-
101 patric species as the number of congeners with breeding ranges that overlap >30% with the focal species’
102 breeding range [25]. Comparisons of the number of sexually-dimorphic plumage patches vs. the number
103 of sympatric species among different breeding range overlap thresholds are provided in Supplementary
104 Figure 2.

105 **Breeding Spacing Model**

106 Species’ breeding range sizes (in km²) were acquired using the *BirdLife International* breeding range maps.
107 Species’ island vs. mainland residence was also determined using breeding ranges from *BirdLife Interna-*
108 *tional*. Mainland residence was assigned if the species had a breeding range on any continent and Japan.
109 Island residence was assigned to species having a breeding range limited to a non-continental landmass
110 entirely surrounded by an oceanic body of water.

111 **Statistical modeling**

112 We used phylogenetically-corrected Bayesian multilevel logistic regression models using the *brms* v2.13.0
113 package [41] in R v4.0.0 [35] where responses, the number of sexually-dichromatic patches >1, 2, and
114 3 chromatic and achromatic JNDs, were modelled as binomial trials (N=5 plumage patch “trials”) to test
115 for associations with breeding timing, breeding sympathy and breeding spacing. For all phylogenetically-
116 corrected models, we used the *Turdus* phylogeny from Nylander et al. (2008) [42] to create a covariance
117 matrix of species’ phylogenetic relationships. All models used a dataset of N=67 out of the *Turdus* species
118 for which all the types of data (see above) were available.

119 Our *breeding timing* models included the following predictors: z-scores of breeding season length
120 (mean-centered by $\mu = 5.4$ months, and scaled by one standard deviation $\sigma = 2.3$ months), migratory
121 behaviour (no migration as the reference category versus partial or full migration), and their interaction.
122 *Breeding sympathy* models included the number of sympatric species with greater than 30% breeding range
123 overlap as the only predictor of the probability of having a sexually-dichromatic plumage patch. *Breeding*
124 *spacing* models included \log_e transformed breeding range size (km²) and breeding landmass (mainland as
125 the reference category versus island). We also ran null models (intercept only) for all responses. All models’
126 intercepts and response standard deviations were assigned a weak prior (Student T: df = 3, location = 0,
127 scale = 10), and predictor coefficients were assigned flat priors. We ran each model for 6,000 iterations
128 across 6 chains and assessed Markov Chain Monte Carlo (MCMC) convergence using the Gelman-Rubin
129 diagnostic (Rhat) [43]. We then performed k-fold cross-validation [44] to refit each model K=16 times.

130 For each k-fold, the training dataset included a randomly selected set of $N - N \frac{1}{K}$ or $N \approx 63$ species,
131 and the testing dataset included $N \frac{1}{K}$ or $N \approx 4$ species not included in the training dataset. Finally, we
132 compared differences between the models' expected log pointwise predictive densities (ELPD) to assess
133 which model(s) best predicted the probability of having a sexually-dichromatic plumage patch. [44].

134 Models' predictor effects were assessed using 90% highest-density intervals of the posterior distribu-
135 tions and probability of direction, the proportion of the posterior distribution that shares the same sign
136 (positive or negative) as the posterior median [45], to provide estimates of the probability of that a pre-
137 dictor has an entirely positive or negative effect on the presence of sexually-dimorphic plumage patches.
138 We assume predictor estimates with a probability of direction ≥ 0.90 to be indicative of a true existence
139 of a predictor's effect on sexually-dimorphic plumage patches [45].

140 Results

141 Model comparisons

142 We obtained $N \geq 4000$ effective posterior samples for each model parameter and all models' Markov
143 Chains (MCMC) successfully converged ($Rhat = 1$ for all models' parameters) (Supplementary Figure 3, 4).
144 All *breeding sympatry*, *breeding timing*, and *breeding spacing* models performed similarly well and substan-
145 tially better than *intercept only* models in predicting the probability of having a sexually dimorphic plumage
146 patch with achromatic JND values > 1 , 2, or 3 (Table 1; all models predicting achromatic plumage patches
147 had ELPD values within 4, following the convention of Burnham and Anderson (2002)[46]). Among mod-
148 els predicting the probability of having a sexually-dichromatic plumage patch with chromatic JND values
149 > 1 , 2, or 3, all *breeding sympatry*, *breeding timing*, and *breeding spacing* models performed much better than
150 *intercept only* models, and *breeding sympatry* models had the top predictive performance (Table 1; *breed-*
151 *ing sympatry* models all have ELPD = 0, only the *breeding spacing* models predicting dichromatic plumage
152 patches had similar predictive performance).

153 Achromatic plumage sexual dimorphism predictors

154 All model predictors' effect estimates are provided as the posterior median odds-ratio (OR) and 90%
155 highest-density interval (HDI) in Table 2. Among predictors of achromatic sexually-dimorphic plumage
156 patches, only predictors included in the *breeding timing* model have predictors with probability of direction
157 (*pd*) values ≥ 0.90 (Table 2). Specifically, longer breeding season length was associated with lower odds of
158 a species having a sexually-dimorphic plumage patch with achromatic JND > 2 (breeding season length,
159 OR [90% HDI] = 0.10 [0.01, 1.1], 89.5% decrease in odds per 2.3-month increase in breeding season) and
160 JND > 3 (breeding season length, OR [90% HDI] = 0.25 [0.03, 1.5], 75% decrease in odds per 2.3-month
161 increase in breeding season). Additionally, full migratory behaviour, rather than no migratory behaviour,
162 was associated with greater odds of a species having a sexually-dimorphic plumage patch with achromatic
163 JND > 1 (full migration, OR [90% HDI] = 4.97 [0.95, 24.4]), JND > 2 (full migration, OR [90% HDI] = 66.5
164 [3.2, 1802.4]) and JND > 3 (OR [90% HDI] = 22.3 [1.6, 307.9]). Finally, both full and partial migratory

behaviour, rather than no migration behaviour, 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 was 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 behaviour 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 was 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 was 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.

Plumage Metric	JND Threshold	Model			
		Breeding Sympatry	Breeding Timing	Breeding Spacing	Intercept Only
Achromatic					
	1 JND	0 \pm 0 (-122.17 \pm 0.67)	-2.51 \pm 2.49 (-124.68 \pm 2.38)	-2.59 \pm 1.01 (-124.76 \pm 1.04)	-21.69 \pm 7.36 (-143.87 \pm 7.51)
	2 JND	0 \pm 0 (-98.94 \pm 7.56)	-1.19 \pm 3.95 (-100.13 \pm 9.22)	-0.7 \pm 1.34 (-99.64 \pm 7.92)	-52.42 \pm 12.67 (-151.36 \pm 13.4)
	3 JND	-0.04 \pm 1.4 (-85.4 \pm 8.91)	-1.7 \pm 4.41 (-87.07 \pm 10.71)	0 \pm 0 (-85.37 \pm 8.76)	-28.54 \pm 10.02 (-113.91 \pm 13.65)
Chromatic					
	1 JND	0 \pm 0 (-115.75 \pm 2.95)	-5.67 \pm 3.55 (-121.42 \pm 2.28)	-2.73 \pm 3.4 (-118.49 \pm 2.67)	-14.8 \pm 7.22 (-130.55 \pm 7.05)
	2 JND	0 \pm 0 (-88.47 \pm 8.77)	-3.8 \pm 4.46 (-92.27 \pm 10.01)	-3.32 \pm 5.29 (-91.79 \pm 10.91)	-50.53 \pm 14.49 (-139 \pm 16.77)
	3 JND	0 \pm 0 (-62.77 \pm 10.41)	-8 \pm 4.32 (-70.77 \pm 12.29)	-4.43 \pm 3.9 (-67.2 \pm 11.72)	-47.63 \pm 15.34 (-110.4 \pm 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 ≥ 0.90 are bolded in **red** for a negative effect and **blue** for a positive effect on plumage dichromatism. Phylogenetic signal (λ) 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
Breeding Timing							
	Intercept	0 (0, 0.54), pd = 0.98	0 (0, 0.19), pd = 0.99	0 (0, 0.19), pd = 0.99	0.41 (0.05, 2.79), pd = 0.78	0 (0, 1.73), pd = 0.95	0 (0, 1.37), pd = 0.96
	Breeding Season Length	0.1 (0.01, 1.05), pd = 0.97	0.25 (0.03, 1.49), pd = 0.91	0.25 (0.03, 1.49), pd = 0.91	0.89 (0.56, 1.4), pd = 0.66	0.14 (0.01, 1.42), pd = 0.94	0.08 (0, 9.14), pd = 0.83
	Partial Migration vs. No Migration	0.76 (0.31, 2.75), pd = 0.53	4.11 (0.3, 61.54), pd = 0.83	3.65 (0.44, 33.64), pd = 0.85	2.2 (0.24, 4.89), pd = 0.94	6.7 (0.42, 134.8), pd = 0.88	71.16 (0.32, 59062.92), pd = 0.92
	Full Migration vs. No Migration	4.37 (0.95, 24.41), pd = 0.96	66.52 (3.19, 1802.4), pd = 0.99	22.34 (1.59, 307.9), pd = 0.98	2.29 (0.69, 7.31), pd = 0.88	80.31 (2.81, 343.86), pd = 0.99	234.71 (0.51, 200382.62), pd = 0.95
	Breeding Season Length x Partial Migration	1.34 (0.48, 3.92), pd = 0.68	20.71 (0.87, 589.09), pd = 0.96	8.28 (0.76, 109.11), pd = 0.94	1.39 (0.65, 31.32), pd = 0.76	9.03 (0.44, 251.36), pd = 0.9	34.46 (0.08, 68228.71), pd = 0.85
	Breeding Season Length x Full Migration	4.34 (0.67, 39.63), pd = 0.9	66.3 (0.59, 11415.7), pd = 0.93	16.41 (0.27, 824.69), pd = 0.89	1.68 (0.31, 8.33), pd = 0.7	160.6 (0.84, 67791.13), pd = 0.95	433.67 (0.01, 371945.69), 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	0 (0, 2.44), pd = 0.95	0 (0, 0.14), pd = 0.98	0 (0, 0.14), pd = 0.98	0.51 (0.03, 9.7), pd = 0.65	0 (0, 7.63), pd = 0.92	0 (0, 8.19), pd = 0.91
	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	0.27 (0.09, 0.89), pd = 0.97	0.03 (0, 3.99), pd = 0.89	0.04 (0, 67.59), 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 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	0.41 (0.03, 5.83), pd = 0.72	0 (0, 0.98), pd = 0.95	0 (0, 0.34), pd = 0.98	0.25 (0.04, 1.35), pd = 0.91	0 (0, 1.12), pd = 0.95	0 (0, 0.29), pd = 0.98
	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	1.4 (1.18, 1.67), pd = 0.99	1.59 (1.01, 2.52), pd = 0.96	2.11 (1.03, 4.46), 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)

186 **Discussion**

187 In support of the species recognition hypothesis for plumage sexual dimorphism, we found that the odds
188 of plumage sexual dimorphism are greater for species that migrate, have short breeding seasons, and are
189 in sympatry with many other congeneric species (Table 1,2).

190 **Conclusions**

191 **Acknowledgements**

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