RAPID SYMPATRY EXPLAINS GREATER COLOR PATTERN DIVERGENCE IN HIGH LATITUDE BIRDS

Paul R. Martin,[1,2,3] Robert Montgomerie,[1,4] and Stephen C. Lougheed[1,5]

[1]*Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3N6*

[2]*Yanayacu Biological Station, Napo, Ecuador*

[3]*E-mail: pm45@queensu.ca*

[4]*E-mail: mont@queensu.ca*

[5]*E-mail: lough@queensu.ca*

Latitudinal variation in patterns of evolution has fascinated biologists for over a century, but our understanding of latitudinal differences in evolutionary processes—such as selection and drift—remains limited. Here, we test for, and find, accelerated evolution of color patterns in bird taxa that breed at higher latitudes compared with those breeding in the tropics, analyzing data from seven diverse avian families. Most important, we show that the extent of overlap of species' breeding ranges (degree of sympatry) explains the elevated rate of color pattern evolution at higher latitudes. We suggest that the dynamic shifts in breeding ranges that accompanied climatic changes during the last 3 million years (Milankovitch Oscillations) resulted in more rapid and more frequent secondary contact at high latitudes. We argue that sympatry among diverging clades causes greater divergence of color traits in birds at higher latitudes through sexual, social, or ecological character displacement that accelerate rates of evolution, and through the selective elimination of weakly differentiated lineages that hybridize and fuse in sympatry (differential fusion).

KEY WORDS: Character displacement, color patterns, differential fusion, latitudinal gradients, rates of evolution, reinforcement, speciation, sympatry.

Patterns of evolution show striking differences between the tropics and higher latitudes, a disparity known to biologists for over a century (Darwin 1859; Wallace 1878). Despite continued interest and active research efforts, our understanding of the evolutionary forces that underlie latitudinal patterns—such as latitudinal variation in natural or sexual selection, gene flow, drift, or mutation—remains limited (Mittelbach et al. 2007). For organisms with generation times and metabolic rates that vary with temperature, rates of evolution appear generally to be highest in the warmer tropics (Rohde 1992, 1999; Allen et al. 2002, 2006; Wright et al. 2006), but in birds and mammals more rapid phenotypic evolution seems to occur at higher, colder latitudes (Chek et al. 2003; Weir and Schluter 2007). This trend in birds and mammals is shown by young sister species with divergent phenotypes at higher latitudes, and by tropical populations that have been separated for long periods of time without evolving phenotypic differences worthy of species recognition (Hackett and Rosenberg 1990; Chek et al. 2003; Weir and Schluter 2007). Thus, rates of phenotypic evolution in birds and mammals appear to contrast with their global patterns of species richness wherein tropical regions have the highest number of species in most clades (Willig et al. 2003; Hillebrand 2004).

What causes accelerated evolution of phenotypes in some high latitude organisms? Possible mechanisms involve rapid and frequent secondary contact and sympatry between differentiated lineages that could (1) increase rates of divergence through

character displacement (Dobzhansky 1937; Brown and Wilson 1956; Coyne and Orr 1989, 2004) and (2) reduce the number of weakly differentiated lineages through hybridization and dissolution ("differential fusion"; Templeton 1981). Character displacement involves divergent evolution among two or more lineages due to selection that directly results from the fitness costs of sharing similar traits in sympatry. These costs may be caused by mixed mating and hybridization (resulting in sexual character displacement, including reinforcement; Dobzhansky 1937; Coyne and Orr 1989, 1997; Servedio and Noor 2003; Coyne and Orr 2004), misdirected intraspecific aggression (resulting in social character displacement; West-Eberhard 1983; Kingston et al. 2001; Tynkkynen et al. 2005), or ecological similarity (resulting in ecological character displacement; Brown and Wilson 1956; Grant and Grant 2006). The frequent spatial shifting of species distributions at higher latitudes through cycles of changing climate (Milankovitch Oscillations; Dynesius and Jansson 2000; Jansson and Dynesius 2002; Bush et al. 2004) creates the potential for rapid secondary range shifts into sympatry, and accelerated divergent evolution by character displacement. Distribution shifts that result in sympatry could also lead to the hybridization and fusion of lineages that are insufficiently diverged. This lineage fusion would not increase rates of evolution within lineages, but could increase the mean rate of evolution among the remaining lineages by selectively eliminating poorly differentiated lineages that fuse together in sympatry (Templeton 1981; Coyne and Orr 2004). Thus, frequent range shifts that result in sympatry could plausibly explain previous evidence for faster phenotypic evolution in some higher latitude organisms through the combined mechanisms of character displacement and differential fusion.

The goals of this study were to (1) test whether the rates of color pattern evolution in birds vary with latitude, and upon finding that they do, (2) test whether the frequency and extent of range shifts resulting in sympatry, character displacement, and differential fusion explains the concomitant latitudinal variation in color pattern evolution better than alternative hypotheses. To accomplish these goals, we used sister-clade estimates of (1) plumage and bare part differences in color patterns (hereafter "color pattern divergence"), (2) the extent of breeding range overlap (degree of sympatry), and (3) the magnitude of sequence divergence in putatively neutral mtDNA markers for high- and low-latitude clades of birds. We examined plumage and bare part color patterns because colors play important roles in reproductive isolation and speciation in birds (Price 2008).

Materials and Methods

We first present a summary of our methods followed by specific details for the selection of taxa, calculation of each metric used

in our analyses, evidence for phylogenetic independence, and phylogenetic and statistical methods.

To do this study, we examined seven phylogenetically and ecologically diverse families of New-World birds that have both tropical and high-latitude species (Picidae, Accipitridae, Tyrannidae, Turdidae, Parulidae, Emberizidae, and Fringillidae), allowing us to compare between latitudinal regions within families. For each family, we defined high-latitude species as those whose breeding ranges have an area-weighted mean (centroid) latitude >40°, and low-latitude species as having their breeding latitude centroid between the Tropics of Cancer and Capricorn. Using only these high- and low-latitude taxa, we estimated color pattern divergence of males in breeding (alternate) plumage by using human observers to rank and rate differences in plumage and bare part color and pattern (see Montgomerie 2006 for review of this methodology) between all pairs of species or subspecies within each region. We then calculated the mean color pattern divergence between paired sister-clades within each region at each successively deeper node in their respective phylogenies. For these paired sister-clades, we also calculated the extent of overlap of their respective breeding ranges.

Within each family, we used homologous regions of mtDNA to calculate mean sequence divergence between focal sister-clades. Assuming that these mitochondrial genes evolved at similar rates within families, this index of sequence divergence is roughly comparable to the time since lineages began to separate (Weir et al. 2008). We repeated this analysis using coalescent-based estimates of time-to-most-recent-common-ancestor (TM-RCA; Drummond et al. 2005) to provide an alternative estimate of phylogenetic divergence. We also performed this analysis using a sister-species approach to ensure that our results were not a spurious consequence of our sister-clade methodology. Our primary analysis did not involve sister-species comparisons because taxonomic effort varies with latitude and can bias analyses that rely upon species-level taxonomy (Weir and Schluter 2007; Tobias et al. 2008). All sequence data were obtained from Genbank, from birds sequenced as part of previous work by many different researchers (Appendix S1).

Our divergence estimates using mtDNA sequences assume that differences among lineages are selectively neutral and do not reflect different rates of evolution over latitude. However, recent evidence for global variation in selection on mtDNA in humans associated with temperature (Balloux et al. 2009), and evidence for selection acting on mtDNA in birds (e.g., Cheviron and Brumfield 2009), suggests that broad-scale variation in mtDNA haplotypes and haplotype diversity may be influenced by natural selection and may thus reflect different rates of evolution. Nonetheless, three lines of evidence indicate that differential selection and rates of evolution of mtDNA across latitudes did not bias our results. First, shifts in mtDNA haplotypes in humans were associated with

major population movements from warm to cold or cold to warm environments (Balloux et al. 2009). Instead of moving into new temperature environments, the distributions of many bird species shift to track changing environmental temperatures to which they are adapted (Root 1988; Thomas and Lennon 1999; Hitch and Leberg 2007; La Sorte and Thompson 2007). Bird species would thus live in similar environmental temperatures during the periods of divergence, so a major shift in mtDNA evolution due to selection by temperature is not expected. Second, previous studies of birds (Bromham and Cardillo 2003; Weir and Schluter 2008) did not find significant variation in rates of mtDNA evolution over latitude. Finally, the relative patterns of relatedness between taxa based on mtDNA have been found to be similar to those incorporating nuclear genes, that should not be under similar selection due to climate (*Picoides*, Weibel and Moore 2002; *Empidonax*, Johnson and Cicero 2002; *Catharus*, Winker and Pruett 2006; *Dendroica*, Rabosky and Lovette 2008).

SELECTION OF TAXA

We focused on seven bird families, each of which included species with both high latitude and tropical breeding ranges, with each family having at least four species in each latitudinal group. No high latitude, southern hemisphere taxa met our criteria so all comparisons are between northern hemisphere high-latitude species and tropical species. We quantified breeding ranges because only these are critical for reproductive isolation and speciation (Mayr 1963). We examined radiations with ≥4 species because they provided at least three nodes for estimating range overlap, color pattern divergence, and genetic differentiation. We excluded (1) taxa endemic to islands, to avoid potential biases of island isolation on latitudinal effects, and (2) all species for which we had DNA sequence data for <80% of congeners within a recent clade (<6% sequence divergence; see below).

We included all taxa from the Americas for which we had >500 DNA base pairs from homologous regions of the mitochondrial genome available for comparable sister-clades in both latitudinal regions (i.e., high latitudes and tropics). This allowed us to align DNA sequences between groups, and to estimate sequence divergence for all sister-clades using the same genes within a family.

To test hypotheses, we examined sister-clades up to and including those with 6% mtDNA sequence divergence. We selected a 6% sequence divergence cutoff because this subset of clades allowed us to examine recent and rapid color pattern divergence over a time period relevant to recent speciation in birds (Johnson and Cicero 2004; Weir and Schluter 2007). Clades (lineages) were compared regardless of their current taxonomic status. Thus, we compared clades that represented subspecies, species, and superspecies whenever DNA sequence data were available and the taxa met our criteria. Our sister-clade comparisons of color pattern divergence and breeding range overlap excluded taxa that occurred outside the focal regions (either high latitudes or tropics), and excluded all island endemics, even when those taxa comprised a lineage within focal clades. We did not compare taxa between high latitudes and the tropics—any high-latitude taxa that occurred within focal clades were excluded from tropical comparisons, and tropical taxa were excluded from high-latitude comparisons.

COLOR PATTERN DIVERGENCE

Color pattern differences between pairs of taxa were estimated by seven human observers unfamiliar with the objectives of the study, using both ranking and rating methods. Both the rankings and ratings were highly repeatable across observers (see below). This method has been used successfully in other studies of bird coloration (Montgomerie 2006), but cannot, of course, take into account colors in the bird-visible UV range (320–400 nm), which are invisible to human observers, or subtle differences in reflectance spectra that would not be easily discerned by the human eye. We employed human observers to quantify the color pattern differences between species because we felt that no other method reliably allowed comparisons of whole plumages with respect to both color and pattern. One alternative would be to define color patches, measure the color of each patch using reflectance spectrometry, and then compare the suite of measurements between species. Endler and Mielke (2005) developed a sophisticated statistical method for comparing bird colors in this fashion, taking into account colors in different patches, ambient light, and bird vision parameters, but this method does not include the comparison of patterns. Armenta et al. (2008) found that various other quantitative measures of sexual dichromatism in birds, using reflectance spectrometry, were significantly correlated with the human assessment of sexual dimorphism. Thus, our method using human observers to quantify species differences in color and pattern has some external validity based on more objective methods to measure color but has the added advantage of comparing pattern as well. Certainly, the use of human observers to make such comparisons is likely to result in some measurement error—especially given that human observers cannot see into the UV range—but there is no reason to believe that such error is biased in favor of the hypotheses we tested in this study.

Each observer ranked all pairs of taxa within each family from least to most different with respect to both plumage and bare part colors and color patterns. Pairs of taxa were compared within high latitudes or low latitudes, not between latitudinal groups. On a different occasion, each of these observers rated the differences in colors and color patterns between pairs of taxa on a scale of 1 (least different) to 7 (vastly different). All observers received the same written instructions (Appendix S2) and a sheet that presented pictures of pairs of taxa showing examples of ratings from 1 to

7, using published illustrations of birds that were not included in our study (Appendix S3). Each observer was also provided with illustrations of three different bird species, with arrows pointing to examples of color patches. Color patches were not predefined for our focal taxa. Color patches illustrated in our examples were regions of feathers or bare parts that had a consistent color and pattern.

Color illustrations were presented to observers as pairs of bird taxa side by side, each pair on a single sheet of paper. The location of each member of the pair (left or right side), and the direction that the birds faced (left or right) was reversed for one-half of the trials. Both illustrations in each pair were from the same source and were painted by the same artist (see Appendix S3).

We averaged rankings for each pair of illustrations across all seven observers and standardized rankings within each family to a value between 0 and 1 by dividing each rank value by the total number of comparisons within a family. We standardized ratings within observers so that all ratings for each observer had a mean of 0 and a standard deviation of 1 within each family. We then averaged standardized ratings for each pair of illustrations across all seven observers. Interobserver reliability, measured as intraclass correlation coefficients (ICC) within each family, was high and highly significant for both rankings (mean ICC across all families = 0.81, range = 0.73–0.91, all $P < 0.0001$) and ratings (mean ICC across all families = 0.75, range = 0.62–0.95, all $P < 0.0001$).

For both ranking and rating measures, we estimated color pattern divergence as the mean difference between all pairwise comparisons of taxa in sister-clades, where all lineages included in the analysis were represented. For example, mean color pattern divergence between two sister-clades, each comprised of three species, would be calculated as the average of all nine between-clade estimates of color pattern divergence. We calculated and analyzed mean color pattern divergence for rankings and ratings separately.

BREEDING RANGE OVERLAP

Breeding range overlap (sympatry) was calculated as the proportion of the smaller range that occurred within the larger range so that values ranged from zero (no overlap) to one (smaller range completely overlapped by the larger range) (Chesser and Zink 1994; Barraclough and Vogler 2000). Breeding range overlap calculations were restricted to breeding ranges within the Americas if the species had a wider breeding distribution. Breeding ranges were taken from previously generated maps (Martin and Tewksbury 2008) with updates from Poole (2009). All calculations were made within ArcGIS 9.1 (ESRI, Redlands, CA) using Xtools Pro 4.2 (Data East, Novosibirsk, Russia).

Species missing from our dataset due to lack of sequence data could artificially increase apparent allopatry because their ranges would not be included in our analysis of range overlaps within focal clades. To correct for this, we incorporated these "missing" taxa into phylogenies using other published data (e.g., anatomical traits, other genes), so that their ranges would be included in our analyses of breeding range sympatry (see Appendix S1 for details).

GENETIC DIVERGENCE

Genetic divergence was estimated as the mean proportion of nucleotide sites that differed between clades (p-distance; Nei and Kumar 2000), calculated using the program MEGA version 4 (Tamura et al. 2007), and a coalescent approach (TMRCA) calculated using the program BEAST version 1.4.6 (Drummond and Rambaut 2007). For TMRCA calculations, we used a GTR + I + G model of evolution with six gamma categories, and a relaxed lognormal clock for all taxa but *Anairetes*, where the HKY + I model of evolution was the best model following MrModeltest version 2.2 (Nylander 2004; see *Phylogenetics section* below). We set the mean substitution rate at 1.0, and used a Yule tree prior, which assumes a constant speciation rate per lineage and has been recommended for species-level phylogenies (Drummond et al. 2005). Thus, TMRCA values of specified internal nodes were estimated as the number of lineages arising from a parent lineage per substitution per site, rather than by employing any particular clock calibration. For each dataset, we conducted three to seven independent runs of 20 million generations each, logging parameter values every 1000 generations. For each run, we discarded the first 10% of logged values as burn-in, and then combined results using the program Tracer version 1.3 (Rambaut and Drummond 2005), verifying that effective sample sizes for each parameter exceeded 100 (and thus that we had adequately sampled the posterior distribution). The details of this analysis for each of the seven examined avian families are as follows: Picidae (four runs, total 80 million generations); Accipitridae (four runs, total 80 million generations); Tyrannidae (three runs, total 60 million generations); Turdidae (seven runs, total 140 million generations); Parulidae (seven runs, total 140 million generations); Emberizidae (two runs, total 40 million generations); Fringillidae (three runs, total 60 million generations).

PHYLOGENETIC INDEPENDENCE

Comparisons of color pattern divergence between high- and low-latitude taxa can be biased if latitudinal comparisons are not phylogenetically independent (Felsenstein 1985). For example, if all high-latitude taxa share a more recent common ancestor that exhibited a particular pattern of phenotypic evolution, we might find differences in color pattern divergence between high- and low-latitude taxa due simply to their phylogenetic history. We controlled for the effects of such phylogenetic dependence by comparing high-and low-latitude taxa within families that shared a

more recent common ancestor, so that all high-latitude taxa shared a more recent common ancestor with low-latitude taxa within a family than they did with other families in our dataset (see Appendix S1 for specific evidence that taxa within families shared a more recent common ancestor). We also made all comparisons between sister-clades at each successively higher node within phylogenies, and thus each comparison was made between equal-aged clades at phylogenetically independent branching points.

PHYLOGENETICS

For *Anairetes* (cyt b + ND2), *Dendroica* (COI), and *Geothlypis* (ND2), we generated our own phylogenies because Bayesian phylogenies that included all focal taxa were not available (see Appendix S1 for details). For these taxa, we generated phylogenies using MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001) with the best of 24 models of evolution chosen using MrModeltest version 2.2 (Nylander 2004). Models selected using the Akaike Information Criterion (AIC) were: *Anairetes* − HKY + I, *Geothlypis* − GTR + G, *Dendroica* − GTR + I + G. For each taxon, we specified the appropriate model but allowed parameter estimates to vary freely and ran two independent, simultaneous Markov chain Monte Carlo (MCMC) chains, with default temperature settings. All runs were for 1 million generations, sufficient for the standard deviation of the split frequencies to reach values less than 0.01, and for the effective sample size for estimated parameters to exceed 100, as calculated by TRACER version 1.3 (Rambaut and Drummond 2005). Trees were sampled every 100 generations. The first 2500 trees were discarded as burn-in, and a 50% consensus tree was built from the remaining 7500 trees.

STATISTICAL METHODS

We tested the prediction that higher latitude clades exhibit greater color pattern divergence, controlling for neutral genetic divergence, using a General Linear Mixed Model (GLMM) fit by maximum likelihood with family as a grouping variable, latitude (high latitude or tropical) as a fixed factor, and neutral genetic divergence (p-distance) as a random factor. A separate analysis was run using TMRCA as an alternative measure of neutral genetic divergence. Color pattern divergence was included as the dependent variable, either as rank values (arcsine transformed to improve the normality of residuals) or ratings, in separate analyses. The GLMM was used because it did not require data to be independent with constant variance within a family (Pinheiro and Bates 2004)—assumptions that were not met by our data. Data were values from each node within focal clades, and thus were phylogenetically independent.

We tested the prediction that higher latitude clades exhibit greater breeding range overlap than tropical clades, controlling for neutral genetic divergence, using a GLMM fit by maximum

likelihood with family as a grouping variable, degree of sympatry as the dependent variable (range: 0–1), latitude (high latitude or tropical) as a fixed factor, and neutral genetic divergence (p-distance or TMRCA in separate analyses) as a random factor. Degree of sympatry was arcsine transformed prior to analysis to improve the normality of residuals.

We tested the prediction that degree of sympatry explains the latitudinal variation in color pattern divergence, controlling for neutral genetic divergence, using a GLMM fit by maximum likelihood with family as a grouping variable, latitude (high latitude or tropical) and degree of sympatry (ranging from 0 to 1) as fixed factors in a saturated model, and neutral genetic divergence (p-distance or TMRCA in separate analyses) as a random factor. Color pattern divergence was included as the dependent variable, either as rank values (arcsine transformed to improve the normality of residuals) or ratings, in separate analyses. We first ran a saturated model, and then evaluated alternative models by comparing bias-adjusted Akaike's information criterion (AICc) values between the saturated model and simplified models that incorporated fewer factors. This information-theoretic approach (Burnham and Anderson 2002) allowed us to compare the strength of evidence for each of the tested hypotheses, given the data. AICc is an adjusted AIC value that corrects for bias associated with small sample sizes. $AICc = AIC + ((2K(K + 1))/(n − K − 1))$, where K is the number of estimated parameters in the model, and n is the sample size (Burnham and Anderson 2002). We used AICc as opposed to AIC values because the ratio of $n/K < 40$ in some of our models.

We performed additional tests of these hypotheses using a sister-species approach that compared only the most closely related pairs of species at high latitudes and low latitudes. To do this, we repeated all GLMM analyses described above using sister species, with rank values for estimates of color divergence and p-distance for estimates of genetic differentiation. This analysis allowed us to verify that our findings were not anomalous results of our sister-clade approach.

Results

For the seven bird families that we studied (Picidae, Accipitridae, Tyrannidae, Turdidae, Parulidae, Emberizidae, and Fringillidae), there were higher rates of color pattern divergence among higher latitude pairs of clades than among tropical clade pairs (color pattern differences controlling for neutral genetic mtDNA—p-distance divergence: GLMM, $t = 3.0$, df = 70, $P = 0.004$; Fig. 1A). Also, across all seven bird families, the degree of breeding range overlap of high latitude clades was greater than that of lower latitude clades (GLMM, $t = 5.0$, df = 70, $P < 0.0001$; Fig. 1B), controlling for levels of mtDNA divergence. However, after controlling for the extent of current breeding range
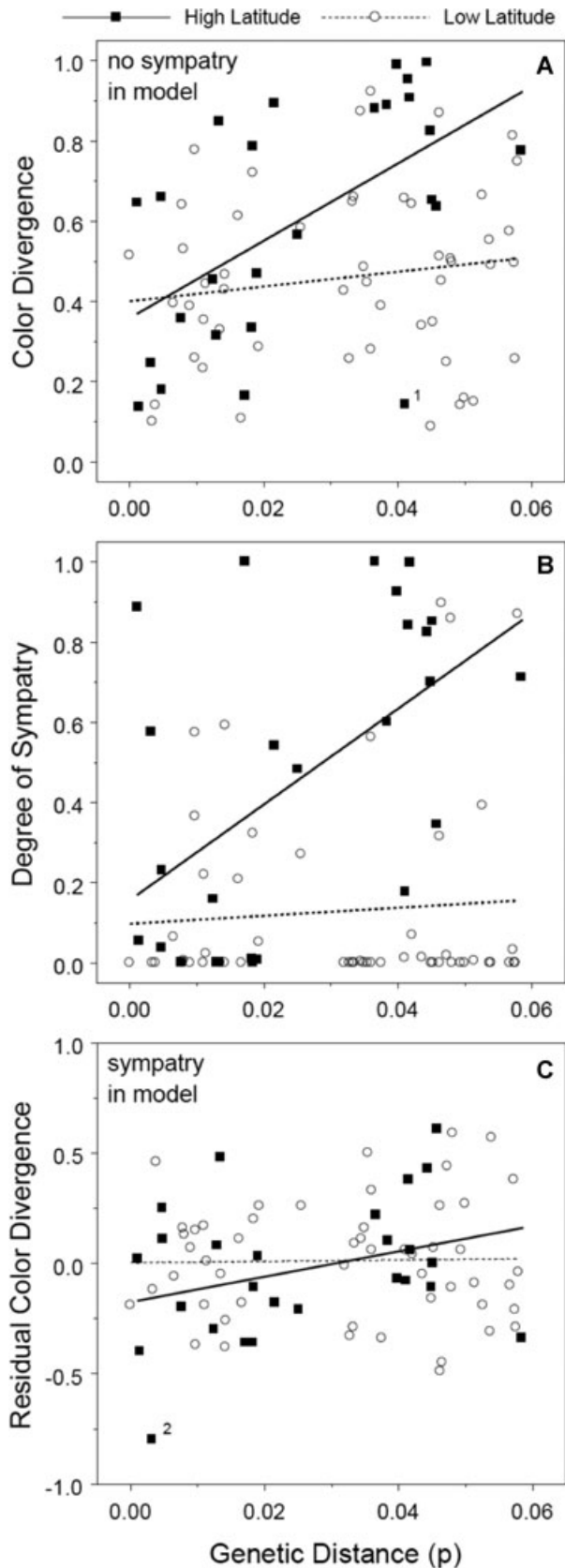
Figure 1. Relations between the mean proportion of mtDNA nucleotide sites that differed (p-distance) and (A) the degree of color pattern divergence (mean rank values), (B) the degree of breeding

overlap (i.e., degree of sympatry), rates of color pattern evolution (Fig. 1A) did not differ significantly between low- and high-latitude clades (saturated GLMM, $t = 0.2$, df = 68, $P = 0.86$; Fig. 1C). Moreover, in both high- and low-latitude clades, the magnitude of color pattern divergence increased with the degree of sympatry (saturated GLMM, $t = 4.3$, df = 68, $P < 0.0001$; Fig. 2), and these relations for high- and low-latitude clades were not significantly different (saturated GLMM, $t = 0.7$, df = 68, $P = 0.49$; Fig. 2). Given our data, the evidence supporting the best model that incorporated only sympatry was 2.2 times stronger than evidence supporting the model with both latitude and sympatry (no interaction term), and 5.2 times stronger than the saturated model incorporating both latitude and sympatry (Table 1). Other models incorporating only latitude or only the intercept received very little support using the IT approach to model evaluation (Table 1).

Analyses using TMRCA to estimate neutral genetic divergence showed similar patterns to analyses that used p-distance (mean proportion of nucleotide sites that differed). Thus, high-latitude clades showed accelerated color pattern divergence (GLMM, $t = 2.9$, df = 70, $P = 0.005$), as well as greater breeding range sympatry controlling for neutral genetic divergence (GLMM, $t = 4.1$, df = 70, $P = 0.0001$). Latitudinal differences in rates of color pattern divergence were again not significantly different once the degree of breeding range sympatry was included in this model (saturated GLMM, $t = 0.2$, df = 68, $P = 0.87$). Moreover, degree of sympatry positively covaried with color pattern divergence when TMRCA was used in the model (saturated GLMM, $t = 4.3$, df = 68, $P = 0.0001$), and this relation did not vary with latitude (saturated GLMM, $t = 0.7$, df = 68, $P = 0.48$). Evidence supporting the best model that incorporated only sympatry was 2.2 times stronger than evidence supporting the model with both latitude and sympatry (no interaction term), and 5.2 times stronger than the saturated model incorporating both

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range overlap (sympatry), and (C) the relative degree of color pattern divergence (mean rank values), controlling statistically for the degree of breeding range sympatry. Each datapoint represents a value for a pair of sister-clades of birds from high (solid squares, solid line, $N = 26$) and low (open circles, dotted line, $N = 52$) latitudes. The rate of color pattern divergence appears to be accelerated at high latitudes compared with the tropics (A; GLMM, $t = 3.0$, df = 70, $P = 0.004$). However, once the latitudinal differences in sympatry (B; GLMM, $t = 5.0$, df = 70, $P < 0.0001$) are taken into account, the latitudinal differences in color pattern divergence are no longer significant (saturated GLMM, $t = 0.2$, df = 68, $P = 0.86$). Outliers are: 1, Tyrannidae: *Empidonax alnorum – E. traillii*; 2, Fringillidae: *Carduelis flammea – C. hornemanni*. For all panels, ordinary least squares regression lines are shown.
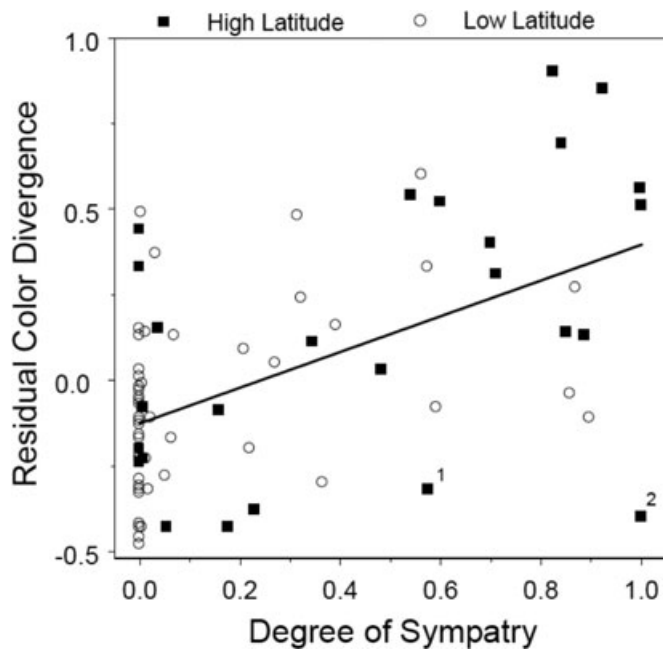
Figure 2. Relation between the extent of breeding range sympatry and mean color pattern divergence (rank values, controlling for genetic distance measured as p–distance) for paired sister-clades of birds at high (solid squares, $N = 26$) and low (open circles, $N = 52$) latitudes. Color pattern divergence increased significantly with the degree of breeding range overlap (saturated GLMM, $t = 4.3$, df = 68, $P < 0.0001$), but high latitude and tropical clade-pairs did not differ significantly (Fig. 1C), nor was there a significant interaction between the degree of sympatry and latitude (saturated GLMM, $t = 0.7$, df = 68, $P = 0.49$). Outliers are: 1, Fringillidae: *Carduelis flammea – C. hornemanni*; 2, Turdidae: *Catharus bicknelli – C. minimus/fuscecens*. An ordinary least squares regression line is shown.

Table 1. AICc values[1], AICc differences (Δ_i)[2], and evidence ratios[3] for GLMM models that examined the effects of latitude and sympatry on color divergence measured by ranking and rating methods.

Model	Ranking method			Rating method		
	AICc	Δ_i	Evidence Ratio	AICc	Δ_i	Evidence Ratio
Sympatry	35.5	min	1.0	183.7	min	1.0
Sympatry + latitude	37.0	1.6	2.2	185.8	2.2	3.0
Sympatry × latitude	38.7	3.3	5.2	188.0	4.4	9.0
Latitude	52.4	16.9	4675	201.1	17.4	6003
Intercept only	58.8	23.3	114,270	203.7	20.0	21,946

[1]AICc = AIC + $((2K(K + 1))/n - K - 1)$, where K is the number of estimated parameters and n is the sample size; AICc adjusts for bias in AIC values caused by small sample sizes (e.g., when $n/K < 40$; Burnham and Anderson 2002).

[2]$\Delta_i = AICc_i - AICc_{min}$.

[3]evidence ratio = $\exp(1/2(\Delta_i))$.

latitude and sympatry. Other models incorporating only latitude or only the intercept received negligible support ($\Delta_i > 17$; see Burnham and Anderson 2002).

Analyses using ratings of color pattern differences (Figs. S1, S2; Table 1) showed similar patterns to those using rankings (Figs. 1 and 2). Thus, color pattern divergence estimated by ratings was significantly greater at higher latitudes (GLMM, $t = 2.2$, df = 70, $P = 0.03$; Fig. S1A), and this difference was not significant once the degree of breeding range sympatry was included in the model (saturated GLMM, $t = 0.1$, df = 68, $P = 0.92$; Fig. S1B). Again, degree of sympatry positively covaried with color pattern divergence as measured by ratings (saturated GLMM, $t = 4.3$, df = 68, $P < 0.0001$; Fig. S2), and this relation did not vary significantly with latitude (saturated GLMM, $t = 0.2$, df = 68, $P = 0.88$; Fig. S2). Evidence supporting the best model that incorporated only sympatry was 3.0 times stronger than evidence supporting the model with both latitude and sympatry (no interaction term), and 9.0 times stronger than the saturated model incor-

porating both latitude and sympatry. Other models incorporating only latitude or only the intercept received negligible support (Table 1).

Further analysis shows that the findings described above were not spuriously caused by our sister-clade methodology. When we used a sister-species approach that compared only the most closely-related species pairs within high and low latitude groups, we found similar results. Thus, high latitude species pairs showed significantly greater color pattern divergence rankings (GLMM, $t = 2.2$, df = 21, $P = 0.039$) and degree of sympatry (GLMM, $t = 3.7$, df = 21, $P = 0.001$) when genetic distance (p-distance) was controlled statistically ($N = 14$ high and 15 low latitude pairs). As before, latitudinal differences in color pattern divergence were no longer significant once the degree of breeding range sympatry was included in the model (saturated GLMM, $t = 0.3$, df = 19, $P = 0.78$). Moreover, the degree of sympatry of sister species positively covaried with color pattern divergence rankings (saturated GLMM, $t = 3.4$, df = 19, $P = 0.003$), and this relation did not vary significantly with latitude (GLMM, $t = 0.9$, df = 19, $P = 0.40$). Evidence supporting the best model that incorporated only sympatry was 3.5 times stronger than evidence supporting the model with both latitude and sympatry (no interaction term), and 8.6 times stronger than the saturated model incorporating both latitude and sympatry. Other models incorporating only latitude or only the intercept received negligible support (Δ_i values were >13).

Our complete dataset is included as Appendix S4.

Discussion

RATES OF COLOR PATTERN EVOLUTION, LATITUDE, AND SYMPATRY

The faster rates of color pattern evolution that we have described in high-latitude taxa (Fig. 1A) provide the first direct evidence of faster phenotypic evolution among high latitude birds compared to those in the tropics. These results are consistent with previous observations that show faster evolution of both species-level differences and the resulting transition times to speciation among high-latitude populations of birds and mammals (Chek et al. 2003; Weir and Schluter 2007). We have shown that more rapid color pattern divergence in high-latitude birds coincided with faster secondary contact and greater breeding range overlap (sympatry) at high latitudes (Fig. 1B). Thus, once we controlled for sympatry, we no longer found a latitudinal difference in rates of color pattern evolution (Fig. 1C). These relations suggest a direct role of breeding range overlap in the divergent and accelerated evolution of color pattern in high-latitude birds.

The ranges of species are dynamic through time, and our analysis assumes that the degree of breeding range overlap among clades approximates the degree of overlap that occurred during the evolution of color patterns (Losos and Glor 2003). Our inability to directly relate specific historical patterns of sympatry to current patterns of color divergence certainly reduces our power to detect the influence of sympatry on rates of evolution, and increases variation in the relation between sympatry and divergence (Fig. 2). Nonetheless, most populations of birds are believed to initially diverge in allopatry and subsequently expand their ranges into sympatry at some later time (Phillimore et al. 2008; Price 2008). Thus, our estimates of present-day breeding range overlap among lineages may provide a relative estimate of the degree to which lineages have moved and expanded their ranges from allopatry into sympatry, and, as a result, provide a relative index of the historical importance of sympatry in the evolution of present-day color patterns.

CHARACTER DISPLACEMENT AND DIFFERENTIAL FUSION OF LINEAGES

We do not know the relative contributions of character displacement and the differential fusion of lineages to the enhanced color pattern divergence of birds at high latitudes. Character displacement uniquely predicts accelerated rates of evolution within lineages that exhibit an increased degree of sympatry (Coyne and Orr 2004). These patterns are evident in our dataset, as there are three instances of color pattern divergence in sympatry that exceed all values found in allopatry (controlling for neutral mtDNA sequence divergence; Fig. 2). Greater rates of color pattern evolution among these three sympatric sister-clades compared to all allopatric clade pairs suggest that character displacement in sym-

patry has likely contributed to the greater color divergence evident at higher latitudes (Fig 1A).

There are several potential causes of character displacement when taxa move into sympatry. First, sexual character displacement (including reinforcement) would occur if costs associated with the reduced fitness of hybrids favored the divergence of color patterns involved in prezygotic isolation (Dobzhansky 1937; Coyne and Orr 1989, 1997; Servedio and Noor 2003). Recent evidence for a significant (mean) effect of assortative mating across 58 studies of avian hybrid zones (Randler 2008) supports a role for reproductive character displacement in the kind of rapid divergent evolution of color pattern that we have documented. Second, social character displacement may result when costs associated with misdirected intraspecific aggression favor the divergence of color patterns involved in species recognition (West-Eberhard 1983; Kingston et al. 2001; Tynkkynen et al. 2005). Third, ecological character displacement requires that ecological costs associated with similarity in color patterns favor divergence in those patterns (Brown and Wilson 1956), for example if similarities in color pattern lead to a positive density-dependent predator response.

In contrast to character displacement, the differential fusion of lineages does not cause faster rates of evolution within lineages (Coyne and Orr 2004; Lukhtanov et al. 2005), but instead can result in higher mean rates of evolution among lineages by selectively eliminating weakly differentiated clades through hybridization (Templeton 1981). The paucity of datapoints in the lower right quadrant of Figure 2 is consistent with the differential fusion of lineages, but is also consistent with character displacement.

Lineages that are fusing in the present-day provide additional evidence for the role of differential fusion in causing faster mean rates of evolution of color pattern in high-latitude birds. For example, current patterns of hybridization, coupled with mtDNA haplotype signatures of historical hybridization, suggest that *Dendroica townsendi* and *D. occidentalis*, both species included in the present analysis, will eventually fuse from two lineages into one (Rohwer et al. 2001). These two lineages apparently came into secondary sympatry so soon after differentiation that they were not different enough to have allowed sexual character displacement or reproductive isolation to occur (Rohwer et al. 2001; Rohwer and Martin 2007). Thus, we conclude that both character displacement and differential fusion could have contributed to the greater rates of color pattern divergence at high latitudes that we document here.

ALTERNATIVE HYPOTHESES FOR GREATER COLOR DIVERGENCE AT HIGH LATITUDES

Although the degree of breeding range sympatry explained much of the variation in rates of color evolution across latitudes that

we describe (Fig. 1), we cannot exclude other factors. Models that incorporated both the degree of breeding range sympatry and latitude received some support in our analysis (Table 1), suggesting that factors that covary with latitude, other than the degree of sympatry, may influence rates of color pattern divergence.

For example, several alternative hypotheses could explain the faster evolutionary divergence of color pattern among high latitude birds. First, extrapair fertilizations may be more prevalent in socially monogamous birds at higher latitudes, due to greater breeding synchrony, faster pair formation, higher breeding density, accelerated adult mortality, or increased female opportunity for such matings (Stutchbury and Morton 1995, 2001; Macedo et al. 2008). Higher extrapair fertilization rates at higher latitudes could thus increase both the intensity of sexual selection and the divergence of color patterns. Second, genetic drift may be more prevalent at higher latitudes because of bottlenecks during the recolonization of breeding habitats following a glacial recession (Hughes and Hughes 2007), or as a result of the isolation of small populations during glaciations (Weir and Schluter 2004). Genetic drift may increase the divergence of populations undergoing sexual selection (Uyeda et al. 2009), thus increasing rates of divergent evolution of color pattern in high-latitude birds. Third, fragmentation and the divergence of populations could also be more common at higher latitudes owing, in part, to the presence of glacial ice sheets (Weir and Schluter 2004) or to the isolation of high-latitude populations during a glacial recession (e.g., relict populations at higher elevations). Greater fragmentation of populations could potentially increase rates of color divergence in birds through divergent selection in the absence of gene flow. However, the absence of phenotypic differentiation among many isolated populations at lower latitudes (Hackett and Rosenberg 1990; Chek et al. 2003; Martin and McKay 2004; Weir and Schluter 2007) does not support a role for greater isolation causing faster rates of color divergence. Fourth, greater taxonomic richness in the tropics may constrain the divergent evolution of color pattern, and thus may reduce rates of color evolution at lower latitudes (Chek et al. 2003). This mechanism assumes that the convergent evolution of color patterns among sympatric taxa results in fitness costs, and thus that regions with higher sympatric species richness are limited in their potential for color pattern evolution (perhaps through mechanisms similar to social or ecological character displacement). Weir (2006), for example, found that the number of sympatric species negatively covaries with diversification rates in lowland but not in highland Neotropical birds, suggesting that high tropical sympatric species richness in the lowlands could constrain diversification rates.

Although these other mechanisms could increase rates of color pattern evolution in high-latitude birds, none of the alternative hypotheses predicts the positive relationship between the degree of breeding range sympatry and rates of color pattern evolution that we have uncovered (Fig. 2), because none of these hypotheses invokes interactions with other sympatric species as the cause of more rapid color pattern evolution. Most of the latitudinal variation in rates of color evolution in our study was explained by the degree of breeding range sympatry (Fig. 1), suggesting that other factors have smaller, if any, effects on rates of color pattern evolution across latitudes.

Rates of evolution may be influenced by variation in generation times and mutation rates, both of which increase with metabolic rate in many organisms (Shigenaga et al. 1989; Martin and Palumbi 1993; Allen et al. 2006; Wright et al. 2006). In contrast to organisms whose generation times and metabolic rates vary with temperature (Rohde 1992; Allen et al. 2006), birds appear to have shorter generation times at higher latitudes, based on lower annual survival rates and higher annual fecundity (clutch size), at least in the northern hemisphere (Ghalambor and Martin 2001). Similarly, metabolic rates of birds appear to be faster at higher latitudes (Wikelski et al. 2003), potentially causing higher rates of mutation (Shigenaga et al. 1989). Both shorter generation times and higher mutation rates could increase rates of evolution (Shigenaga et al. 1989; Martin and Palumbi 1993; Allen et al. 2006), and thus could contribute to the patterns that we found in our study. However, we expect shorter generation times and higher mutation rates to increase rates of evolution for both putatively neutral mitochondrial genes and phenotypic traits such as color pattern. Thus, shorter generation times and faster metabolic rates in high-latitude birds cannot explain the accelerated rates of color pattern evolution relative to mtDNA divergence that we show (Fig. 1A).

RAPID SYMPATRY, COLOR DIVERGENCE, AND RATES OF SPECIATION

Rates of speciation are generally thought to be higher in the tropics (Jablonski 1993; Jablonski et al. 2006; Mittelbach et al. 2007). However, recent controversial work has suggested that speciation rates may be higher in high-latitude birds and mammals (Weir and Schluter 2007, 2008; Tobias et al. 2008; see also Gillman et al. 2009).

Speciation rates are defined as the number of new (reproductively isolated) lineages per clade per unit time (Coyne and Orr 2004), and thus we can ask how a rapid shifting into sympatry and accelerated rates of phenotypic evolution at higher latitudes can influence the number of new lineages per clade per unit time. Rapid range shifts into sympatry at high latitudes—and the resulting reproductive character displacement—may increase rates of evolution among diverging lineages and thus reduce the amount of time required for full reproductive isolation to evolve. Accelerated rates of phenotypic evolution could thus reduce transition or lag times to speciation, consistent with patterns documented in high-latitude birds and mammals (Chek et al. 2003; Weir and Schluter

2007). However, more frequent reproductive character displacement at higher latitudes does not necessarily increase the number of new lineages, and, as a result, the overall rates of speciation. Accelerated evolution by character displacement at higher latitudes could be consistent with higher rates of speciation if character displacement increased the birth rate of new lineages, perhaps by causing spatially divergent selective pressures on conspecific populations that were sympatric with different species in different regions of their range (e.g., Galápagos finches, Grant and Grant 2006; *Pseudacris* frogs, Lemmon 2009). This scenario would lead to phenotypic divergence among allopatric sister species at high latitudes, a pattern that was evident in few taxa in our dataset.

In contrast, the differential fusion of lineages reduces the number of diverging lineages through hybridization, and thus should reduce speciation rates by fusing incipient species that are in the early stages of differentiation. The pattern of fewer subspecies per bird species occurring at high latitudes (Martin and Tewksbury 2008) is consistent with this mechanism.

Overall, rapid range shifts that result in increased sympatry among high latitude clades could reduce speciation rates through the loss of lineages by fusion (Dynesius and Jansson 2000; Jansson and Dynesius 2002; Jansson 2003) while simultaneously causing greater average phenotypic divergence at high latitudes through the combined effects of character displacement and the loss of weakly differentiated lineages through fusion. Thus, our results provide support for the hypothesis that more frequent range shifting at higher latitudes due to Milankovitch Oscillations reduces speciation rates at higher latitudes (Dynesius and Jansson 2000; Jansson and Dynesius 2002; Jansson 2003), but does not exclude other hypotheses to explain higher tropical speciation rates (Mittelbach et al. 2007; Schemske 2009).

Our results further suggest that accelerated climate change in the present day will not only result in range shifts (Walther et al. 2002), but also in accelerated phenotypic evolution through character displacement and the loss of weakly differentiated lineages through fusion. Our evidence for character displacement supports the widespread importance of this phenomenon in birds (Sætre et al. 1997; Seddon 2005; Grant and Grant 2006; Price 2008), and is consistent with patterns from other taxonomic groups (Coyne and Orr 1989, 1997; Schluter 2000; Servedio and Noor 2003; Coyne and Orr 2004; Lukhtanov et al. 2005; Davies et al. 2007; Kay and Schemske 2008; Lemmon 2009). We suggest that character displacement and differential fusion may act in concert to influence broad patterns of evolutionary differentiation.

ACKNOWLEDGMENTS

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Supporting Information

The following supporting information is available for this article:

Figure S1. Relations between the mean proportion of mtDNA nucleotide sites that differed (p-distance) and (A) the degree of color pattern divergence (mean ratings), and (B) the relative degree of color pattern divergence (mean ratings), controlling statistically for the degree of breeding range sympatry.

Figure S2. Relation between the extent of breeding range sympatry and mean color pattern divergence (ratings, controlling for genetic distance, measured as p-distance) for paired sister-clades of birds at high (solid squares, $N = 26$) and low (open circles, $N = 52$) latitudes.

Appendix S1. Evidence for the phylogenetic placement of species and phylogenetic independence of families examined in this study.

Appendix S2. Instructions given to human observers who ranked and rated color pattern differences among birds.

Appendix S3. The rating examples of Asian birds given to human observers to assist in rating color pattern differences among pairs of birds, and the sources for illustrations used in our ranking and rating of color pattern.

Appendix S4. The complete dataset used in our study.

Supporting Information may be found in the online version of this article.

(This link will take you to the article abstract).

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Supporting Figure Legends

Supporting Figure S1. Relations between the mean proportion of mtDNA nucleotide

sites that differed (p-distance) and (A) the degree of color pattern divergence (mean

ratings), and (B) the relative degree of color pattern divergence (mean ratings),

controlling statistically for the degree of breeding range sympatry. Each data point

represents a value for a pair of sister clades of birds from high (solid squares, solid line,

N = 26) and low (open circles, dotted line, N = 52) latitudes. Using ratings as estimates of

color divergence, the rate of color pattern divergence appears to be accelerated at higher

latitudes compared with the tropics (A; GLMM, t = 2.2, df = 70, P = 0.032). However,

once the latitudinal differences in sympatry (Fig. 1B) are taken into account, the

latitudinal differences in color pattern divergence are no longer significant (saturated

GLMM, t = 0.1, df = 68, P = 0.92). Outliers are: 1, Tyrannidae: *Empidonax alnorum – E.

traillii*, 2, Turdidae: *Catharus bicknelli – C. minimus/fuscecens*. For all panels, ordinary

least squares regression lines are shown.

Supporting Figure S2. Relation between the extent of breeding range sympatry and

mean color pattern divergence (ratings, controlling for genetic distance, measured as p–

distance) for paired sister clades of birds at high (solid squares, N = 26) and low (open

circles, N = 52) latitudes. Color pattern divergence measured using ratings increased

significantly with the degree of breeding range overlap (saturated GLMM, t = 4.3, df =

68, P < 0.0001), but high latitude and tropical clade-pairs did not differ significantly

(Supporting Figure S1B), nor was there a significant interaction between the degree of

sympatry and latitude (saturated GLMM, t = 0.2, df = 68, P = 0.88). Outliers are: 1,

Fringillidae: *Carduelis flammea – C. hornemanni*, 2, Turdidae: *Catharus bicknelli – C. minimus/fuscecens*. An ordinary least squares regression line is shown.
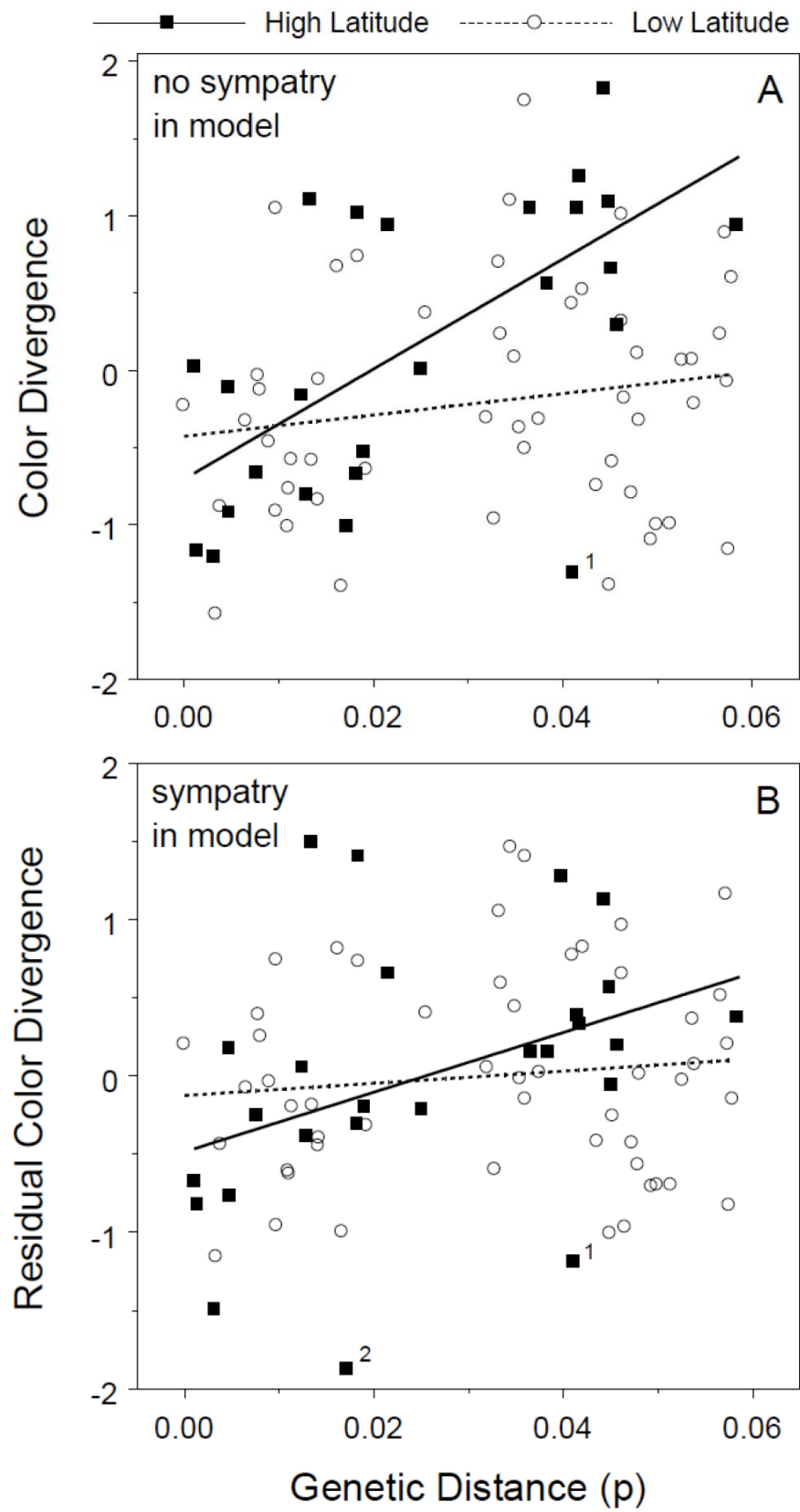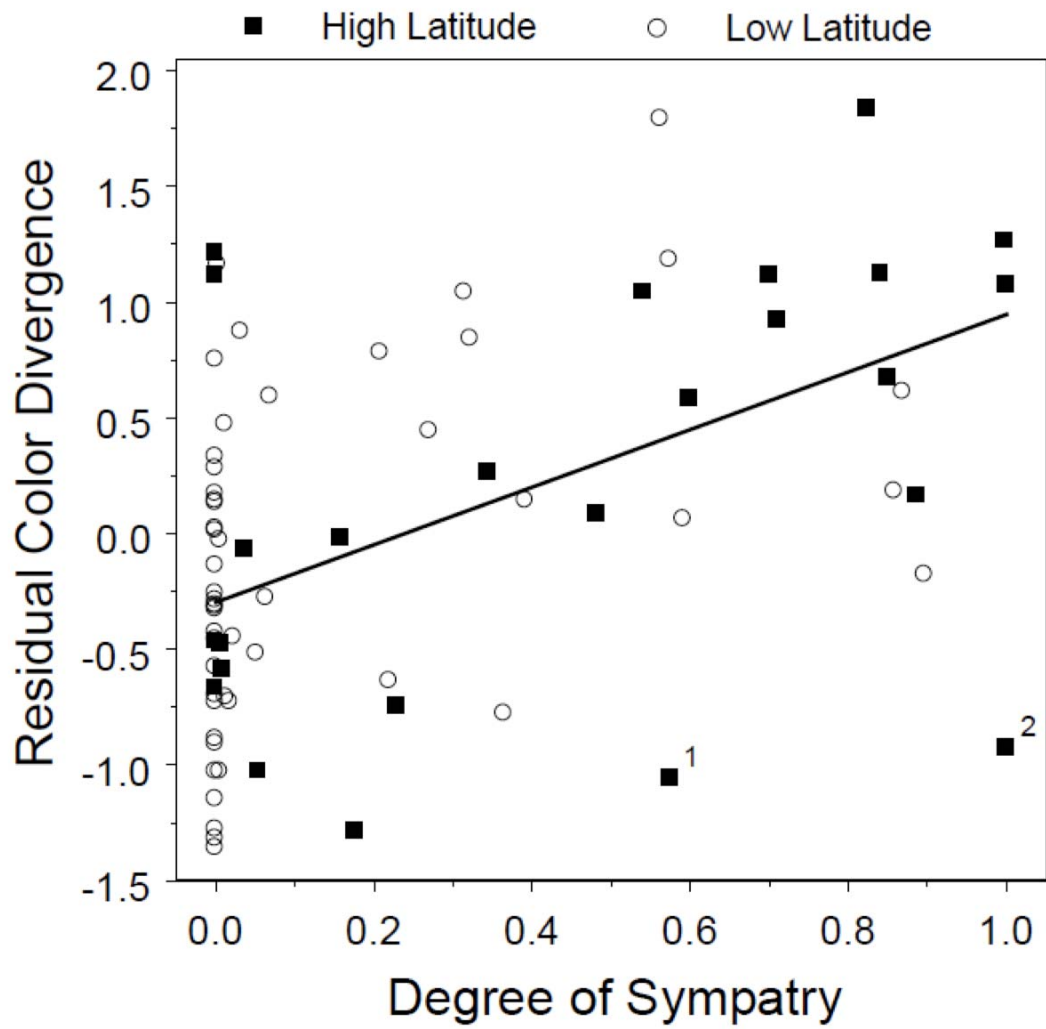
Fig. S1

Fig. S2

Supporting Appendix S1. Evidence for the phylogenetic placement of species and phylogenetic independence of families examined in this study.

(1) Picidae. Comparisons were phylogenetically independent following Webb and Moore (2005). High latitude taxa included two clades involving the genera *Sphyrapicus* and *Picoides*, with all high latitude taxa represented. Tropical taxa included two clades involving the genera *Veniliornis* and *Campephilus*. In *Veniliornis*, we lacked DNA sequence data for *V. maculifrons* and *V. sanguineus*; in *Campephilus*, we lacked sequence data for *C. robustus*. We treated *V. maculifrons* as a sister taxon to *V. affinis* and *V. sanguineus* as a sister taxon to *V. passerinus* following Short (1982) and Moore et al. (2006) (see also Sibley and Monroe 1990: p.55; Burn 2002). We treated *C. robustus* as a sister taxon to *C. rubricollis* following Short (1970: p.127). We followed published phylogenies for *Sphyrapicus* (Cicero and Johnson 1995: Fig. 6), *Picoides* (Weibel and Moore 2002: Fig. 2b), *Veniliornis* (Moore et al. 2006: Fig. 1, amended by the inclusion of *V. chocoensis*; see p.618), and *Campephilus* (Fleischer et al. 2006: Fig. 1). We estimated raw sequence divergence (mean p-distance) and time to most recent common ancestor (TMRCA) for focal clades using a combined 1386 base pairs of cytochrome *b* (cyt b) and cytochrome oxidase I (COI).

(2) Accipitridae. Comparisons were phylogenetically independent following Riesing et al. (2003) and do Amaral et al. (2006). High latitude taxa included one clade involving the genus *Buteo*, where all high latitude taxa were represented (Riesing et al. 2003). Tropical taxa included two clades (do Amaral et al. 2006) involving *Leucopternis* (clades

2 and 3 in Fig. 1, do Amaral et al. 2006) that included all taxa. A third clade, involving a variety of genera (clade 1 in Fig. 1, do Amaral et al. 2006), was missing several taxa (*Buteogallus aequinoctialis*, *B. anthracinus*, *B. subtilis*, *Harpyhaliaetus solitarius*); the best location of these taxa on the phylogeny was difficult to discern, particularly given the paraphyly of the genus *Buteogallus*. Thus, we excluded this clade. We followed published phylogenies of Riesing et al. (2003: Fig. 3, supplemented with data from Fig. 2 for node IV), and do Amaral et al. (2006: Fig. 1). We estimated sequence divergence and TMRCA using 519 base pairs of NADH dehydrogenase subunit 6 (ND6).

(3) Tyrannidae. Comparisons were phylogenetically independent following Fitzpatrick (2004). High latitude taxa included one clade involving the genus *Empidonax*, where all high latitude taxa were represented (Johnson and Cicero 2002). Tropical taxa included one clade involving the genus *Empidonax* (Johnson and Cicero 2002) where all taxa were represented, and one clade involving the genus *Anairetes* (including *Uromyias*) (Roy et al. 1999), where sequence data were missing for one species, *Anairetes (Uromyias) agraphia*. We treated *A. (U.) agraphia* as a sister taxon to *A. (U.) agilis* following most references that regard the two *Uromyias* species as most closely-related (Ridgely and Tudor 1994) and potentially conspecific (Sibley and Monroe 1990: p.345, 1993: p.48). We followed a published phylogeny for *Empidonax* (Johnson and Cicero 2002: Fig. 1). For *Anairetes*, we generated our own Bayesian phylogeny (Genbank Accession Numbers: AF067001 - AF067007, AF066992 - AF066998; see Phylogenetics below). The topology for focal taxa was consistent with Roy et al. (1999: Fig. 3c). We estimated sequence

divergence and TMRCA using a combined 592 base pairs cyt b and NADH

dehydrogenase subunit 2 (ND2).

(4) Turdidae. Comparisons were phylogenetically independent following Jønsson and

Fjeldså (2006). High latitude taxa included one clade involving the genus *Catharus*,

where all taxa were represented (Outlaw et al. 2003). Tropical taxa included one clade

involving the genus *Turdus* (including *Platycichla* and *Nesocichla*) (Voelker et al. 2007),

also with all taxa represented. We followed published phylogenies for both *Catharus*

(Outlaw et al. 2003: Fig. 2) and *Turdus* (Voelker et al. 2007: Fig. 1). We estimated

sequence divergence and TMRCA using a combined 1859 base pairs of cyt b and ND2.

(5) Parulidae. Comparisons were phylogenetically independent following Jønsson and

Fjeldså (2006). High latitude taxa included two clades involving the genera *Dendroica*

(Lovette and Bermingham 1999; Klein et al. 2004) and *Vermivora* (Klein et al. 2004).

For *Vermivora*, all species were represented, while for *Dendroica*, sequence data (for

focal genes) were missing for *D. kirtlandii*. Sequence data were available for all focal

Dendroica (including *D. kirtlandii*) for COI (Genbank Accession Numbers: AY327389,

AY650183 - AY650186, AY650188 - AY650191, AY650193, AY650194, AY650198,

AY650199, AY650205, AY650208, AY650212 - AY650214, AY650218, AY650222 -

AY650224, AY666185, AY666186, AY666188, AY666204, AY666217, AY666226,

AY666243, AY666299, AY666301, AY666313, AY666384, AY666392, AY666395,

AY666396, AY666442, AY666446, AY666447, AY666453, AY666457, AY666458,

AY666462, AY666465, AY666582, AY666592, DQ432885 - DQ432897, DQ433024,

DQ433059, DQ433181, DQ433575 - DQ433578, DQ433567 - DQ433574, DQ433579 -

DQ433592, DQ433802, DQ433864, DQ434068, DQ434561 - DQ434584, DQ434679,

DQ434698, DQ434699, DQ434700, DQ434741), so we generated a phylogeny for

Dendroica and related taxa (*Parula*, *Setophaga*, *Mniotilta*) using this gene (see

Phylogenetics below), and this analysis placed *D. kirtlandii* as basal to other focal

Dendroica. COI could not be used for tropical-temperate comparisons because COI

sequence data were not available for tropical taxa. Tropical taxa included two clades

involving the genera *Myioborus* (Pérez-Emán 2005) and *Geothlypis* (unpublished data

from Genbank; Accession Numbers: AF290135, AF447283, AY030147, AY650195,

DQ233480 - DQ233487). For both clades, all tropical taxa were represented. We

followed published phylogenies for *Dendroica* (Lovette and Bermingham 1999: Fig. 2),

Vermivora (Klein et al. 2004: Fig. 3) and *Myioborus* (Pérez-Emán 2005: Fig. 4). For

Geothlypis, we knew of no published phylogeny, so we estimated our own phylogeny

(see Phylogenetics below). We estimated sequence divergence and TMRCA using 1041

base pairs of ND2. Data for cyt b were not available for *Geothlypis*, so these data were

not included in our overall analyses.

(6) Emberizidae. Comparisons were phylogenetically independent following Jønsson and

Fjeldså (2006) (*Melospiza* to *Chlorospingus* clade within Passeroidea Clade 20). High

latitude taxa included two clades, one involving the genus *Melospiza*, *Passerculus*, and

some species of the paraphyletic genus *Ammodramus* (Zink and Avise 1990; Carson and

Spicer 2003; Klicka and Spellman 2007), and a second clade involving the genera

Zonotrichia, *Junco*, *Passerella*, and *Spizella arborea* (Carson and Spicer 2003; Zink and

Weckstein 2003). For both high latitude clades, all taxa were represented (Zink and Avise 1990; Weckstein et al. 2001; Carson and Spicer 2003; Zink and Weckstein 2003; Klicka and Spellman 2007). Tropical taxa included one clade of *Chlorospingus* (Weir et al. 2008) where ND2 data were missing for *C. inornatus*. We followed the phylogeny of Weir et al. (2008) for *C. inornatus* based on other gene sequences. We followed published phylogenies for the two temperate clades (Weckstein et al. 2001: Fig. 3; Carson and Spicer 2003: Fig. 4; Zink and Weckstein 2003: Fig. 1 including *Pipilo chlorurus* as an outgroup) and for the tropical *Chlorospingus* (Weir et al. 2008: Fig. 4). We estimated sequence divergence and TMRCA using 667 base pairs of ND2. For *Zonotrichia*, ND2 data came from published sequences and from McKereghan-Dares (2008) (Genbank Accession Numbers: GQ205467-GQ205562).

(7) Fringillidae. Comparisons were phylogenetically independent following Jønsson and Fjeldså (2006). High latitude taxa included one clade involving the genus *Carduelis*, where all high latitude taxa were represented (Arnaiz-Villena et al. 1998). Tropical taxa included the same clade of *Carduelis* (Arnaiz-Villena et al. 1998). For tropical taxa, sequence data were missing for *C. atriceps* and *C. siemiradzkii*. We treated *C. atriceps* as a sister taxon to *C. pinus* because the two hybridize in western Guatemala and are often considered conspecific (Sibley and Monroe 1990: p.706). We treated *C. siemiradskii* as a sister taxon to *C. magellanica* following concerns that the two species may be conspecific (Sibley and Monroe 1990: p.706; Clement et al. 1993; van den Elzen 2001), and the many similarities and likely close relationship between *siemiradskii* and *magellanica* (Ridgely and Tudor 1989: p.485; Clement et al. 1993). We followed a published

phylogeny for all *Carduelis* (Arnaiz-Villena et al. 1998: Fig. 1). We estimated sequence divergence and TMRCA using 924 base pairs of cyt b.

For all other avian taxa for which published DNA sequences are available, data did not meet our criteria of phylogenetic independence with at least 500 base pairs of sequence in common between tropical and high latitude groups.

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Supporting Appendix S2. Instructions given to human observers who ranked and rated color pattern differences among birds. Observers were unaware of the purpose of the study.

Plumage Scoring Instructions

Please read all instructions before beginning. Refer to the example pictures to see what is meant by 'patches'. Start with either the RANKING task or the RATING task as indicated at the top of the datasheet. Please use <u>only</u> the information provided in the pictures.

RANKING: Please rank the pairs of species with respect to their overall appearance, taking into account both the **colour & pattern**. Include considerations of both plumage and bare parts like eye, bill and legs. Lay the pictures out so that they rank from most similar to most different. If you have trouble deciding on the ranks of some pictures just make your best guess.

On the data sheet, please record the letter from each picture (located on the back) in the order that you have ranked them from 1(=most similar) to the end (=most different).

RATING: Please assign a rating to each picture showing a pair of species following the 1-7 scale below.

1 = identical, or nearly so; birds would be indistinguishable from 2 m away.
2 = very similar, having differences only in one or very few patches of colour; virtually indistinguishable from 5 m away.
3 = different enough to be easily distinguished but having most of the same colours in most of the same places.
4 = as different as they are similar, having the same colours in the same places in about half of the patches on the body.
5 = clearly different, many patches of colour differ between the two birds, but there are still similarities in more than a few patches of colour.
6 = quite different; having similarities only in one or very few patches of colour.
7 = vastly different, easily distinguishable at any distance with virtually no colours in common in any of the same patches.

Beware that postures, tail fanning, shape, etc. vary according to the artist's taste. Please ignore these differences when ranking the pictures and focus only on the colours and patterns of colour on the birds. In addition, please ignore morphological differences between species, such as bill size and shape. Note that crests are illustrated correctly in all cases, and thus the colour and pattern of crests (if present) should be included. Take your time – it may take >60 minutes to finish one family.

When you are done, please write your name and the envelope information on the top of the data sheet.

Thanks very much!!!

Supporting Appendix S3. The rating examples of Asian birds given to human observers to assist in rating color pattern differences among pairs of birds, and the sources for illustrations used in our ranking and rating of color pattern.

1 = identical, or nearly so; birds would be indistinguishable from 2 m away (Grimmett et al. 1999, Plate 102: 8a, 9a)

2 = very similar, having differences only in one or very few patches of color; virtually indistinguishable from 5 m away (Grimmett et al. 1999, Plate 104: 4a, 4c)

3 = different enough to be easily distinguished but having most of the same colors in most of the same places (Grimmett et al. 1999, Plate 104 5a, 7a)

4 = as different as they are similar, having the same colors in the same places in about half of the patches on the body (Grimmett et al. 1999, Plate 104 5c, 5a)

5 = clearly different, many patches of color differ between the two birds, but there are still similarities in more than a few patches of color (Grimmett et al. 1999, Plate 104 2a, 3a)

6 = quite different; having similarities only in one or very few patches of color (Grimmett et al. 1999, Plate 104 6a, 2a)

7 = vastly different, easily distinguishable at any distance with virtually no colors in common in any of the same patches (Grimmett et al. 1999, Plate 104 6c, 6a)

Illustrations of species and subspecies used in the present study came from the following references: Picidae (del Hoyo et al. 2002), Accipitridae (del Hoyo et al. 1994), Tyrannidae (del Hoyo et al. 2004), Turdidae (del Hoyo et al. 2005), Parulidae, tropics

(Curson et al. 1994), Parulidae, temperate (Sibley 2000), Fringillidae (Clement et al. 1993), Emberizidae, tropics (Isler and Isler 1987; Ridgely and Greenfield 2001), Emberizidae, temperate (Sibley 2000). Taxa for which comparable illustrations could not be located (e.g., some subspecies) were not included in the color pattern divergence analysis.

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Supporting Appendix S4. The complete dataset used in our study.

N	sequential number of independent samples in the analysis
Family	taxonomic family for sister-clades
Genus	taxonomic genus for sister-clades
Clade.A	the taxa within the first of the two sister-clades; includes only the species or subspecies that fall within the latitudinal region of interest (high or low latitudes - see Latitude below)
Clade.B	the taxa within the second of the two sister-clades; includes only the species or subspecies that fall within the latitudinal area of interest (high or low latitudes - see Latitude below)
Latitude	high or low, based on the species distributions (centroid latitude > 40 degrees = high; centroid latitude between tropics of Cancer and Capricorn = low)
Sympatry	the proportion of the smaller range clade that falls within the distribution of the larger range clade (breeding ranges only); includes only the species that fall within the latitudinal area of interest (high or low latitudes - see Latitude above)
TMRCA	estimated time to most recent common ancestor measured in number of lineages born from a parent lineage per substitution per site
p.Distance	mean raw nucleotide distance (p distance) between members of the two clades, measured using the program MEGA 4
p.Distance.SE	standard error of the mean nucleotide distance (p distance) between members of the two clades, measured using the program MEGA 4 (bootstrap, 1000 replicates)
mtDNA.Genes	genes used to estimate genetic distance
Base.Pairs	number of base pairs used to estimate genetic distance
Rank	mean ranking of color pattern differences across 7 observers, ranging from 0 (similar) to 1 (different); ranked within families; standardized to between 0 and 1
Rating	mean rating of color pattern differences across 7 observers, rated from 1 (similar) to 7 (different); rated within families, standardized within observers within each family (mean = 0, SD = 1.0)

Notes:
data sets include only clades with p distance values between 0 - 0.06
subspecies/allopatric populations are included
incl = lineage includes a taxon whose phylogenetic placement is based on other evidence (e.g., morphometrics, other genes) and for which genetic data for the gene(s) of interest are not available
excluding = lineage excludes a taxon that is sometimes included within a species but is phylogenetically independent based on sequence evidence

N	Family	Genus	Clade.A	Clade.B	Latitude	Sympatry	TMRCA	p.Distance	p.Distance.SE	mtDNA.Genes	Base.Pairs	Rank	Rating
1	Picidae	*Picoides*	*albolarvatus*	*villosus*	high	0.842	2.362	0.04157	0.00489	cyt b, COI	1386	0.95238	1.04668
2	Picidae	*Sphyrapicus*	*ruber*	*nuchalis*	high	0.037	0.745	0.00479	0.00136	cyt b, COI	1386	0.65873	-0.11458
3	Picidae	*Sphyrapicus*	*ruber/nuchalis*	*varius*	high	0.007	1.552	0.01907	0.00316	cyt b, COI	1386	0.46825	-0.53583
4	Picidae	*Veniliornis*	*affinis (incl maculifrons)*	*nigriceps*	low	0.018	0.865	0.04731	0.00582	cyt b, COI	1386	0.24802	-0.79732
5	Picidae	*Veniliornis*	*callonotus*	*dignus*	low	0.003	0.493	0.03448	0.00438	cyt b, COI	1386	0.87302	1.09642
6	Picidae	*Veniliornis*	*affinis (incl maculifrons)/nigriceps*	*callonotus/dignus*	low	0.069	1.215	0.04215	0.00371	cyt b, COI	1386	0.64220	0.51961
7	Picidae	*Veniliornis*	*frontalis*	*passerinus (incl sanguineus)*	low	0.064	0.673	0.00655	0.00223	cyt b, COI	1386	0.39484	-0.33031
8	Picidae	*Veniliornis*	*affinis (incl maculifrons)/nigriceps/callonotus/*	*frontalis/passerinus (incl sanguineus)*	low	0.859	1.710	0.04794	0.00424	cyt b, COI	1386	0.50529	0.10588
9	Picidae	*Campephilus*	*melanoleucos*	*gayaquilensis*	low	0.000	0.406	0.04496	0.00561	cyt b, COI	1386	0.08730	-1.39387
10	Picidae	*Campephilus*	*melanoleucos/gayaquilensis*	*guatemalensis*	low	0.000	0.484	0.04937	0.00501	cyt b, COI	1386	0.14087	-1.09983
11	Picidae	*Campephilus*	*melanoleucos/gayaquilensis/guatemalensis*	*pollens*	low	0.392	0.870	0.05264	0.00467	cyt b, COI	1386	0.66402	0.06202
12	Accipitridae	*Buteo*	*lagopus*	*regalis*	high	0.000	0.223	0.00771	0.00365	ND6	519	0.35714	-0.66732
13	Accipitridae	*Buteo*	*lagopus/regalis*	*jamaicensis*	high	0.345	1.077	0.04578	0.00835	ND6	519	0.63571	0.28802
14	Accipitridae	*Buteo*	*lagopus/regalis/jamaicensis*	*swainsoni*	high	1.000	1.096	0.03662	0.00656	ND6	519	0.88095	1.04508
15	Accipitridae	*Leucopternis*	*melanops*	*kuhli*	low	0.052	0.263	0.01927	0.00579	ND6	519	0.28571	-0.64411
16	Accipitridae	*Leucopternis*	*albicollis costaricensis*	*albicollis ghiesbreghti*	low	0.244	0.000	0.00000	0.00000	ND6	519	0.51429	-0.23221
17	Accipitridae	*Leucopternis*	*albicollis*	*occidentalis*	low	0.000	0.546	0.01354	0.00472	ND6	519	0.32857	-0.58596
18	Accipitridae	*Parabuteo*	*unicinctus harrisi*	*unicinctus unicinctus*	low	0.000	0.424	0.00337	0.00211	ND6	519	0.10000	-1.58169
19	Tyrannidae	*Empidonax*	*alnorum*	*traillii*	high	0.177	0.528	0.04110	0.00772	cyt b, ND2	592	0.14286	-1.31520
20	Tyrannidae	*Empidonax*	*atriceps*	*fulvifrons*	low	0.000	0.480	0.03547	0.00699	cyt b, ND2	592	0.44643	-0.37511
21	Tyrannidae	*Empidonax*	*flavescens flavescens*	*flavescens salvinii*	low	0.000	0.450	0.01098	0.00410	cyt b, ND2	592	0.23214	-1.01495
22	Tyrannidae	*Anairetes*	*nigrocristatus*	*reguloides*	low	0.000	0.230	0.01418	0.00477	cyt b, ND2	592	0.42857	-0.84189
23	Tyrannidae	*Anairetes*	*nigrocristatus/reguloides*	*agilis (incl agraphia)*	low	0.032	0.564	0.05722	0.00942	cyt b, ND2	592	0.81250	0.88679
24	Turdidae	*Catharus*	*fuscescens*	*minimus*	high	0.008	1.223	0.01829	0.00242	cyt b, ND2	1859	0.33333	-0.67750
25	Turdidae	*Catharus*	*bicknelli*	*fuscescens/minimus*	high	1.000	1.592	0.01722	0.00221	cyt b, ND2	1859	0.16369	-1.01609
26	Turdidae	*Turdus*	*serranus*	*fuscater*	low	0.563	0.219	0.03604	0.00403	cyt b, ND2	1859	0.92262	1.74214
27	Turdidae	*Turdus*	*serranus/fuscater*	*olivater*	low	0.315	0.731	0.04626	0.00410	cyt b, ND2	1859	0.86905	1.00576
28	Turdidae	*Turdus*	*ignobilis*	*maranonicus*	low	0.006	0.313	0.00807	0.00228	cyt b, ND2	1859	0.52976	-0.13073
29	Turdidae	*Turdus*	*amaurocholinus*	*ignobilis/maranonicus*	low	0.271	0.659	0.02555	0.00380	cyt b, ND2	1859	0.58333	0.36709
30	Turdidae	*Turdus*	*amaurocholinus/ignobilis/maranonicus*	*lawrenceii*	low	0.869	1.179	0.05792	0.00495	cyt b, ND2	1859	0.74802	0.59701
31	Turdidae	*Turdus*	*fumigatus*	*hauxwelli*	low	0.013	0.263	0.04362	0.00499	cyt b, ND2	1859	0.33929	-0.74907
32	Turdidae	*Turdus*	*haplochrous*	*nudigenis (excluding n. maculirostris)*	low	0.000	0.293	0.03604	0.00404	cyt b, ND2	1859	0.27976	-0.50953
33	Turdidae	*Turdus*	*grayi*	*haplochrous/nudigenis (excluding n. maculirosti*	low	0.000	0.532	0.03497	0.00378	cyt b, ND2	1859	0.48512	0.08246
34	Turdidae	*Turdus*	*grayi/haplochrous/nudigenis (excluding n. ma*	*nudigenis maculirostris*	low	0.000	0.808	0.03281	0.00336	cyt b, ND2	1859	0.25595	-0.96591
35	Turdidae	*Turdus*	*grayi/haplochrous/nudigenis*	*rufiventris*	low	0.012	1.163	0.04102	0.00371	cyt b, ND2	1859	0.65625	0.42914
36	Turdidae	*Turdus*	*infuscatus*	*nigrescens*	low	0.000	0.275	0.05756	0.00479	cyt b, ND2	1859	0.25595	-1.16364
37	Parulidae	*Dendroica*	*occidentalis*	*townsendi*	high	0.158	0.383	0.01249	0.00335	ND2	1041	0.45408	-0.16754
38	Parulidae	*Dendroica*	*occidentalis/townsendi*	*virens*	high	0.000	0.443	0.01297	0.00284	ND2	1041	0.31378	-0.80891
39	Parulidae	*Dendroica*	*petechia*	*striata*	high	0.925	0.617	0.03992	0.00564	ND2	1041	0.98980	2.08190
40	Parulidae	*Dendroica*	*pensylvanica*	*petechia/striata*	high	0.999	0.715	0.04182	0.00512	ND2	1041	0.90689	1.24827
41	Parulidae	*Dendroica*	*coronata coronata*	*coronata auduboni*	high	0.230	0.488	0.00480	0.00207	ND2	1041	0.17857	-0.92587
42	Parulidae	*Vermivora*	*celata*	*ruficapilla*	high	0.542	0.959	0.02161	0.00451	ND2	1041	0.89286	0.93474
43	Parulidae	*Vermivora*	*chrysoptera*	*pinus*	high	0.600	0.730	0.03843	0.00552	ND2	1041	0.88776	0.55387
44	Parulidae	*Myioborus*	*cardonai*	*castaneocapillus castaneocapillus*	low	0.000	1.192	0.03330	0.00545	ND2	1041	0.64796	0.69663
45	Parulidae	*Myioborus*	*albifacies*	*cardonai/castaneocapillus*	low	0.000	1.689	0.05373	0.00654	ND2	1041	0.55230	0.06603
46	Parulidae	*Myioborus*	*melanocephalus ruficoronatus*	*ornatus*	low	0.000	1.576	0.00785	0.00243	ND2	1041	0.64031	-0.03677
47	Parulidae	*Myioborus*	*melanocephalus melanocephalus*	*melanocephalus ruficoronatus/ornatus*	low	0.000	1.837	0.00901	0.00217	ND2	1041	0.38776	-0.46739
48	Parulidae	*Myioborus*	*melanocephalus/ornatus*	*albifrons*	low	0.000	2.630	0.03754	0.00525	ND2	1041	0.38861	-0.32207
49	Parulidae	*Myioborus*	*torquatus*	*albifrons/melanocephalus/ornatus*	low	0.000	2.874	0.05741	0.00641	ND2	1041	0.49554	-0.07577
50	Parulidae	*Myioborus*	*albifacies/cardonai/castaneocapillus/pariae/fl*	*torquatus/melanocephalus/ornatus/albifrons*	low	0.000	3.057	0.05669	0.00456	ND2	1041	0.57429	0.23062
51	Parulidae	*Myioborus*	*miniatus comptus*	*miniatus ballax*	low	0.000	1.975	0.01667	0.00292	ND2	1041	0.10714	-1.40231
52	Parulidae	*Myioborus*	*miniatus comptus/miniatus ballax*	*miniatus miniatus*	low	0.000	2.484	0.05393	0.00647	ND2	1041	0.48980	-0.21874
53	Parulidae	*Geothlypis*	*flavovelata*	*nelsoni*	low	0.000	0.465	0.00384	0.00202	ND2	1041	0.14031	-0.88606
54	Parulidae	*Geothlypis*	*semiflava*	*speciosa*	low	0.000	0.683	0.04995	0.00647	ND2	1041	0.15816	-1.00300
55	Parulidae	*Geothlypis*	*flavovelata/nelsoni*	*semiflava/speciosa*	low	0.005	1.521	0.05139	0.00578	ND2	1041	0.14923	-0.99642
56	Emberizidae	*Melospiza*	*georgiana*	*lincolnii*	high	0.700	0.025	0.04498	0.00745	ND2	667	0.82488	1.08567
57	Emberizidae	*Melospiza*	*melodia*	*georgiana/lincolnii*	high	0.711	0.042	0.05847	0.00772	ND2	667	0.77419	0.93758
58	Emberizidae	*Zonotrichia*	between all 4 high latitude subspecies of *leuc*	between all 4 high latitude subspecies of *leucop*	high	0.055	0.006	0.00144	0.00110	ND2	667	0.13594	-1.17681
59	Emberizidae	*Zonotrichia*	*atricapillus*	*leucophrys*	high	0.887	0.006	0.00115	0.00032	ND2	667	0.64516	0.01537
60	Emberizidae	*Zonotrichia*	*albicollis*	*leucophrys/atricapilla*	high	0.482	0.023	0.02513	0.00566	ND2	667	0.56452	0.00212
61	Emberizidae	*Zonotrichia*	*querula*	*albicollis/leucophrys/atricapilla*	high	0.851	0.032	0.04517	0.00675	ND2	667	0.65131	0.65383
62	Emberizidae	*Passerella*	*fuliginosa*	*schistacea*	high	0.000	0.011	0.01342	0.00352	ND2	667	0.84793	1.09897
63	Emberizidae	*Passerella*	*fuliginosa/schistacea*	*iliaca*	high	0.000	0.014	0.01841	0.00410	ND2	667	0.78571	1.01320
64	Emberizidae	*Chlorospingus*	*o. phaeocephalus*	*semifuscus*	low	0.000	0.031	0.03349	0.00679	ND2	667	0.65899	0.23089
65	Emberizidae	*Chlorospingus*	*o.phaeocephalus/semifuscus/inornatus*	*tacarcunae*	low	0.000	0.032	0.04527	0.00729	ND2	667	0.34793	-0.59559

66	Emberizidae	*Chlorospingus*	*o.phaeocephalus/semifuscus/inornatus/tacar*	*o. cinereocephalus*	low	0.000	0.035	0.04626	0.00680	ND2	667	0.51152	0.31408
67	Emberizidae	*Chlorospingus*	*o.phaeocephalus/semifuscus/inornatus/tacar*	*o. jacqueti*	low	0.000	0.041	0.04811	0.00603	ND2	667	0.49770	-0.32616
68	Fringillidae	*Carduelis*	*flammea*	*hornemanni*	high	0.576	0.087	0.00325	0.00129	cyt b	924	0.24490	-1.21157
69	Fringillidae	*Carduelis*	*pinus*	*tristis*	high	0.825	0.308	0.04437	0.00640	cyt b	924	0.99490	1.81945
70	Fringillidae	*Carduelis*	*xanthogastra*	*olivacea*	low	0.209	0.167	0.01623	0.00425	cyt b	924	0.61224	0.66786
71	Fringillidae	*Carduelis*	*magellanicus (incl siemiradskii)*	*yarrellii*	low	0.023	0.190	0.01139	0.00283	cyt b	924	0.44260	-0.58183
72	Fringillidae	*Carduelis*	*crassirostris*	*magellanicus(incl siemiradskii)/yarrellii*	low	0.365	0.195	0.00975	0.00247	cyt b	924	0.25765	-0.91534
73	Fringillidae	*Carduelis*	*crassirostris/magellanicus(incl siemiradskii)/y*	*spinescens*	low	0.220	0.196	0.01110	0.00273	cyt b	924	0.35268	-0.77013
74	Fringillidae	*Carduelis*	*atrata*	*crassirostris/magellanicus(incl siemiradskii)/yar*	low	0.574	0.196	0.00975	0.00235	cyt b	924	0.77704	1.04472
75	Fringillidae	*Carduelis*	*xanthogastra/olivacea*	*atrata/crassirostris/magellanicus(incl siemiradsk*	low	0.592	0.211	0.01426	0.00262	cyt b	924	0.46620	-0.06275
76	Fringillidae	*Carduelis*	*cucullata*	*xanthogastra/olivacea/atrata/crassirostris/mage*	low	0.322	0.211	0.01841	0.00366	cyt b	924	0.72003	0.73453
77	Fringillidae	*Carduelis*	*cucullata/xanthogastra/olivacea/atrata/crassi*	*notata*	low	0.000	0.237	0.03200	0.00548	cyt b	924	0.42602	-0.31133
78	Fringillidae	*Carduelis*	*cucullata/xanthogastra/olivacea/atrata/crassi*	*atriceps*	low	0.897	0.287	0.04655	0.00651	cyt b	924	0.45051	-0.18304