Color Patterns of Closely Related Bird Species Are More Divergent at Intermediate Levels of Breeding-Range Sympatry

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abstract: Closely related species of birds often differ markedly in their color patterns. Here we examine the influence of breeding-range overlap (breeding sympatry) on the evolution of color pattern differences in a sample of closely related bird species. We used a sister-lineage method to analyze 73 phylogenetically independent comparisons among 246 species and 39 families of birds worldwide. We found that divergence of color patterns among closely related species was greater between sympatric than between allopatric lineages, but only at intermediate levels of sympatry (50%–80% breeding-range overlap). This pattern suggests that closely related species incur costs at intermediate levels of sympatry if they exhibit similar color patterns—costs that could include hybridization, interspecific aggression, competition for signaling space, or ecological interactions that secondarily influence color patterns. The decline in color pattern divergence with further increase in sympatry suggests either the relaxation of divergent selection, increased impediment of gene flow, or an increased role for counteracting selection at higher levels of sympatry. We also found that the differences in color pattern between sympatric and allopatric sister species were greatest at lower latitudes. The global scale and broad taxonomic coverage in our study suggest that the divergence of color patterns between sympatrically breeding closely related species is widespread in birds.

Keywords: sympatry, color pattern, character displacement, differential fusion, differential expansion, hybridization.

Introduction

Birds are renowned for the diversity of their color patterns (Stoddard and Prum 2011), even differing markedly between closely related species (e.g., tanagers [Isler and Isler 1987], wood warblers [Curson et al. 1994], and birds of paradise [Frith and Beehler 1998]). While various social, sexual, and natural-selection pressures may influence the divergence of color patterns as species evolve, closely related species whose breeding ranges overlap (i.e., species that breed in sympatry) have long been thought to exert strong selection on each other's color patterns, possibly to minimize the risk of hybridization (e.g., Wallace 1889; Dobzhansky 1937; Mayr 1942).

We expect divergence among close relatives in breeding sympatry if there is a cost of exhibiting similar color patterns, including the costs of hybridization (Servedio and Noor 2003; Coyne and Orr 2004), interspecific aggression (Lorenz 1962, 1966; Grether et al. 2009; Anderson and Grether 2010), competition for signaling space (Nelson and Marler 1990; Endler 1992), or other ecological interactions, such as density-dependent predation (Holt and Lawton 1994). Alternatively, we might expect more similar color patterns in closely related species when they live in the same habitat, because they are subject to many of the same local selection pressures (e.g., selection on signal efficacy; Morton 1975; Endler 1992; Marchetti 1993; Ey and Fischer 2009) and because competitive interactions among species may favor the convergence of color signals (Cody 1969, 1973; Rainey and Grether 2007; Grether et al. 2009).

Previous studies of birds have found evidence that color patterns can either diverge or converge among closely related species that occur together. For example, meadowlark (genus *Sturnella*) color patterns converge in areas of breeding sympatry, compared to areas of allopatry (Rohwer 1973), and phylogenetic studies in several other bird genera similarly show that color patterns have converged in sympatry (e.g., toucans, genus *Ramphastos*; Weckstein 2005; see also Cody 1969, 1973). Also, hybridizing species regularly converge in color pattern as a direct result of hybridization and genetic introgression (McCarthy 2006), which might be more likely to occur in younger lineages during early stages of breeding-range overlap.

Conversely, studies of Old World flycatchers (genus *Ficedula*) document greater divergence of color pattern in breeding sympatry, compared with that in allopatry, as the result of sexual and ecological character displacement (Sætre et al. 1993, 1997; Vallin et al. 2011). Divergence of color pattern between closely related species breeding in sympatry

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has also been noted in other avian genera (e.g., caciques, genus *Cacicus*; Kiere et al. 2009).

Our own comparative study (Martin et al. 2010) found a positive relationship between the degree of breeding sympatry and the divergence of color patterns among closely related taxa in seven bird families that breed in the New World, suggesting that this phenomenon may be common. Studies that have found either convergence or divergence in color patterns contrast with a comparative study of Australasian birds that found no difference in male plumage color between closely related species in breeding sympatry and those in allopatry (McNaught and Owens 2002).

The lack of consensus in previous work led us to use a global data set and a sister-lineage approach to address the problem generally. We used a simple but powerful method of isolating the importance of sympatry on the evolution of traits, proposed by Noor (1997) in work on *Drosophila*. Noor's method focuses on pairs of closely related lineages that differ from a third, more distant close relative in the extent of their breeding-range overlap (fig. 1). This sister-lineage approach requires an estimate of evolutionary relationships. It does not, however, require data on the time since divergence, because the focal sister species or lineages have, by definition, been evolving from their common ancestor—and from their more distantly related relative (lineage A)—for the same amount of time. If closely related species of birds incur costs from having similar color patterns in breeding sympatry, then we predicted that there would be greater divergence between species whose breeding ranges overlap that of a close relative when compared with sister species or lineages whose breeding ranges do not overlap. If, on the other hand, closely related species acquire benefits from having similar color patterns in sympatry, then we would predict the opposite pattern.

Material and Methods

Selection of Species

Using a recent avian taxonomy (Gill and Donsker 2010), we searched the literature for genera that had three or more species where at least 80% of the species were included in a

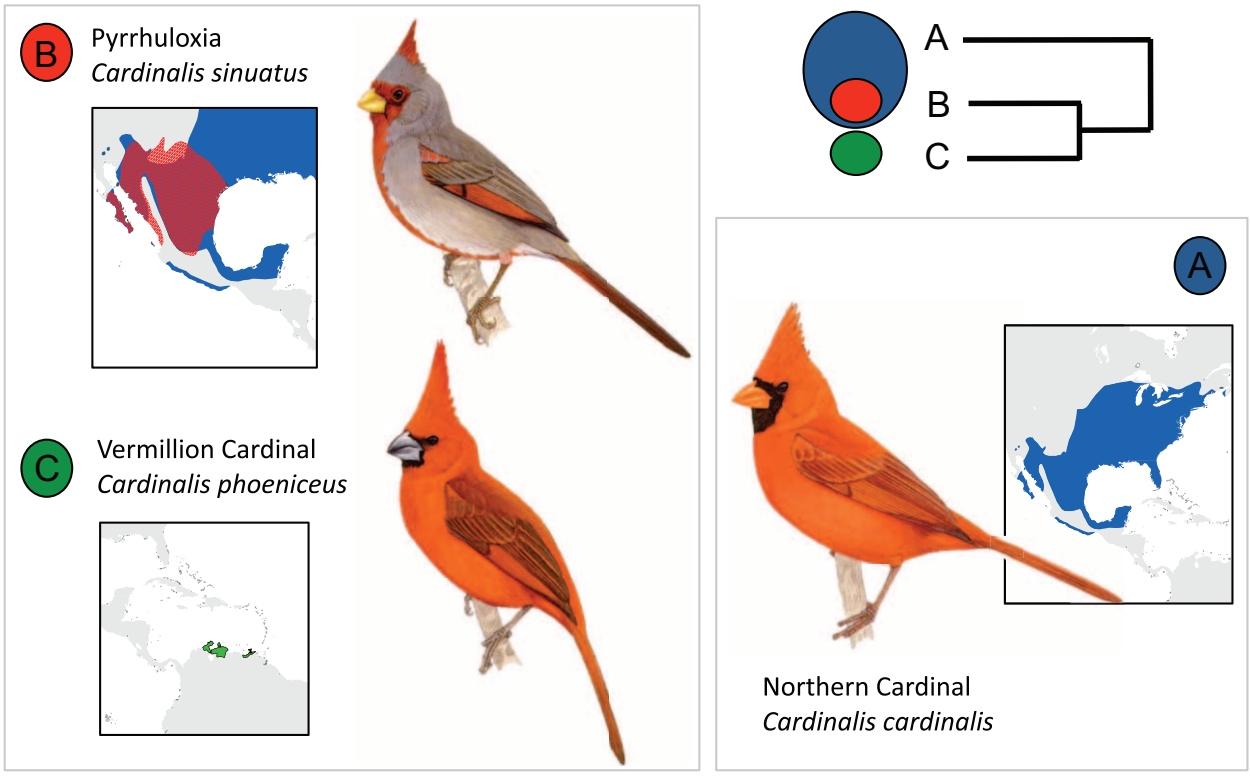

Figure 1: An example of our methods (following Noor 1997) in the genus *Cardinalis*. Each comparison consists of two sister species (or lineages) B and C, where the breeding range of B overlaps with that of a closely related species (A), while the breeding range of C does not. If similar color patterns in sympatry are costly, then we predicted that differences between A and B should exceed those between A and C. If similar color patterns in breeding sympatry are beneficial, then we predicted that the color pattern differences between A and C should exceed those between A and B. *Cardinalis* illustrations are from the *Handbook of the Birds of the World* (del Hoyo et al. 2011) and were painted by Brian Small (reproduced with permission).

phylogeny based on DNA sequence data and also met the following three criteria with respect to their breeding ranges (fig. 1): (1) clades B and C are mostly allopatric, with less than 10% of their breeding ranges overlapping, (2) clades A and B are mostly sympatric, with more than 50% of the breeding range of B overlapped by that of A, and (3) clades A and C are mostly allopatric, with less than 10% of the breeding range of C overlapped by that of A. Some of our comparisons involved lineages containing more than one species. For example, in the genus *Lophura*, the range of lineage A (*L. nycthemera*) overlaps that of lineage B (which includes two sister species, *L. edwardsi* and *L. hatinhensis*) but does not overlap that of lineage C (*L. swinhoii*). For comparisons, we compared A-B versus A-C, but the difference between A and B equals the mean of the difference between *L. nycthemera* (A) and *L. edwardsi* (B1) and that between *L. nycthemera* (A) and *L. hatinhensis* (B2). Overall, we found 73 phylogenetically independent comparisons that met all of our criteria, involving 246 species of birds from 39 families on all continents but Antarctica.

Color Pattern Divergence

We assessed color pattern divergence among birds, using human observers who ranked and rated the differences in color patterns from published color illustrations of both males and females of focal species, following methods used in our previous study of color pattern divergence (Martin et al. 2010; also see the appendix, available online, for more detail on why these illustrations are suitable for our study). We used both ranking and rating methods because ranking assesses the sign of differences between lineages while rating assesses the relative magnitude of that difference. We asked 15 observers to rank which species pair (A-B or A-C) was more divergent and seven observers to rate the differences between species pairs A-B and A-C on a scale of 1–7 (1 = virtually identical, 7 = vastly different), scoring males and females separately for sexually dimorphic species. For both the ranking and rating tasks, we presented pictures of all of the birds in each comparison simultaneously to the observers.

For ratings, we standardized among observers so that all ratings for each observer had a mean of 0 and a standard deviation of 1. Color pattern divergence assessed by humans positively covaries with assessments using spectrometry (e.g., Armenta et al. 2008; Seddon et al. 2010) but has the added benefit that humans incorporate information on the location, shape, and internal patterning of color patches. Humans do not see into the ultraviolet, nor did the pictures we used reflect in the ultraviolet, so our estimates of color pattern divergence do not incorporate any potential differences in ultraviolet coloration among species. See the appendix for detailed information on our methods. Our written instructions to observers are available in a zip file, available online.

One limitation of our study is that we examined only one phenotype within each species, whereas some species show geographic variation in color pattern. For geographically variable species that comprised either lineages A or B, we preferentially selected subspecies that were sympatric with the opposite species, thus capturing the geographic variation most relevant to our study. Otherwise, we selected the nominate subspecies. We note also that within-species variation in color and pattern is usually smaller than interspecific variation among closely related species of birds (see discussion in Price 2008). Thus, the variation captured in comparisons of sympatric versus allopatric species will typically exceed within-species variation. Importantly, any bias caused by using the nominate subspecies in our study could not have produced the patterns that we describe in this article, because these illustrations were created without regard to the hypothesis that we tested. Nonetheless, we recognize that comparisons of within-species patterns of divergence would be interesting and informative (particularly if they diverged in the face of gene flow) and would be an excellent focus for future work.

Geographic Ranges

We assessed the degree of breeding-range overlap between species by using ranges from Martin and Tewksbury (2008) and BirdLife International and NatureServe (2011). We measured both range size (km^2) and overlap with ArcGIS 9.2 (ESRI, Redlands, CA). We measured breeding-range overlap only (rather than global or wintering ranges) because these ranges are critical for reproductive isolation and speciation (Mayr 1963) and because many of our plumage and bare-part color patterns are evident only during the breeding season (see the appendix for details).

Phylogenetic Relationships

We obtained molecular phylogenetic relationships among species from the published literature (see the appendix for sources). A few genera (e.g., *Cyanerpes*) had DNA sequence data but no molecular phylogeny, so we generated our own phylogeny for these groups, using Bayesian phylogenetic methods (see the appendix for methods).

Predictor Variables

Because other factors could interact with breeding-range overlap to influence color pattern evolution, we measured and assessed 10 predictor variables in our statistical models (details and justifications in the appendix; fig. 1 shows how we defined lineages A, B, and C): (1) mean Tamura-Nei ge-

netic distance (mitochondrial DNA) between lineages A and BC, (2) mean Tamura-Nei genetic distance between lineages B and C, (3) maximum number of congeners (besides A) whose breeding ranges overlapped substantially with those of either B or C (i.e., where (area of breeding-range overlap)/(breeding-range size of B or C) > 0.50), (4) proportion of the breeding range of A that overlapped with the breeding range of B (area of breeding-range overlap of A and B)/(breeding-range size of A), (5) proportion of the breeding range of B that overlapped with the breeding range of A (area of breeding-range overlap of A and B)/(breeding-range size of B), (6) mean latitude of the breeding ranges of A, B, and C (mean of the absolute latitude of the centroid of the separate breeding ranges), (7) breeding-range size of species B, (8) breeding-range size of species C, (9) sex (male, female, or "both" for monomorphic species), and (10) continent occupied by the majority of the breeding range of species B.

Statistical Methods

We used generalized linear models with either a quasi-binomial (ranking measures) or a Gaussian (rating measures) error distribution (see the appendix and the R code available in the zip file) to test the prediction that color patterns differed between closely related species in sympatry, compared with closely related species in allopatry. We used R (ver. 3.0.3; R Development Core Team 2014) for all analyses.

For ranking measures, we used a statistical approach for proportional data where we knew the bivariate outcomes for each case. This approach is often used for analyzing counts of successes versus failures and individuals that are alive versus dead, infected versus uninfected, or male versus female (in sex ratio studies; Crawley 2013). In our study, we compared the following two outcomes to the rankings: (1) observers ranked the sympatric pair (A-B) as more different, and (2) observers ranked the allopatric pair (A-C) as more different. Our 15 observers each ranked sympatric versus allopatric pairs for each independent comparison ($n = 73$), yielding a minimum of 15 outcomes per comparison. For lineages that had multiple species (e.g., *Lophura*, where lineage B included two species, B1 and B2), the number of rankings per comparison exceeded 15 because observers ranked allopatric and sympatric lineages for all species (for *Lophura*, the observers ranked the pair A-C against both A-B1 and A-B2, yielding 30 ranking outcomes). We then analyzed the bivariate outcomes of rankings, using a two-vector response variable in a binomial model. We entered predictors without interactions because we had no a priori reason to expect interactions, and we did not have a sufficient sample size of comparisons to test all pairwise interactions.

For rating measures, we subtracted the rating for the allopatric pair (A-C) from the rating for the sympatric pair (A-B) for each independent comparison ($n = 73$). In cases where a lineage contained multiple species, we averaged the ratings for each species pair within a comparison (e.g., rating for A-B = average of the ratings for A-B1 and A-B2 when lineage B contained two species, B1 and B2). We then used these differences as the response variable, with the predictors again entered without interaction terms.

For both ranking and rating analyses, we standardized each continuous predictor variable before analysis by subtracting the mean and dividing by 2 standard deviations. We thus standardized continuous predictor variables so that the effect sizes of different predictors would be comparable. We compared the performance of models with all possible combinations of predictor variables and assessed the performance of models, using either the Akaike information criterion adjusted for small sample size (AICc for Gaussian generalized linear models) or QAICc to estimate AICc values for quasi models (Bolker 2013). We determined the top models (where ΔAICc or ΔQAICc < 2) in each set and report the best-fitting model in the text and all of the top models and an averaged model in the appendix. See the appendix for details of model diagnostics and the transformations of variables, and see table A1 (tables A1–A3 available online) for a list and definitions of variables. Data that we used in our analyses and figures are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.8dc26 (Martin et al. 2015). R code for our analyses is available in the zip file.

Results

Ranking Analyses

In the best-fitting model from the ranking analysis (table 1), the probability (predicted value [95% confidence limits (CL)] = 0.65 [0.53–0.75]) that an observer would rank sympatric breeding birds (lineages A and B) as more different in their color patterns than allopatric breeding birds (lineages A and C) was significantly greater than 0 when 50% of the range of B was overlapped by the range of A (our minimum criterion for sympatry). This prediction controls for the number of nonfocal congeners overlapping lineages B or C, which was also a significant predictor in this model (see table A2 for a list of the top models in this set and an averaged model). This probability declined significantly as both the extent of sympatry and the number of nonfocal congeners overlapping lineages B or C increased (tables 1, A2). Figure 2 shows the effect of degree of sympatry on the rankings of color patterns and illustrates significantly greater divergence of color pattern (based on 95% CLs calculated from the best-fitting model) in sympatric than in al-

Table 1: The best-fitting linear models to predict divergence in color patterns between closely related bird species

	Estimate	95% CL	*t*	*P*
Ranking analysis:[a]				
Intercept	1.50	.33, 2.70	2.50	.01
No. of nonfocal congeners overlapping breeding range of either lineage B or C	−.09	−.15, −.03	2.77	.007
Proportion of breeding range of lineage B overlapped by breeding range of lineage A	−1.75	−3.23, −.30	2.35	.02
Rating analysis:[b]				
Intercept	1.65	.56, 2.74	3.02	.004
Mean latitude of breeding ranges of lineages A, B, and C	−.02	−.03, −.006	2.99	.004
Proportion of breeding range of lineage B overlapped by breeding range of lineage A	−1.62	−2.88, −.36	2.57	.01
Sex (female)	−.22	−.68, .24	.97	.34
Sex (male)	.29	−.18, .74	1.24	.23

Note: Both analyses tested whether color pattern differences were larger or smaller among sympatric lineages, as compared with allopatric lineages. $N = 73$ phylogenetically independent comparisons. 95% CL = 95% confidence limits.

[a] Generalized linear model with quasi-binomial error; response = binomial variable (y_1 = no. of observers scoring sympatric pair more different; y_2 = no. of observers scoring allopatric pair more different); units are log odds $[p/(1 - p)]$ where $p = y_1/(y_1 + y_2)$, so when response = 0, then $y_1 = y_2$. See figure A1*B*, available online, for test of residuals.

[b] Generalized linear mixed model with Gaussian error; response = (rated difference in color pattern between sympatric (A-B) pair of lineages) − (rated difference in color pattern between allopatric (A-C) pair of lineages); random effect = comparison; rated differences were standardized within each observer ($N = 7$ observers) such that the mean = 0 and the standard deviation = 1. See figure A2*B*, available online, for test of residuals.

lopatric lineages when sympatry ranged from our minimum value of 50% overlap to approximately 70% overlap.

Overall, observers ranked sympatric species as more different than allopatric species in 40 of 73 (55%) comparisons of males and 35 of 73 (48%) comparisons of females. As shown in figure 2*A*, 2*B*, the difference between sympatric and allopatric species pairs is most pronounced at intermediate levels of sympatry (50%–75% overlap) and when no nonfocal congeners overlapped lineages B or C. Thus, for breeding-range overlap of lineage B by A between 50% and 75% and no nonfocal congeners overlapping either B or C, observers ranked sympatric species as more different than allopatric species in 16 of 22 (73%) comparisons of males and 15 of 22 (68%) comparisons of females.

Rating Analyses

The rating analysis revealed a very similar pattern: the ratings of differences in color pattern among sympatric compared with allopatric breeding birds declined significantly with both the degree of overlap of lineage B by lineage A and the absolute latitude of the breeding ranges of A, B, and C (table 1). For a breeding-range overlap between A and B equal to 0.5 (with the mean latitude of lineages A, B, and C set to 0), sympatric lineages were rated as more different than allopatric lineages by a value significantly greater than 0, where the ratings would be the same (predicted value [95% CL] = 0.84 [0.29–1.39]).

In the rating analysis, for all eight of the top models (ΔAICc < 2), the greater difference in color pattern among sympatric, compared with allopatric, breeding birds declined with overlap of lineage B by A and with the mean latitude of lineages A, B, and C (table A3). In the averaged model, only those two variables were significant (table A3), and the other five predictors appear to be relatively unimportant. Figure 2 shows the effect of degree of sympatry on the ratings of color patterns and illustrates significantly greater divergence of color pattern (based on 95% CLs calculated from the best-fitting model) in sympatric than in allopatric lineages when sympatry ranged from our minimum value of 50% overlap to approximately 80% overlap.

Discussion

Closely related species of birds breeding at intermediate levels of sympatry are more divergent in color pattern than are those in allopatry (fig. 2), suggesting that there are costs associated with exhibiting similar color patterns when closely related species breed in the same geographic range. Our results are consistent with some previous studies that found greater divergence of color patterns in breeding sympatry in different groups of birds (e.g., genus *Ficedula* [Sætre et al. 1997; Vallin et al. 2011]; New World birds [Martin et al. 2010]) and provide the first evidence from a global data set that divergent color patterns in breeding sympatry are a general pattern among closely related birds.

Our results are not consistent with those of McNaught and Owens (2002), who found no difference in male plumage color between closely related allopatric and sympatric Australasian birds during the breeding season. McNaught and Owens (2002) examined color reflectance spectra from five general plumage regions of 65 species. Unlike our study, they did not control for differences in time since divergence

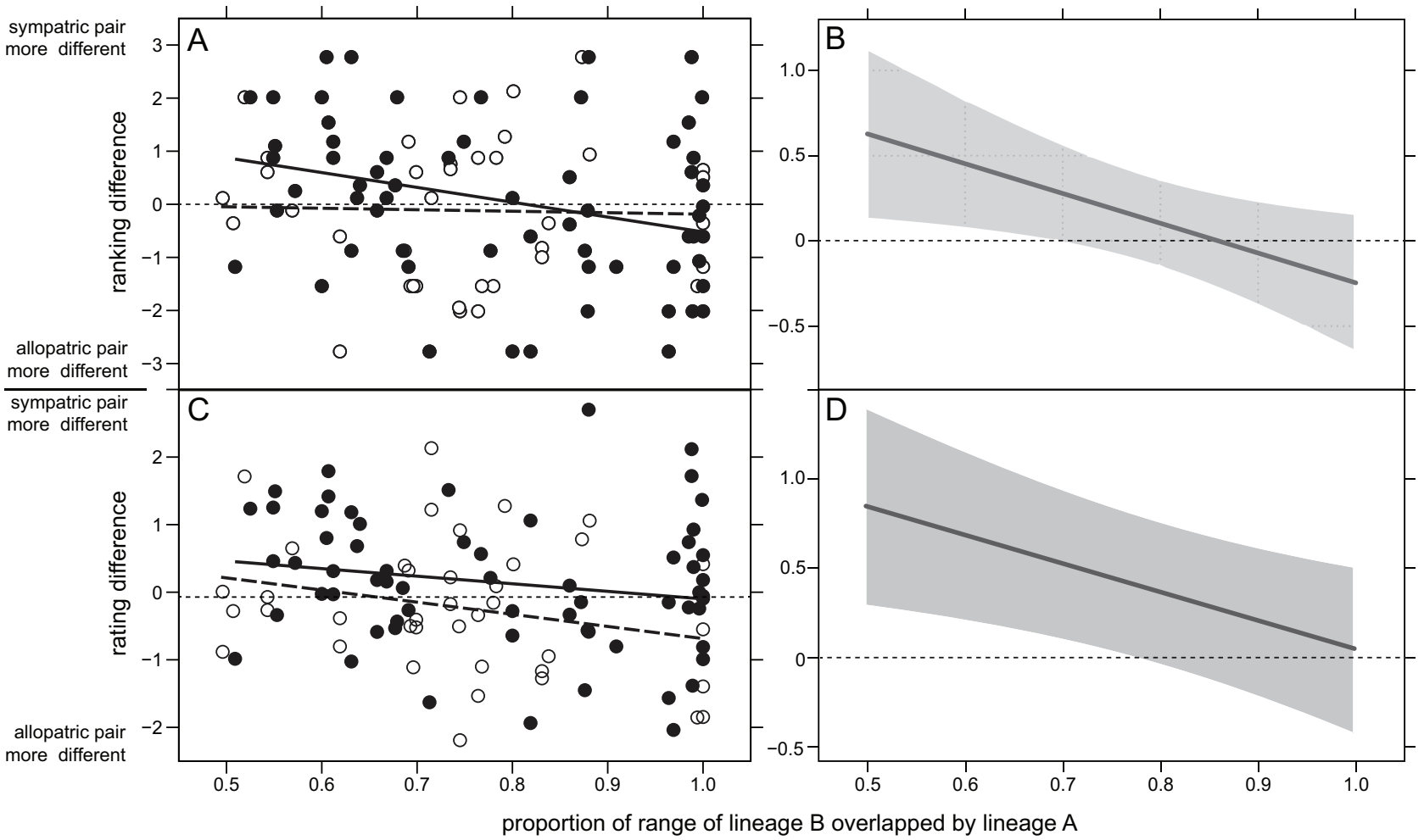

Figure 2: Rankings (*A*, *B*) and ratings (*C*, *D*) of color pattern differences between pairs of closely related species across the extent of sympatry analyzed in this study (50%–100% breeding-range overlap of lineage B by lineage A). Raw data (*A*, *C*) for the relationship between degree of sympatry (*X*-axis) and color pattern difference (*Y*-axis) for comparisons where either some (long-dashed lines, open circles) or none (solid lines, filled circles) of the nonfocal congener breeding ranges overlap the breeding range of lineage B or C. Ranking differences = ln[(no. of sympatric pairs ranked as most different + 1)/(no. of allopatric pairs ranked as most different + 1)]; rating differences = (rated difference in color patterns between sympatric lineages) − (rated difference in color patterns between allopatric lineages). Rating differences were standardized within observers and transformed (generalized logarithmic) to normalize (see the appendix and the R code available in the zip file, both available online). Horizontal short-dashed lines indicate equal differences for sympatric and allopatric lineages; in *C*, this is slightly below 0 because of the data transformation. Both *B* and *D*, illustrating predicted values and their approximate 95% confidence limits, were calculated from the best-fitting model in each set, controlling for the number of nonfocal congeners whose breeding range overlaps the breeding range of either lineage B or C (*B*) or for mean latitude, excluding the (nonsignificant) effect of sex to facilitate calculations (*D*). See figure A3, available online, for plots of residuals from *B* and *D*.

between allopatric and sympatric pairs, degree of range overlap, or overlap by other nonfocal congeners. These differences in methodologies and sampling could explain the differences in our results. Alternatively, because our studies share no species in common, it is possible that the taxa studied by McNaught and Owens (2002) simply do not diverge in color when closely related species are sympatric.

Differences in color patterns between bird species breeding in sympatry, compared to those between species breeding in allopatry, varied with several factors. Ranked differences in color pattern declined as additional congeners overlapped the breeding ranges of sister lineages (table 1). This suggests that other congeners may also have exerted selective pressures on color patterns of our focal species, forcing them to evolve in response to interactions with multiple similar species simultaneously and weakening their response to each species individually (see discussion in Noor 1997). Such multispecies interactions are rarely considered in studies of color pattern evolution, although they have been widely appreciated in multispecies coevolutionary models (e.g., Thompson 2005; Guimarães et al. 2011). Our results imply that multispecies interactions might be important for the evolution of color pattern in birds and deserve further attention.

The importance of sympatry for color pattern divergence varies with latitude in an interesting way. Closely related lineages of birds at higher latitudes come into sympatry more quickly than do tropical lineages, causing rapid divergence of color pattern among high-latitude lineages (Martin et al. 2010). Our new results from the ratings analysis suggest that, once those lineages come into breeding sympatry, the degree of divergence in color pattern is proportionately greater in the tropics, even though all lineages showed greater divergence in sympatry than in allopatry, regardless of latitude (table 1). The latitudinal difference in the degree of color pattern divergence in sympatry, relative to that in allopatry, suggests that other selective pressures acting on both sympatric and allopatric lineages may be relatively more important at high latitudes (e.g., sexual selection; Macedo et al. 2008; Bonier et al. 2014) or that other signals, such as song, may play a more important role in species recognition at higher latitudes (see Weir and Wheatcroft 2011; Lawson and Weir 2014). Such a pattern is expected if there is a general trade-off between song and plumage as targets of sexual selection, as has been suggested and documented (Darwin 1871; Shutler and Weatherhead 1990; Badyaev et al. 2002).

Maximum divergence of color pattern between sympatric and allopatric lineages occurred at the lowest levels of breeding sympatry that we measured (50% overlap), declining to no divergence at higher levels of sympatry (fig. 2). This result suggests that higher levels of sympatry are associated with either (1) a relaxation of divergent selection and a return of color patterns toward ancestral states, (2) increased levels of gene flow that impede divergence (Nosil 2013), or (3) an increased role for counteracting selection, such as local adaptation, that promotes convergence. A similar pattern of divergence peaking at intermediate levels of sympatry (~50%–70%) was recently described for prezygotic isolation in *Drosophila* (Nosil 2013) and should be looked for in other taxa.

Our analysis of color pattern divergence includes colors that result from pigments (e.g., carotenoids, melanins) and those that result from nanostructural arrangements of keratin, melanosomes, or other components of the integument. The evolutionary constraints and opportunities offered by pigments versus structural colors differ, with pigments more constrained in their expression and more likely to show phenotypic convergence than structural colors (Maia et al. 2013). We do not know the relative importance of pigments versus structural colors in either the divergence of color patterns among sympatric species or the apparent convergence, or lack of divergence, among closely related species at high levels of sympatry. However, we recognize that pigments and structural colors may differentially influence the evolution of color patterns among closely related species and that assessing their relative importance may be a rewarding avenue for future work.

Our results cannot distinguish whether the divergence of color pattern occurred before breeding sympatry, after sympatry was established, or a combination of the two (Templeton 1981; Rice and Pfennig 2007). Closely related species that have diverged in color pattern before range overlap are predicted to be better able to expand their breeding ranges into sympatry (differential expansion), including cases where incipient species with similar color patterns hybridize and fuse into a single species after secondary contact (differential fusion; Templeton 1981). Evidence to support such differential breeding-range expansion in birds comes from incipient species (or distinct lineages) in the process of fusing, apparently unable to coexist in sympatry without hybridizing (e.g., genus *Setophaga* [Rohwer et al. 2001]; genus *Corvus* [Webb et al. 2011]).

Our results are also consistent with character displacement (including reinforcement; Brown and Wilson 1956; Grant 1972; Pfennig and Pfennig 2009), where color patterns diverge after breeding ranges overlap. Evidence to support character displacement in the color patterns of birds comes from studies that show greater divergence of color pattern for populations within the same species that are sympatric with congeners than for populations that are allopatric during the breeding season (e.g., genus *Ficedula*; Sætre et al. 1993, 1997). The evidence to date suggests that both differential expansion and character displacement contribute to the greater divergence of color pattern in breeding sympatry that we found in this study.

Several different selective pressures may produce costs for co-occurring birds that have similar color patterns. A review of 58 studies of hybrid zones in birds suggests significant assortative mating consistent with selection against hybridization and sexual character displacement (Randler 2008). Detailed work on *Ficedula* flycatchers illustrates costs of hybridization (Sætre et al. 1997) and of interspecific aggression and ecological interactions (Sætre et al. 1993; Alatalo et al. 1994; Vallin et al. 2011), all of which may favor color pattern divergence in breeding sympatry over the time course of secondary contact and divergence (Vallin et al. 2011).

Other ecological interactions—such as competition for resources driving divergence in ecological traits that secondarily affect color pattern—are also likely, given the causal links between habitat characteristics and color. For example, studies of *Phylloscopus* warblers in the Himalayas of Kashmir found that closely related species occupied different habitats (Richman and Price 1992), likely reflecting adaptive ecological partitioning to reduce the costs of living together. The habitats used by these species differed in light levels that favored the divergence of color patterns, with brighter birds in darker habitats (Marchetti 1993). Thus, there is evidence for both direct and indirect factors favoring the divergence of color patterns among closely related species of birds breeding in sympatry. We await future work that can test the relative contributions of these possible selection pressures for the divergence of color pattern among sympatric birds.

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Appendix from P. R. Martin et al., "Color Patterns of Closely Related Bird Species Are More Divergent at Intermediate Levels of Breeding-Range Sympatry" (Am. Nat., vol. 185, no. 4, p. 000)

Supplementary Methods and Results

Supplementary Methods

Color Pattern Divergence

The methods described here were used previously in Martin et al. (2010). To score the degree of color divergence between pairs of species, we used human observers who had no knowledge of either breeding-range overlap or evolutionary divergence of the species studied. We provided each observer with illustrations of pairs of species (A-B and A-C; e.g., fig. 1), alternating the order of presentation between comparisons (A-B first or A-C first) and alternating the position of each species on the illustrations (A on left or A on right) between observers, to control for potential biases. Color illustrations of birds were scanned from the *Handbook of the Birds of the World* (del Hoyo et al. 1992–2010) with an Epson V500 scanner at 800 dpi (Epson America, Long Beach, CA). For species that were not yet illustrated at the time of measurements (families Emberizidae, Cardinalidae, Thraupidae, and Icteridae), illustrations were scanned from Isler and Isler (1987), Ridgely and Tudor (1989), Howell and Webb (1995), Jaramillo and Burke (1999), or Sibley (2000). In all cases but one, both species in each pair were illustrated by the same artist.

We considered a species to be sexually dimorphic if the sexes were different enough to be illustrated separately by del Hoyo et al. (1992–2010) or the other references listed above. For dimorphic species, we scored the males and females separately. For all species, we scored adults in breeding (alternate) plumage. For species with multiple morphs (e.g., hawks with dark and light morphs), we scored the most common morph in nature according to del Hoyo et al. (1992–2010). For geographically variable species that comprised lineages A or B, we preferentially selected subspecies that were sympatric with the opposite species. Otherwise, we selected the nominate subspecies.

Human observers ranked and rated differences between pairs of species according to written instructions (available in the zip file). We gave observers digital files of the illustrations, and observers assessed differences by viewing these illustrations on their personal computer screens (computers and monitors varied across observers). We provided observers with examples of rating differences (1–7 scale) used previously in Martin et al. (2010). We used seven observers to rate the difference between species and 15 observers to rank them.

While we were able to take advantage of the ability of human observers to distinguish among colors and patterns, it would certainly be desirable to repeat these analyses with objective measures of color patterns as perceived by the birds. Such a study, however, would be very difficult with currently available methods, for three reasons. First, while there are some excellent visual models to predict how birds see colors (e.g., Osorio and Vorobyev 2008), we have the relevant measurements to make a quantitative assessment for only a small number of taxa so far. Second, there are few empirical data on the ability of birds to discriminate between similar colors (e.g., Goldsmith et al. 1981). Third, and possibly most important, there are no methods for describing color patterns in a way that is relevant to bird's ability to discriminate between them (but see Endler and Mielke 2005 for a potential start at doing this). Thus, there is as yet no way to quantify the differences among the myriad color patterns that birds exhibit in a way that is relevant to a bird's ability to discriminate among them (see, e.g., Lazareva et al. 2005).

Geographic Ranges

We used the breeding ranges of focal species in Martin and Tewksbury (2008) and BirdLife International and NatureServe (2011) to estimate degree of sympatry. We used ArcGIS 9.2 (ESRI) to estimate the degree of sympatry of those breeding ranges, by measuring the area (km^2) of each breeding range, then intersecting the ranges to generate a shapefile for measuring the area of overlap (sympatry) in square kilometers. The degree of breeding-range sympatry was calculated as (area of overlap)/(breeding-range area of the focal species).

Phylogenies

We used the phylogenetic relationships described in the following references for each of these genera: *Lophura* (Randi et al. 2001), *Anas* (Eo et al. 2009; Gonzalez et al. 2009), *Pelecanoides* (Nunn and Stanley 1998), *Ciconia* (Slikas 1997), *Platalea* (Chesser et al. 2010), *Circaetus* (Lerner and Mindell 2005), *Hieraaetus* (Lerner and Mindell 2005), *Thalasseus* (Bridge et al. 2005), *Gallicolumba* (Jønsson et al. 2011), *Brotogeris* (Ribas et al. 2009), *Amazona* (Russello and Amato 2004), *Heliangelus* (this study; see also Para et al. 2010), *Pharomachrus* (this study), *Corythornis* [*Alcedo*] (Moyle et al. 2007; Melo and Fuchs 2008), *Todus* (Overton and Rhoads 2004), *Merops* (Marks et al. 2007), *Picoides* (Weibel and Moore 2002), *Veniliornis* (Moore et al. 2006), *Campephilus* (Fleischer et al. 2006), *Ochetorhynchus* (Chesser et al. 2007), *Cinclodes* (Sanín et al. 2009), *Dendrocincla* (Weir et al. 2009), *Dendrocolaptes* (Weir et al. 2009), *Xiphorhynchus* (Aleixo 2002), *Cercomacra* (Gómez et al. 2010), *Pteroptochos* (Chesser 1999), *Empidonax* (Johnson and Cicero 2002), *Acanthiza* (Nicholls et al. 2000; Gardner et al. 2010), *Oriolus* (Jønsson et al. 2010), *Cyanolyca* (Bonaccorso 2009), *Tachycineta* (Whittingham et al. 2002), *Petrochelidon* (Sheldon et al. 2005), *Phylloscopus* (Olsson et al. 2005), *Acrocephalus* (Fregin et al. 2009), *Xanthomixis* [*Bernieria*] (Moyle and Marks 2006), *Sylvia* (Voelker and Light 2011), *Regulus* (Päckert et al. 2003), *Campylorhynchus* (Barker 2007; Vázquez-Miranda et al. 2009), *Toxostoma* (Zink et al. 1999), *Mino* (this study), *Sturnia* [*Temenuchus*] (Lovette et al. 2008; Zuccon et al. 2008), *Lamprotornis* (Lovette and Rubenstein 2007), *Turdus* (Voelker et al. 2007), *Luscinia* (Sangster et al. 2010), *Oenanthe* (Outlaw et al. 2010), *Monticola* (Outlaw et al. 2007), *Bradornis* (Sangster et al. 2010), *Anthus* (Alström and Mild 2003, p. 102), *Loxia* (this study), *Icterus* (Omland et al. 1999; Jacobsen et al. 2010), *Quiscalus* (Powell et al. 2008), *Ammodramus* (Klicka and Spellman 2007), *Peucaea* (DaCosta et al. 2009), *Melozone* [*Pyrgisoma*, *Pipilo*] (DaCosta et al. 2009), *Paroaria* (Sedano and Burns 2010; we did not use Dávalos and Porzecanski 2009 because they incorporated phenotypic characters), *Rampholocelus* (Burns and Racicot 2009), *Chlorochrysa* (Sedano and Burns 2010), *Tangara* (Sedano and Burns 2010), *Cyanerpes* (this study), *Diglossa* (Mauck and Burns 2009), *Piranga* (Burns 1998), *Calcarius* (Klicka et al. 2003), and *Cardinalis* (figs. 1, 2 in Klicka et al. 2007).

Phylogenetics

For five genera, we could not find a suitable published phylogeny, so we generated our own, using mitochondrial DNA (mtDNA) sequence data, as follows: *Heliangelus* (outgroups = *Oreotrochilus chimborazo*, *Metallura theresiae*; 1,041 base pairs [bp] of ND2; Genbank accession numbers: GU167230, GU167231, GU167232, AY830489, EU042556, GU166849, GU166850, GU166851, AY830506, GU166853), *Pharomachrus* (outgroups = *Apaloderma aequatoriale*, *Trogon viridis*, *Harpactes erythrocephalus*; 1,041 bp of ND2; Genbank accession numbers: AY625218, AY625219, AY625220, EU603915, EU603917, EU603918, EU603920, EU603919, EU603916, HQ380007, EU603907, EU603908), *Mino* (outgroups = *Gracula religiosa*, *Gracula ptilogenys*; 825 bp of ND2; Genbank accession numbers: DQ469050, DQ469049, DQ469048, DQ469047, DQ469046, DQ469045, DQ469044, EF468161, EF468160, DQ466868, EF468237, EF468159), *Loxia* (outgroup = *Carduelis hornemanni*; 1,143 bp of cytochrome-*b* [cyt*b*]; Genbank accession numbers: AF171652, AF171653, AF171654, AF171655, AF171656, AF171657, AF171658, AF171659, AF171660, AF171661, AF171662, AF171663, AF171664), and *Cyanerpes* (outgroup = *Dacnis cayana*; 719 bp of cyt*b*; Genbank accession numbers: GU215305, GU215302, FJ899500, FJ899499, FJ899498, FJ899497, AF006225, GU215303, GU215299, GU215298, FJ799873, EF529958, AY190167, GU215301). We aligned the sequences with the homologous gene from the chicken (Desjardins and Morais 1990), using Clustal X, version 2.0.10 (Larkin et al. 2007); visually inspected the sequence, using MacClade, version 4.08 (Maddison and Maddison 2005); and removed any sequence that did not align with the relevant gene from the chicken. For each data set, we used jModelTest, version 1.0 (Guindon and Gascuel 2003; Posada 2008), to identify the preferred model of evolution for subsequent Bayesian phylogenetic analysis. AICc values were used to rank 24 models. Best models of evolution for each genus were as follows: for *Pharomachrus*, GTR + G (gamma shape = 0.236); for *Cyanerpes*, HKY + I (proportion of invariant sites = 0.762); for *Loxia*, HKY + I (proportion of invariant sites = 0.830); for *Mino*, HKY + I (proportion of invariant sites = 0.677); and for *Heliangelus*, GTR + I (proportion of invariant sites = 0.644).

For all phylogenetic analyses, we used MRBAYES, version 3.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003), running each analysis for 1 million generations and sampling every 100 generations, with default settings and the model selected by jModelTest specified. One million generations were sufficient to achieve values of the standard deviation of the split frequencies less than 0.01 and for the potential scale reduction factors to approach 1. We

discarded the first 25% of sampled generations as burn-in and constructed 50% majority-rule consensus trees from the remaining 7,500 trees.

Genetic Distance

We calculated the genetic distance (1) between lineages B and C and (2) between lineages A and BC (fig. 1), using mtDNA sequence obtained from GenBank (accession numbers below). We preferentially used the cyt*b* sequence (58 comparisons) because good clock calibrations of this gene were available for birds (Weir and Schluter 2008); however, there was no cyt*b* sequence available for 15 of our comparisons. For those 15 comparisons, we used ND2 (11 comparisons), COI (2 comparisons), or COII (2 comparisons). We aligned the sequence with the homologous gene from the chicken (Desjardins and Morais 1990), using Clustal X, version 2.0.10 (Larkin et al. 2007); visually inspected the sequence, using MacClade, version 4.08 (Maddison and Maddison 2005); removed any sequence that did not align with the relevant gene from the chicken; and then measured genetic distance, using MEGA, version 5.0 (Tamura et al. 2011). We calculated between-group mean Tamura-Nei genetic distances (from B to C and from A to BC) because this measure corrects for multiple substitutions at the same site, incorporates differences in substitution rates between nucleotides, and does not assume equal nucleotide frequencies (Tamura and Nei 1993). We included transitions and transversions and all codon positions. We assumed uniform rates among sites and homogeneous patterns among lineages, and we used pairwise deletion to address gaps or missing data (Tamura et al. 2011).

The Genbank accession numbers for sequences used to calculate genetic distances are as follows: *Lophura* (cyt*b*; AF314644, AF314640, AF314638, AF534558, AF534557, NC_012895, AF314643, EU417810), *Anas* (cyt*b*; EU585609, AF059081, AF059095, AF059093, AF059091, AF059088, AF059083, AF059082, AF059079, AF059078, AF059074, AF059069, EU914150, AF059092), *Pelecanoides* (cyt*b*; AF076074, AF076075, AF076076), *Ciconia* (cyt*b*; NC_002196, NC_002197, DQ485896, AY567910, AY567909, U70822, AB026193, AB026818), *Platalea* (cyt*b*; GU346979, GU346980, GU346984, GU346985, GU346986, GU346987), *Circaetus* (cyt*b*; AY987252, AY987254, AY987253), *Hieraaetus* (cyt*b*; AJ604500, AJ604499, AJ604497, AJ604493, AY754045, AY754044, AY987290, AY987289, AY987288, Y15761, Y15760, AY987291, AY987292, AY987293), *Thalasseus* (cyt*b*; AY631299, AY631298, AY631309), *Gallicolumba* (ND2; EF373332, HQ630232, HQ630220, HQ630213), *Brotogeris* (cyt*b*; FJ652902, FJ652901, FJ652900, FJ652899, FJ652898, FJ652897, FJ652896, FJ652895, FJ652859, FJ652858, FJ652857, FJ652856, FJ652854, FJ652853, FJ652852, FJ652851, FJ652850, AF370777, AF370776), *Amazona ochrocephala-dufresniana-rhodocorytha* (COI; AY301458, AY301439, AY301451), *Amazona autumnalis-viridigenalis-finschi* (cyt*b*; AY283456, AY283455, AY283453, AY283452, AY283451, AY283461), *Amazona vinacea-pretrei-tucumana* (COI; AY301459, AY301457, AY301462), *Amazona agilis-collaria-leucocephala/ventralis/vittata* (cyt*b*; AY283489, AY283493, AY283494, AY283490, AY283488, AY283487, AY283484, AY283483, AY283482, AY283481, AY283480, AY283479, AY283478, AY283477, AY283476, U89178, AY283486, AY283474, AY283473, AY283491, AY283485), *Heliangelus* (ND2; AY830489, GU166849, EU042556, GU167230), *Pharomachrus* (ND2; EU603916, EU603915, EU603917, AY625219, AY625218), *Corythornis* [*Alcedo*] (ND2; AY998900, AY998899, AY998898, AY998897, AY998896, AY998895, DQ640780, AY998917, AY998918, GQ861188, EF585384, EF585383, EF585375, EF585374, DQ111834, EF585381, EF585380), *Todus* (cyt*b*; AF441615, AF441616, AF441617, AF441618, AF441619, AF441620, AF441621, AF441622, AF441623, AF441624, AF441625, AF441626, AF441627, AF441628, AF441629, U89186, AF407450), *Merops* (ND2; EU021525, EU021520, EU021519, EU021526), *Picoides* (cyt*b*; AF389305, AF389304, AF425070, AF425067, AF425064, AF425058, AF425055, AF425052, AF425049, AF425046, AF389331, AF389330, AY863147, AY701066), *Veniliornis* (cyt*b*; AY927220, AY927219, AY927209, AY942893, AF389337), *Campephilus* (cyt*b*; DQ521895, DQ521894, AY940798), *Ochetorhynchus* (cyt*b*; GQ140082, GQ140078, GQ140074), *Cinclodes* (COII; AY613377, AY613376, AY613383, AY613382, AY613385, AY613384), *Dendrocincla* (cyt*b*; GU215186, GU215182, GU215181, GU215184, GU215180, GU215179, GU215178, GU215177, AY442986, AY442985, AY065713), *Dendrocolaptes* (cyt*b*; GU215187, JF276383, JF276381, JF276384, JF276382, JF276385, AY442991, AY089817, EF212896, EF212895), *Xiphorhynchus* (cyt*b*; AY504924, AY504912, AY504891, AY504880, AY089804, AY089820, EF190607, AY089831), *Cercomacra* (cyt*b*; HM637182, DQ294490, HM637188, GU215217, HM637187, HM637186, EF639940, EF639941, GU215216, GU215218, GU215219, GU215220), *Pteroptochos* (COII; AF111826, AF111825, AF111824, AF111821, AF111820, AF111819, AF111818), *Empidonax* (cyt*b*; AY143199, AY143198, AY143194, AY143182, AY030103), *Acanthiza* (cyt*b*; AF129236, AF129235, AF129234, AF129233, AF129232), *Oriolus* (ND2; GQ901758, GQ901759, GQ901764, GQ901767, GQ901775, GQ901781), *Cyanolyca* (ND2; DQ912606, FJ598175,

FJ598174, FJ598173, FJ598177), *Tachycineta* (cyt*b*; GU460236, AY052451, AY052449, AY052448, AY052447, AY052446), *Petrochelidon* (cyt*b*; AF074591, GU460235, AY825985, AY825983, AY825984, AF182391, AF182389, AF182381, AF182380, AF182379, AF182385), *Phylloscopus* (cyt*b*; AY635056, AY887681, HQ608822, AY903607, AB362459, AY887677, AB362458, AB362446, AB362426), *Acrocephalus* (cyt*b*; AJ004294, AJ004293, AJ004304, AJ004300, AJ004236, FJ883024, AJ004769, AJ004244, AJ004243, AJ004242, AJ004291, AJ004290, AJ004292, HQ608855, AJ004258, AJ004257), *Xanthomixis* [*Bernieria*] (cyt*b*; AF199388, AF199389, AF199391, HQ706181), *Sylvia* (cyt*b*; AJ534533, AJ534531, AJ534532), *Regulus* (cyt*b*; AY894876, AY894877, AY894878, AY894882, AY894883, AY894884, AY894886, AY894887, AY894888), *Campylorhynchus* (cyt*b*; DQ004889, DQ004888, DQ004884, DQ004882), *Toxostoma* (cyt*b*; AF130235, AF130237, DQ241266, DQ241262, DQ241251), *Mino* (ND2; DQ466868, DQ469044, DQ469045, DQ469047, DQ469048, DQ469049, DQ469050, EF468160, EF468161, DQ469046), *Sturnia* [*Temenuchus*] (ND2; EU551960, EU403598, EU403597, EU551961, EF468187), *Lamprotornis* (ND2; EF468238, EF468240, EF468124, EF468122, EF468121, AY329425), *Turdus* (cyt*b*; EU154627, DQ910956, EU154623, DQ910951, EU154634, DQ910960, EU154628, DQ910957, EU154616, DQ910945, DQ910949, EU154620, EU154625, DQ910954, EU154604, DQ910936, EU154659, EU154658, DQ910984), *Luscinia* (cyt*b*; HM633322, AB353338, HM633317, DQ119522, DQ119521, HM633315), *Oenanthe* (cyt*b*; EU154592, GU055483, GU055482, GU055481, GU055475, DQ285433, GU055469), *Monticola* (cyt*b*; EF434532, EF434533, EF434527, EF434516, AF276786, AF276785, AF276784), *Bradornis* (cyt*b*; AY329450, AY329463, HM633325, HM633395), *Anthus* (cyt*b*; U46774, U46772, U46773), *Loxia* (cyt*b*; AF171660, AF171661, AF171655, AF342878, AF171663, AF171662, AF171658, AF171657, AY495386), *Icterus* (cyt*b*; AF089033, AF099301, AF099300, AF089030, AF310064, AF099304), *Quiscalus* (cyt*b*; AF089056, GU215210, FJ389570, AF089054, GU215209, GU215208, GU215211, FJ389558), *Ammodramus* (cyt*b*; DQ459520, DQ459519, DQ459522), *Peucaea* (cyt*b*; FJ547265, FJ547264, FJ547263, FJ547266), *Melozone* [*Pyrgisoma, Pipilo*] (cyt*b*; AF314644, EU325776, FJ547262, EF529937), *Paroaria* (cyt*b*; EU647990, EU647989, EU647988, FJ715681, FJ715672, FJ715671, FJ715670, FJ715664, FJ715663, FJ715662), *Ramphocelus* (cyt*b*; FJ799881, EF529964, U15721, U15723, GU215320, AF310048), *Chlorochrysa* (cyt*b*; AY383094, AY383095, EU647981), *Tangara* (cyt*b*; AY383156, AY383145, AY383144, AY383121, AY383125), *Cyanerpes* (cyt*b*; GU215303, GU215298, GU215296, AF006225, AY190167, GU215302), *Diglossa* (cyt*b*; EU647907, EU647906, EU647901, EU647899, EU647896, EU647895, EU647893, AF310050), *Piranga* (cyt*b*; AY124545, EU325775, EF529998, AF011760, AF011759, EF530000, AF011768, AF011768, AF011767, AF011766, AF011765, AF011764, AF011763, AF011762), *Calcarius* (cyt*b*; EF529928, EF529927, DQ489372, DQ489371, DQ489370, DQ489369, DQ489368, DQ489367), *Cardinalis* (cyt*b*; EU325777, EF530009, EF530008, EF530007).

Overlapping Nonfocal Congeners

Our study tests the importance of breeding sympatry among closely related species for the evolution of color patterns. However, in some cases the breeding ranges of nonfocal closely related species overlapped the breeding ranges of our focal species, thus potentially influencing their patterns of evolution and obscuring the interactions between focal species. The potential bias of nonfocal closely related species should be particularly acute when these species' breeding ranges differentially overlap that of either species B or C. Closely related species that overlap species A should cause the color pattern of A to diverge from that of both B and C and thus should not have unduly biased our results. Similarly, any closely related species whose breeding range overlapped those of both B and C, or those of A, B, and C could cause these species to evolve differences in color but should not have unduly biased our results.

We considered a nonfocal congener as sympatric with B or C during the breeding season if [(area of breeding sympatry of nonfocal species and either B or C)/(breeding-range size of B or C)] exceeded 0.50. We summed the number of nonfocal congeners that were sympatric with either B or C during the breeding season for each phylogenetically independent comparison and used this number as a predictor in our statistical models. For example, if congener X overlaps B and congeners Y and Z overlap C, then the value of this predictor was 3.

Degree of Breeding-Range Sympatry

We measured the degree of breeding-range overlap between A and B from the perspective of both species and included these measures as predictors in our statistical models. We predicted that an increase in the overlap of the breeding range of species B on that of species A would cause species A to diverge in color pattern from both species B and C,

thus reducing the likelihood of divergence between B and C. We predicted that an increase in breeding-range overlap of species A on species B would increase the potential for divergent color pattern evolution in species B, because more populations of species B would be subject to selection by species A. Overlap of species A was measured as [(area of breeding-range overlap of A and B [km^2])/(breeding-range size of A [km^2])]. Overlap of species B was measured as [(area of breeding-range overlap of A and B [km^2])/(breeding-range size of B [km^2])].

Mean Latitude of Breeding Range

We used ArcGIS 9.2 (ESRI) to measure the mean latitude of each breeding range as the absolute value of the latitude of that range's centroid (area-weighted mean). We included mean latitude of lineages A, B, and C as a predictor in our models to test whether the influence of breeding sympatry varied with latitude.

Breeding-Range Size

The breeding-range sizes of sympatric species could influence the likelihood of divergent evolution because small range sizes increase the potential for evolution by genetic drift and reduce the likelihood of adaptive evolution. Thus, we measured breeding-range sizes (km^2) with ArcGIS 9.2 (ESRI) and included breeding-range size as a predictor in our statistical models.

Continent

We tested for large-scale geographic variation in our results by including continent as a predictor in our statistical models. We focused on species B for this analysis because species B was the species most likely to evolve because of sympatry with a close relative (A) and thus was most informative for geographic variation. Thus, "continent" was scored as the continent that held the majority of the breeding range of species B. We considered Europe and Asia together because they share large proportions of their breeding avifauna, and we included the Caribbean and Central America in North America. Our sample sizes (number of phylogenetically independent comparisons) for the various continents were as follows: Africa ($n = 9$), Australia ($n = 4$), Eurasia ($n = 16$), North America ($n = 17$), and South America ($n = 27$).

Statistical Methods: Model Building

We constructed models, using R 3.0.3 to predict rankings or ratings. For rankings analyses, we used the *glm* function in the base *stats* package (ver. 3.0.3); for ratings analyses we used the *lme* function in the *nlme* package (ver. 3.1–117).

In each model set shown in tables A2 and A3, we list all models with ΔQAICc or ΔAICc less than 2. These top models were used to create an averaged model with the *model.avg* function in the *MuMin* package (ver. 1.10.0) and the *rescale* function in the *arm* package (ver. 1.7–03) to standardize raw data.

Supplementary Results

Supplementary Figures and Tables

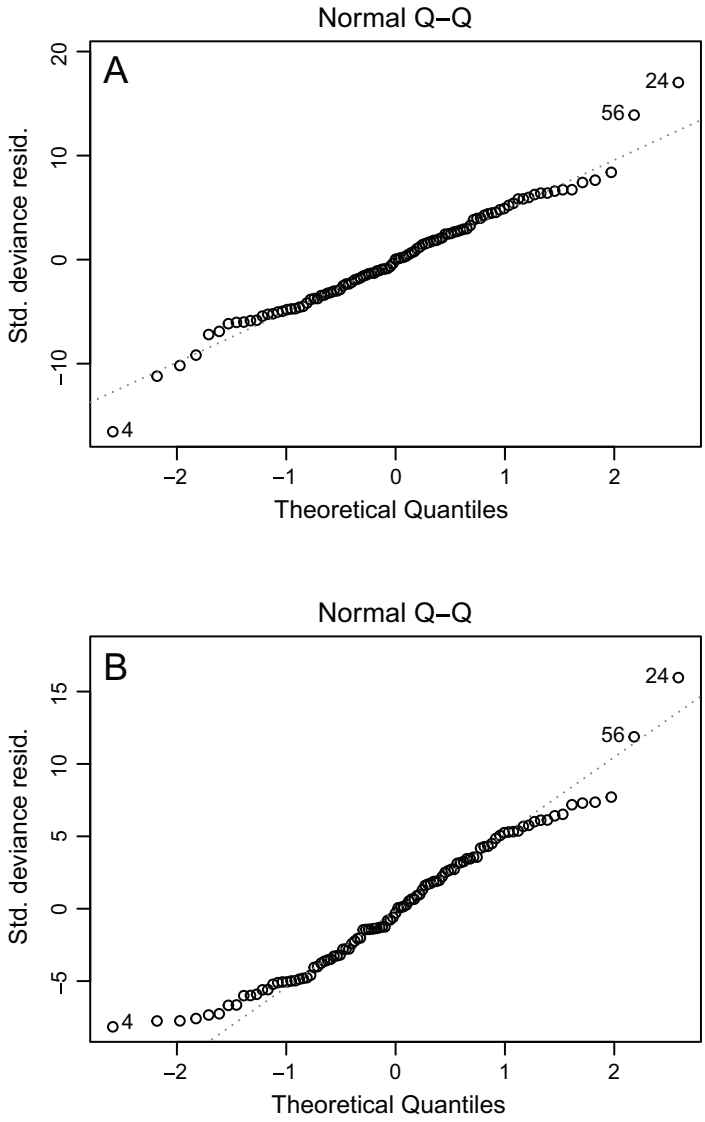

Figure A1: *A*, Q-Q plot of the residuals (resid.) from the full model to predict rank differences from standardized predictors; Shapiro-Wilk test: $W = 0.98$, $P = .16$. *B*, Q-Q plot of the residuals from the best-fitting model to predict rank differences from untransformed predictors; see table 1 for model details; Shapiro-Wilk test: $W = 0.98$, $P = .06$.

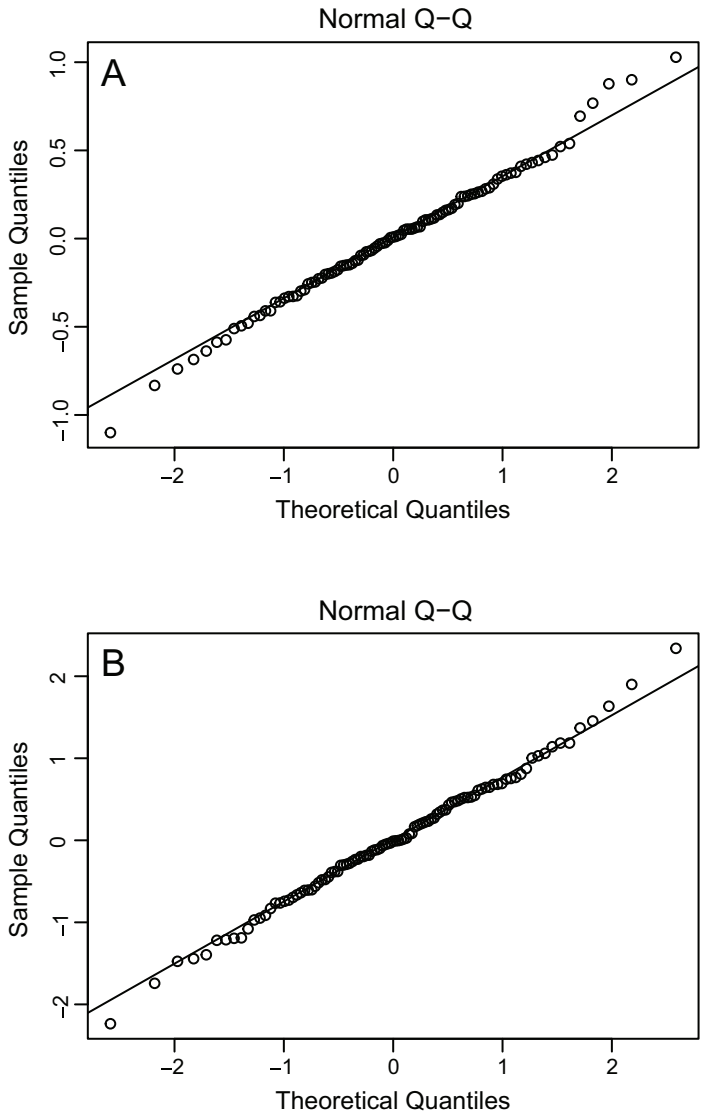

Figure A2: *A*, Q-Q plot of the residuals from the full model for rating differences, with standardized predictors; Shapiro-Wilk test: $W = 0.99$, $P = .88$. *B*, Q-Q plot of the residuals from the best-fitting model for rating differences, with predictors not standardized; see table 1 for model details; Shapiro-Wilk test: $W = 0.996$, $P = .99$.

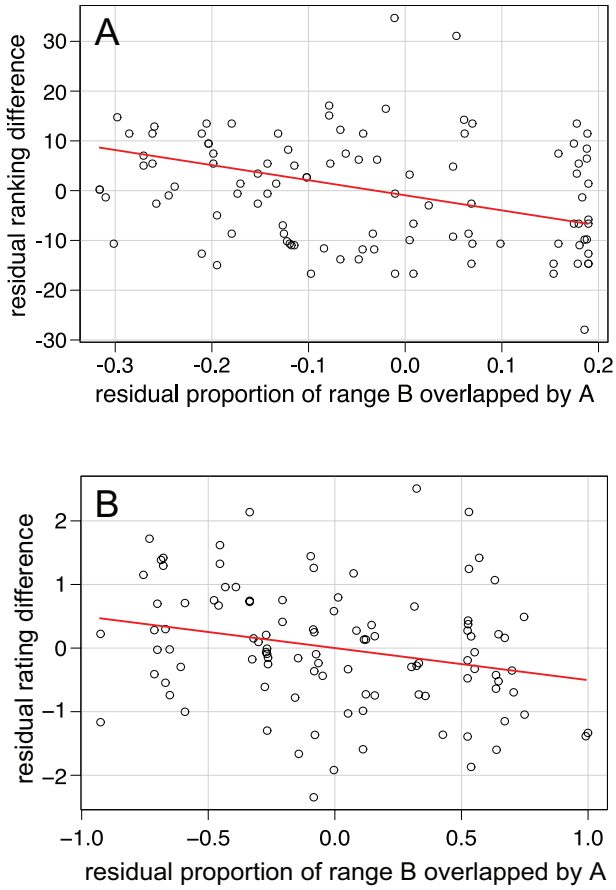

Figure A3: *A*, Partial regression plot of residual ranking difference as a function of residual proportion of range of lineage B overlapped by that of lineage A, from the model shown in figure 2*B*. *B*, Partial regression plot of residual rating difference as a function of residual proportion of range of lineage B overlapped by that of lineage A, from the model illustrated in figure 2*D*.

Table A1: Variables in the data set used in our analyses

Variable	Description
number	Unique number for each phylogenetically independent comparison
Family	Taxonomic family, following the taxonomy of Gill and Donsker 2010
Genus	Taxonomic genus, following the taxonomy of Gill and Donsker 2010
Species.A	Species in lineage A (see fig. 1); species in parentheses[a] are part of lineage A but do not overlap lineage B and thus were not included in our analysis; taxonomy follows Gill and Donsker 2010
Species.B	Species in lineage B (see fig. 1); species in parentheses[a] are part of lineage B but do not overlap lineage A and thus were not included in our analysis
Species.C	Species in lineage C (see fig. 1)
symp.diff	Number of cases where an observer ranked the sympatric (A-B) pair of species as more different for color pattern than the allopatric (A-C) pair of species ($N = 15$ observers)
allo.diff	Number of cases where an observer ranked the allopatric (A-C) pair of species as more different for color pattern than the sympatric (A-B) pair of species ($N = 15$ observers)
color.rating	(Rated difference between sympatric (A-B) pair of species)−(rated difference between allopatric (A-C) pair of species) for color pattern, where rated difference is on a scale of 1–7 (1 being most similar, 7 being most different); all ratings were standardized among observers so that all ratings for each observer had a mean of 0 and a standard deviation of 1; values for each comparison represent these standardized ratings averaged across 7 observers
overlap	Number of additional (nonfocal) congeners that overlap breeding ranges with either B or C, where overlap with B or C > 0.5; thus, if congener X overlaps B, and congeners Y and Z overlap C, then overlap $= 3$; any congener that overlapped both species B and C was not included in this tally because it would exert similar pressures for differentiation on both B and C

Table A1 (*Continued*)

Variable	Description
gen.dist.A	Tamura-Nei genetic distance between lineage A and lineage BC based on mtDNA sequence divergence
gen.dist.BC	Tamura-Nei genetic distance between lineage B and lineage C based on mtDNA sequence divergence
mean.lat.ABC	Average of the absolute centroid (area-weighted mean) latitudes of the breeding ranges of A, B, and C
overlp.A	(Area of breeding-range overlap of A and B)/(breeding-range area of A)
overlp.B	(Area of breeding-range overlap of A and B)/(breeding-range area of B)
range.size.B	Area (km^2) of breeding range of B; if more than one species comprise lineage B, then this value is the average
range.size.C	Area (km^2) of the breeding range of C; if more than one species comprise lineage C, then this value is the average
sex	Sex used in comparison; both = monomorphic species
continent.B	Continent where the majority of the breeding range of species B occurs (North America includes Central America and the Caribbean)

Note: "Data set" refers to the data deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.8dc26 (Martin et al. 2015). These variable names are used in tables A2 and A3.

[a] "Species in parentheses" refers to species names in the data set.

Table A2: Generalized linear models to predict rankings

A. Top models (ΔQAICc < 2)

Model rank[a]	Predictors	ΔQAICc	Weight
1	*overlap*, *overlp.B*	0	.30
2	*overlap*, *overlp.B*, *mean.lat.ABC*	.90	.19
3	*overlap*, *overlp.B*, *range.size.C*	1.45	.15
4	*overlap*, *overlp.B*, *gen.dist.BC*	1.67	.13
5	*overlap*, *overlp.B*, *sex*	1.84	.12
6	*overlap*, *overlp.B*, *overlp.A*	1.96	.11

B. Averaged model, with shrinkage to reduce estimates on weaker terms thereby improving predictions

Coefficient	Estimate [95% CL]	*z*	*P*	Relative importance
Intercept	.08 [−.19, .35]	.58	.56	
overlap	−.36 [−.64, −.08]	2.49	.01	1.0
overlp.B	−.58 [−1.06, −.10]	2.35	.02	1.0
mean.lat.ABC	−.06 [−.82, .21]	.35	.73	.19
range.size.C	−.03 [−.69, .26]	.26	.79	.21
gen.dist.BC	.02 [−.28, .62]	.22	.82	.13
sex (female)	−.05 [−.97, .11]	.31	.76	.12
sex (male)	−.008 [−.60, .47]	.08	.93	.12
overlp.A	.01 [−.33, .57]	.15	.88	.11

Note: Binomial response with standardized predictors (see zip file for R code), using a quasi-binomial distribution to correct for overdispersion. See table A1 for definitions of variables. ΔQAICc = change in Akaike information criterion for quasi models, adjusted for small sample size; 95% CL = 95% confidence levels.

[a] Response: (y_1 = no. of observers scoring sympatric pair more different, y_2 = no. of observers scoring allopatric pair more different).

Table A3: Generalized linear mixed models to predict ratings

A. Top models (ΔAICc < 2)

Model rank[a]	Predictors	ΔAICc	Weight
1	*mean.lat.ABC*, *overlp.B, sex*	0	.25
2	*mean.lat.ABC*, *overlp.B*	.27	.22
3	*mean.lat.ABC*, *overlp.B*, *overlp.A*, *sex*	1.57	.12
4	*mean.lat.ABC*, *overlp.B*, *overlap*, *sex*	1.71	.11
5	*mean.lat.ABC*, *overlp.B*, *overlap*	1.80	.10
6	*mean.lat.ABC*, *overlp.B*, *overlp.A*	1.83	.10
7	*mean.lat.ABC*, *overlp.B*, *range.size.C*, *overlp.A*	1.98	.09

B. Averaged model, with shrinkage to reduce estimates on weaker terms thereby improving predictions

Coefficient	Estimate [95% CL]	*z*	*P*	Relative importance
Intercept	.005 [−.13, .12]	.08	.93	
mean.lat.ABC	−.29 [−.49, −.09]	2.89	.004	1.0
overlp.B	−.25 [−.45, −.06]	2.51	.01	1.0
sex (male)	.08 [−.09, .37]	.71	.47	.57
sex (female)	−.06 [−.34, .12]	.60	.55	.57
overlp.A	.02 [−.11, .28]	.31	.76	.22
overlap	−.02 [−.27, .11]	.30	.76	.21
range.size.C	−.006 [−.27, .15]	.16	.88	.09

Note: Response and all predictors standardized (except sex and continent.B), with comparison entered as a random effect. See table A1 for definitions of variables. ΔAICc = change in Akaike information criterion adjusted for small sample size; 95% CL = 95% confidence levels.

[a] Response: (rating of color difference between sympatric lineages A and B)−(rating of color difference between allopatric lineages A and C).

Combining Sexes

Results were similar if we combined sexes (i.e., rankings summed across males and females for dimorphic species, ratings averaged across males and females for dimorphic species), such that each phylogenetically independent comparison was represented only once in the data set. For both ranking and rating analyses, the best-fitting model using a response variable with sexes combined retained the same predictors: ranking analysis (overlap of nonfocal congeners: best model, predicted value = −0.08 [95% CL: −0.15 to −0.02], $P = .008$; averaged model, $P = .016$; proportion of overlap of lineage B by A: best model, predicted value = −1.75 [−3.26 to −0.27], $P = .02$, averaged model, $P = .02$); rating analysis (mean latitude of lineages A, B, and C: best model, predicted value = −0.02 [−0.03 to −0.01], $P = .007$; averaged model, $P = .007$; proportion of overlap of lineage B by A: best model, predicted value = −1.83 [−3.17 to −0.49], $P = .008$, averaged model, $P = .009$).

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