doi:10.1111/evo.12706

Closely related species of birds differ more in body size when their ranges overlap—in warm, but not cool, climates

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Received June 3, 2014
Accepted June 3, 2015

Differences in body size are widely thought to allow closely related species to coexist in sympatry, but body size also varies as an adaptive response to climate. Here, we use a sister lineage approach to test the prediction that body size differences between closely related species of birds worldwide are greater for species whose ranges are sympatric rather than allopatric. We further test if body size differences among sympatric versus allopatric species vary with geography, evolutionary distance, and environmental temperatures. We find greater differences in size among sympatric compared with allopatric lineages, but only in closely related species that live where mean annual temperatures are above 25°C. These size differences in warm environments declined with the evolutionary distance between sister lineages. In species living in cooler regions, closely related allopatric and sympatric species did not differ significantly in size, suggesting either that colder temperatures constrain the evolutionary divergence of size in sympatry, or that the biotic selective pressures favoring size differences in sympatry are weaker in colder environments. Our results are consistent with suggestions by Wallace, Darwin, and Dobzhansky that climatic selective pressures are more important in cooler environments (e.g., high elevations and latitudes) whereas biotic selective pressures dominate in warm environments (e.g., lowland tropics).

KEY WORDS: **Abiotic selective pressures, biotic selective pressures, body mass, competition, latitude, range overlap.**

Evolutionarily young species whose geographic ranges overlap (i.e., occur in sympatry) encounter a significant challenge—they share many ecological traits and preferences through recent common ancestry, and yet must partition resources to survive and reproduce (Violle et al. 2011). One solution to this challenge is the evolution of differences in key ecological traits that allow closely related species to partition resources when they live together (Brown and Wilson 1956; Grant 1972; Schluter 2000; Dayan and Simberloff 2005). In animals, body size has long been considered one such trait (Hutchinson 1959; Peters 1983; Bonner 2006), influencing the diversity of usable prey, the risk of predation, caloric requirements, life history strategies, behavior, and physiological tolerances, among many other traits (Peters 1983; Vézina 1985; Schmidt-Nielsen 1984; Bonner 2006; Dial et al. 2008). Divergence in body size might thus allow closely related species to partition resources in diverse ways, reducing the fitness costs of living in sympatry (Brown and Wilson 1956; Hutchinson 1959). As a result, studies of ecologically similar, closely related species often find greater differences in body size in sympatry relative to allopatry (reviewed by Dayan and Simberloff 2005).

While divergence in body size may allow closely related species to coexist, the evolution of body size is also influenced by climate—a selective pressure shared by species living in sympatry. The trend to larger size in colder environments is found both within species and among closely related species of birds and mammals (Ashton et al. 2000; Ashton 2002; Meiri and Dayan 2003; Olson et al. 2009; Clauss et al. 2013). Body sizes of some birds and mammals also decline as climates warm over time (Van Buskirk et al. 2010; Gardner et al. 2011; Sheridan and Bickford 2011), further supporting a link between temperature and size.

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The selective benefit of larger size in colder climates is thought to involve relative heat loss, with the lower surface-area-to-volume ratios in larger organisms allowing homeotherms to retain relatively more heat energy as a proportion of their total energy budgets (Bergmann 1848; Meiri and Dayan 2003; Clauss et al. 2013). Other factors may also favor larger sizes in colder climates (Blackburn et al. 1999)—for example, enabling organisms to withstand the longer periods of limited food availability that characterize some cold environments (Lindsey 1966; Calder 1974; Lindstedt and Boyce 1985; Ashton 2002).

Shared climate favoring body size convergence, and the ecological interactions favoring divergence, thus present opposing selective pressures acting upon closely related species living in sympatry. The relative importance of these conflicting selective pressures should vary both geographically and over evolutionary time. For example, the relative importance of competition versus climate has long been thought to vary with both elevation and latitude—with biotic interactions suggested to be more important in warmer regions (Darwin 1859; Wallace 1878; Dobzhansky 1950; Schemske et al. 2009). If shared climate favors convergence in body size among sympatric species, then we might expect stronger selection for convergence at higher latitudes and elevations, where climatic selective pressures are more prevalent. Similarly, the relative importance of competition favoring divergence versus local adaptation favoring convergence may vary with the evolutionary distance between species (i.e., the amount of time since two species shared a common ancestor). As species diverge in body size due to competition, those species are likely to accumulate differences in other ecologically relevant traits (e.g., Richman and Price 1992; Schluter 2000) that could potentially reduce the costs of sharing similar body sizes in the same environment.

Here, we provide a test of the hypothesis that similar body sizes directly or indirectly entail fitness costs for closely related species living in sympatry, and that those costs vary with geography, climate, and evolutionary time. To test our hypotheses, we used a simple but powerful method for isolating the importance of sympatry on the evolution of traits, proposed by Mohamed Noor (1997) in work on *Drosophila*. Noor's method focuses on sister species—or closely related lineages—that differ in their geographic overlap with a third, more distant, but still close, relative (Fig. 1). This sister lineage approach allows us to control for evolutionary time—the focal sister lineages (lineages B and C; Fig. 1) have, by definition, been evolving from their common ancestor for exactly the same amount of time. Similarly, both sister lineages (B and C) have been evolving from the third more distant lineage (A) for the same amount of time, thus facilitating comparisons of trait evolution between species occurring in sympatry (A–B) and allopatry (A–C) (Fig. 1; see also Martin et al. 2015).

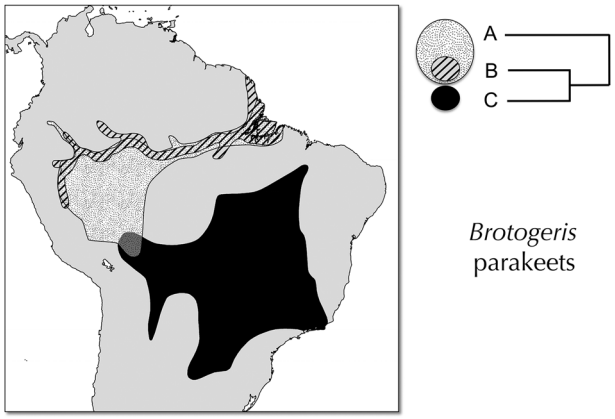


Figure 1. An example of methods (following Noor 1997) using the genus *Brotogeris*. Lineages B and C are sister lineages whose ranges are mainly allopatric (overlap less than 10%), but differ in their overlap with a more distant congener, lineage A. Thus, the geographic range of B overlaps with the range of A, whereas the range of C does not. If similar body sizes in sympatry are costly, then we predicted that differences between the sympatric lineages (A and B) would exceed those between the allopatric lineages (A and C). If similar body sizes in sympatry are beneficial, then we predicted that the difference between the allopatric lineages (A and C) would exceed that of the sympatric lineages (A and B). In this example, lineage A is *B. sanctithomae*, lineage B is *B. versicolurus*, and lineage C is *B. chiriri*.

The Noor method has several distinct advantages. First, it obviates a recent concern that error associated with estimates of time since sharing a common ancestor creates spurious relationships between sympatry and trait divergence in statistical models that include time, sympatry, and trait divergence (Hudson and Price 2014). Such models are the basis of most comparative studies of the effects of sympatry (e.g., Davies et al. 2007; Martin et al. 2010). The Noor method also helps to control for ecology and phylogeny by testing the importance of sympatry versus allopatry within clades of ecologically similar, closely related species, and includes divergence in allopatry as a benchmark for comparison within every clade. Although such control may be unnecessary for species within ecological guilds (e.g., Davies et al. 2007), our analysis includes diverse groups (e.g., pheasants, spoonbills, parrots, hummingbirds, hornbills, woodpeckers, tanagers, and finches), and thus comparisons of trait evolution between sympatry and allopatry within closely related clades could be important. Although the Noor method does not compare sympatric sister species (Fig. 1), most sister species of birds have allopatric ranges (e.g., Hudson and Price 2014) and thus can be uninformative in the study of the effects of secondary sympatry. In contrast, the sympatric lineages in our study represent the youngest co-occurring lineages within each clade—exactly the lineages that we would expect to interact ecologically because of their

shared traits and preferences through recent common ancestry (Violle et al. 2011). We might also expect that these relatively young species would experience and respond to climatic selective pressures in similar ways due to their close evolutionary relations and ecological similarities, such that local adaptation to climate might be expected to favor similar evolutionary solutions. The Noor method also has advantages over evolutionary models of trait evolution in that it makes no assumptions about either lineage birth–death rates or particular models of trait evolution (e.g., there is no assumption about equivalent, stochastic change over time across all lineages). Given the diversity of our focal species, particularly with respect to life histories and generation times, avoiding these assumptions could be important.

A major disadvantage of the Noor method is the restrictive biogeographic and phylogenetic criteria that limit the number of comparisons that can be made. Indeed, from the approximately 10,000 extant species of birds, we found only 64 independent comparisons that met our criteria. These comparisons, however, represent 64 phylogenetically independent contrasts of closely related bird species living in sympatry versus allopatry (Fig. 1), involving 211 species, representing 11 orders and 36 families worldwide. The dataset also includes 6% of the genera of the world's birds that have at least three species per genus (Gill and Donsker 2010–2012), as required for our analysis. Our analysis includes a reasonable sampling of tropical clades ($N = 47$ comparisons) including some of the most diverse avian radiations (e.g., genera *Turdus*, *Tangara*). Ultimately, every method for testing the association between potential selective pressures and trait evolution has advantages and disadvantages. The Noor method provides a robust approach that complements other popular methods for evolutionary discovery (e.g., Davies et al. 2007; Harmon et al. 2008; Lawson and Weir 2014).

Using Noor's method, we predicted that if closely related species of birds living in sympatry incur costs from having similar body sizes, then we should find greater divergence between closely related species whose ranges overlap (lineages A–B) compared with closely related species whose ranges do not overlap (lineages A–C). Simultaneously, we tested the prediction that the relationship between sympatry and differences in body size varies with the time since those lineages shared a common ancestor, with the geographic context of that sympatry (continent and latitude), and with the average environmental temperature across the range of each clade.

Materials and Methods

CHOICE OF SPECIES

We searched a recent taxonomy of the world's birds (Gill and Donsker 2010–2012) to find genera that had three or more species with available data on body size where ≥80% of the species in that genus had been included within a published molecular phylogeny (see Appendix S1 for sources). We chose 80% as a cutoff because we wanted to avoid genera whose phylogenetic relationships were potentially biased by a large proportion of missing species. Focal genera also had to meet three biogeographic criteria (Fig. 1; following Martin et al. 2015) (1) that lineages B and C are mostly allopatric, overlapping less than 10% of their ranges, (2) that lineages A and B are mostly sympatric, with at least 50% of the range of B overlapped by A, and (3) that lineages A and C are mostly allopatric, with less than 10% of the range of C overlapped by A. For migratory species, both the breeding and wintering ranges (scored separately) had to meet our three criteria because interactions on the wintering range may also have influenced body size evolution. In cases where we included genera where all species were not included in molecular phylogenies, we ensured that missing species did not differentially overlap our focal lineages (B and C), potentially biasing our results. We also required that lineage A was the youngest lineage overlapping lineage B, allowing us to focus on the most closely related species that were sympatric. We selected a cutoff of 50% range overlap to define sympatric species because we felt that species would be less likely to influence each other's body size evolution if fewer than half of their populations co-occurred with the other species. We selected a cutoff of 10% range overlap as a maximum for our allopatric species because we felt that species with <10% overlap would be unlikely to influence each other's body size evolution, and a cutoff of 10% (rather than zero) allowed us to include additional comparisons, thus increasing our sample size.

BODY MASS

We used body mass as an index of body size, following many previous studies (e.g., Peters 1983). We compiled body mass data from the literature (mostly Dunning 2008), supplemented with unpublished data from museum collections and ornithologists who kindly shared their data. We preferentially used body mass data collected in the areas of sympatry for species A and B and allopatry for species C. In cases where a lineage was represented by more than one species, we used the average mass of the species in that lineage for analyses. We excluded mass data for immature birds, and used the average of male and female body masses in analyses when the data were distinguished by sex. See Appendix S1 for more details on our methods.

GEOGRAPHIC RANGES

We assessed the degree of range overlap among species using ranges from BirdLife International and NatureServe (2011). We measured range size and overlap using ArcGIS 10.1 (ESRI, Redlands, CA; see online Supporting Information, Appendix S1 for details). Our measure of range overlap does not provide a direct index of species interactions because species could use

different habitats—or be active at different times of day—and thus never encounter each other. Such a scenario (i.e., sympatry without historical or current interactions between the species) would be a source of error in our study, and would reduce the likelihood of finding a difference between allopatric and sympatric species. However, habitat partitioning could also be one of the mechanisms by which species diverge, if competitive interactions among species favor occupying different habitats in sympatry, that in turn favor the evolution of different body sizes. Data from other studies that include many of our focal, sympatric species suggest that they do encounter each other and interact, and thus are not completely segregated within their sympatric ranges (e.g., Pierpoint 1986; Lebbin 2008; Freshwater et al. 2014).

PREDICTOR VARIABLES

We evaluated 10 predictor variables in our statistical models to examine how differences in body size in sympatry and allopatry varied with genetic distance and geography, and to control for potentially confounding factors (details and justifications in Appendix S1; see Fig. 1 for definitions of lineages A–C). These 10 predictor variables (including potentially confounding factors) are (1) mean Tamura–Nei genetic distance (mtDNA) between lineages A and BC, (2) mean Tamura–Nei genetic distance (mtDNA) between lineages B and C, (3) maximum number of congeners (besides A) that overlapped B or C where [(area of range overlap)/(range size of B or C) $>$ 0.50], (4) relative sympatry of A [(area of range overlap of A and B)/(range size of A)], (5) relative sympatry of B [(area of range overlap of A and B)/(range size of B)], (6) mean latitude of the clade (mean of the area-weighted centroid of the ranges for lineages A–C), (7) continental area that included the range of lineage B (Africa, Australia, Eurasia, North America, South America; definitions follow Martin and Tewksbury 2008), (8) average annual environmental temperature (hereafter, environmental temperature) encountered by each clade (mean of the average temperatures experienced by lineages A–C, based on intersections of ranges with climate data from New et al. 2002), (9) relative difference in environmental temperatures between lineages A and B compared with A and C {ln [(absolute value (environmental temperature for lineage A – environmental temperature for lineage B))/(absolute value (environmental temperature for lineage A – environmental temperature for lineage C))]}, and (10) geographic distance between the centroids of the ranges of lineages A and C. See Supporting Information Methods (Appendix S1) for details on how these variables were calculated.

STATISTICAL METHODS

We tested our prediction that body masses should be more different in sympatry compared with allopatry using generalized linear models in R (version 3.1.2; R Core Team 2014). We calculated the response variable as the natural log of the ratio of body mass differences between lineages A and B to that of lineages A and C for each phylogenetically independent comparison: response = ln{[absolute value (mass of lineage A – mass of lineage B)]/[absolute value (mass of lineage A – mass of lineage C)]}. Values of this response variable above zero indicate greater differences in body mass in sympatry, whereas values below zero indicate greater differences in body mass in allopatry.

In each model, we included initially the 10 predictor variables described above, with no interaction terms. Continuous variables were standardized by subtracting the mean from each observation and dividing the result by 2 SDs, using the rescale command in the *arm* package (version 1.7-07; Gelman et al. 2013). We checked the fit to normality of each covariate using Shapiro–Wilk tests, and transformed all variables that were significantly different from normal (for details, see Appendix S1 and R code archived in Dryad, http://dx.doi.org/10.5061/dryad.v5h5f).

The relationship between environmental temperature and our response variable suggested a threshold response, with distinct patterns above and below 24–26°C. Thus, we ran a piecewise regression analysis following Lemoine (2012) and Crawley (2013) (R code for this analysis is archived in Dryad, http://dx.doi.org/10.5061/dryad.v5h5f) to identify the breakpoint in the relationship between temperature and the response variable. The breakpoint was approximately 25°C, and thus we subsequently treated temperature as a bivariate predictor variable (warm $>$ 25°C, cool $<$ 25°C).

After running the full model, we checked model fit by plotting residuals against predicted values and then separately against each predictor, using Bartlett's tests to look for significant differences in residual variance among predictors, and Shapiro–Wilk tests to identify significant deviations of the residuals from a normal distribution. We then compared the performance of models with all possible combinations of predictors using the *dredge* command in the *MuMIn* package (version 1.13.4; Bartoń 2015). We present results for the best-fitting model (lowest corrected Akaike Information Criterion, AICc; Table 1), and include the results from all top models (delta AICc $<$ 2) in Table S1. We checked the fit of our best-fitting model in the same way that we checked model fit for the full model. The intercept tests whether body masses were more different between species in sympatry (intercept $>$ 0) or allopatry (intercept $<$ 0).

Although our comparisons between allopatric and sympatric lineages were phylogenetically independent, our results could have been influenced by the phylogenetic relationships among our comparisons, for example, if different clades of birds show different patterns of body size evolution in sympatry versus allopatry. To address this issue, we ran a Bayesian phylogenetic mixed effects model using *MCMCglmm* (version 2.21; Hadfield 2014) with the same predictor and response variables as our best-fitting model from above, but with the phylogenetic relationships between our

Table 1. Results of our best-fitting statistical model (lowest AICc) testing the prediction that body mass differences are larger (intercept > 0) or smaller (intercept < 0) among sympatric lineages compared to allopatric lineages.

Generalized linear model[1]	Estimate	SE	*t*	*df*	*P*
Intercept[2]	1.536	0.356	4.32	63	<0.0001
Genetic distance between lineages B and C[3]	−0.770	0.372	−2.07	63	0.043
Average temperature of lineage ABC[4]	−1.746	0.418	−4.17	63	<0.0001

Bayesian phylogenetic mixed effects model[1]	Estimate	Lower 95% CI[5]	Upper 95% CI[5]	Effective sample size	*P*
Phylogeny (random effect)	0.088	0.0002	0.429	1000	
Intercept[2]	1.524	0.760	2.348	979	0.002
Genetic distance between lineages B and C[3]	−0.780	−1.461	−0.107	764	0.032
Average temperature of lineage ABC[4]	−1.728	−2.584	−0.895	1000	<0.001

The Bayesian phylogenetic mixed effects model controlled for the significant effects of phylogenetic relationships among our comparisons. *N* = 64 phylogenetically independent comparisons.

[1]Response variable = ln[(absolute value (mass of lineage A − mass of lineage B))/(absolute value (mass of lineage A − mass of lineage C))]; continuous predictors were standardized prior to analysis, see Methods.

[2]Intercept > 0 indicates larger differences in body mass among sympatric, compared with allopatric, lineages at warm temperatures (above 25°C).

[3]Tamura–Nei genetic distances based on mitochondrial sequences.

[4]Categorical (warm > 25°C, cold < 25°C); estimates are for cold temperatures relative to warm temperatures.

[5]CI = confidence interval.

comparisons entered as a random factor. We downloaded 1000 phylogenetic trees for our focal comparisons from Jetz et al. (2012; http://birdtree.org) based on the Hackett sequence-based dataset, and calculated a maximum clade credibility tree using *TreeAnnotator* (version 1.8.1; Drummond et al. 2012) with posterior probability limit = 0, burnin = 0 trees, and node heights = mean heights. For this model, we followed the methods and model checks of Cornwallis et al. (2010) and Horváthová et al. (2012).

Our main analysis tested the predictions of our central hypothesis by examining the relative differences in body mass between sympatric versus allopatric lineages. Because the results of this analysis could be caused by changes in sympatric lineages, allopatric lineages, or both, we ran additional tests to estimate the contribution of both sympatric (lineage B) and allopatric (lineage C) lineages to the significant differences that we found in our main analysis. To do this, we calculated the absolute values of the differences in body mass between lineages A and B, and A and C, both standardized for body mass of the lineage, as: mass difference = [absolute value (mass of lineage A – mass of lineage B or C)]/(average mass of lineages A–C). We evaluated a linear mixed-effects model with the *nlme* package (version 3.1-120; Pinheiro et al. 2015) following Zuur et al. (2009), with body mass difference as the response variable, and the differences between lineage A and B (sympatric) and between A and C (allopatric) entered separately. Sympatry (yes or no), environmental temperature, genetic distance between lineages B and C, and interactions between sympatry and both temperature and genetic distance between lineages B and C were entered as predictors, because they were included in our best-fitting model from the main analysis (Table 1). We included the environmental temperature experienced by lineage B or C as the predictor—as opposed to the average of temperatures experienced by lineages A–C (in the main analysis)—to allow us to assess the importance of temperature experienced by allopatric and sympatric lineages separately. See Appendix S1 for details of our methods.

Results

Within the 64 clades that we analyzed, body size differences between closely related lineages of birds living in sympatry were greater than among those living in allopatry (Fig. 2, Table 1). This body size difference between sympatric and allopatric lineages declined with genetic distance between sister taxa (i.e., lineages B and C; Fig. 2A), and occurred only when the average temperature experienced across the geographic range of the clade was above 25°C (Fig. 2B, Table 1; piecewise regression breakpoint = 25.34°C; Appendix S1). The declines in body size differences between sympatric and allopatric lineages with increased genetic distance (Fig. 2A) were due to the increasing divergence of allopatric lineages from lineage A over evolutionary time, with differences among sympatric lineages remaining stable (Table 2, Fig. 3A). Controlling for phylogeny did not alter our results substantially, even though the phylogenetic relationships among our comparisons had some effect on our results (Table 1).

The greater divergence of sympatric species relative to allopatric species (Fig. 2B) was the result of greater divergence among sympatric rather than allopatric lineages for ranges

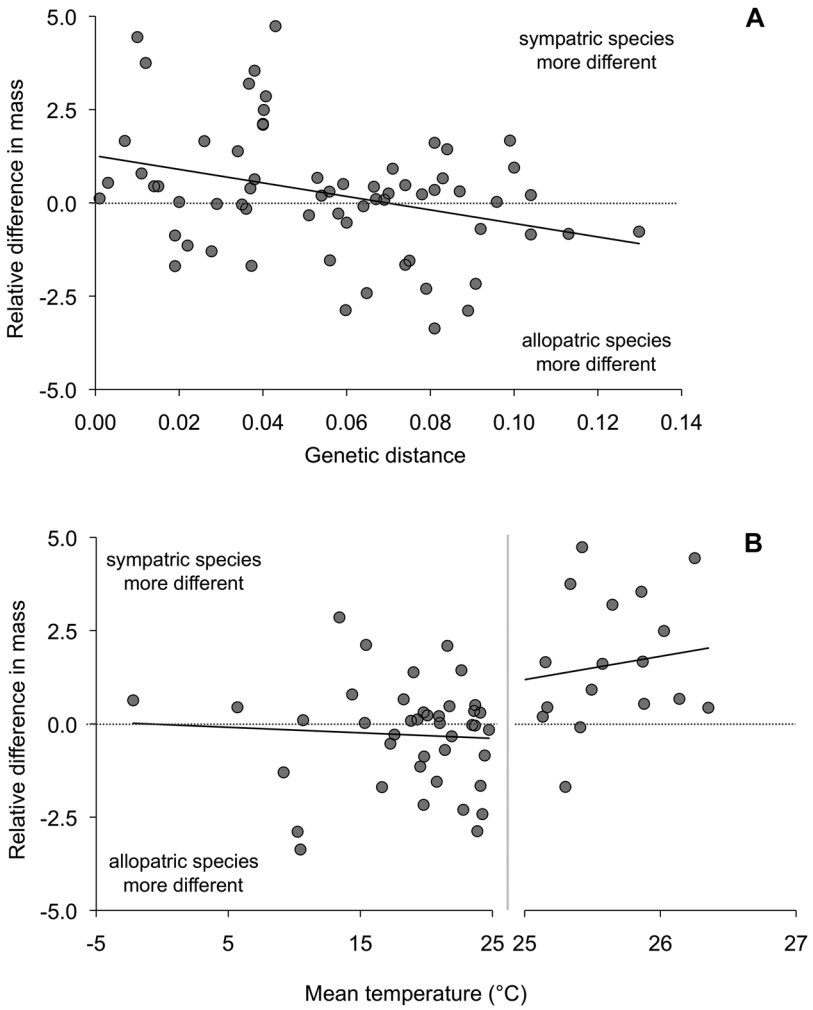


Figure 2. **Variation in the body mass differences between sympatric versus allopatric congeners of birds. Sympatric lineages show greater differences in their mass compared with allopatric lineages (panels A, B), but these differences declined with the genetic distance between sister lineages B and C (panel A), and were only evident in clades that live in warmer environments, where average environmental temperatures exceeded 25°C (panel B). *Y*-axis values are ln [(absolute value of the difference in mass between sympatric lineages A and B)/(absolute value of the difference in mass between allopatric lineages A and C)]. *Y*-axis values above zero indicate greater differences among sympatric lineages, whereas values below zero indicate greater differences among allopatric lineages. We identified the breakpoint at 25°C in panel (B) using a piecewise regression analysis. In panel (A), a genetic distance of 0.02 represents a divergence time of approximately 1 million years before present (Weir and Schluter 2008). In panel (B), the *x*-axis is the environmental temperature (°C) across the range of the focal species, averaged across lineages A–C.**

experiencing warmer temperatures (Table 2, Fig. 3B). Body size differences between sympatric and allopatric species within clades did not vary significantly (1) among continents, (2) with the overlap of nonfocal congeners, (3) with the amount of overlap with lineage A, or (4) with the relative difference in average environmental temperature experienced by lineages in sympatry (A–B) versus allopatry (A–C). The best-fitting model (lowest AICc; Table 1) did not include (1) genetic distance between lineages A and BC, (2) the degree of range overlap with lineage B, (3) latitude, or (4) the geographic distance between lineages A and C, though they were included in other top models (i.e., those with delta AICc < 2; Table S1). In those other models, the greater difference in body size in sympatry compared with allopatry declined with (1) the genetic distance between lineages A and BC, (2) latitude, and (3) the degree to which lineage B was sympatric with A, but increased with the geographic distance between lineages A and C (Table S1). All but one of the top models showed a negative relationship for the genetic distance between lineages A and BC, or between lineages B and C, suggesting that one or the other of these factors was important for the evolutionary divergence of size in sympatry (Table S1).

All top models had significant intercepts and significant effects of temperature (Tables 1 and S1). The greater divergence of sympatric species relative to allopatric species

Table 2. Results of a supplementary test of the contribution of change in sympatry versus allopatry to our main result (Table 1).

Linear mixed effects model[1]	Estimate	SE	*t*	*df*	*P*
Genetic distance[2] effect in sympatry	−0.130	0.549	−0.24	62	0.81
Genetic distance[2] effect in allopatry	1.314	0.547	2.40	62	0.02
Temperature effect[3] in sympatry	−0.105	0.049	−2.14	60	0.04
Temperature effect[3] in allopatry	0.056	0.050	1.12	60	0.27

***N* = 64 phylogenetically independent comparisons.**

[1]Response variable = (absolute value (mass of lineage A − mass of lineage B or C))/(average mass of lineages A–C), intercept = warm (above 25°C).

[2]Tamura–Nei genetic distances based on mitochondrial sequences.

[3]Average environmental temperature of lineage B or C as a bivariate predictor (warm > 25°C, cold < 25°C).

declined with latitude (Fig. 4A), but this relationship was not retained in our best-fitting model that included environmental temperature (Table 1). Sympatric species pairs in cool tropical environments (e.g., high elevations) did not show greater differences in mass relative to allopatric species pairs, a pattern similar to that among higher latitude taxa, and distinct from the greater divergence of body size among sympatric lineages in the warm tropics (Fig. 4B).

Discussion

In regions where the mean annual temperature is above 25°C, closely related species of birds living in sympatry differed more in their body masses than closely related species living in allopatry (Table 1, Fig. 2). These results support the hypothesis that closely related species suffer fitness costs when they share similar body sizes in sympatry, in warm environments. Although we did not measure fitness directly, our results suggest that selection acts on body size in sympatry, implying a fitness cost when sympatric species are closely related and have similar body sizes. Such fitness costs could include exploitative or interference competition for limited resources, negative interactions through shared predators or parasites, or factors that favor the divergence of other traits that secondarily affect body size, such as habitat use. Costs of similar body sizes in sympatry could also arise from reproductive interference (e.g., hybridization) or agonistic interactions independent of ecological overlap (e.g., misdirected aggression) if body size plays an important role in species recognition (Grether et al. 2009; Pfennig and Pfennig 2012). Our results are consistent with both ecological sorting, where contemporary differences in body size allowed species to expand their ranges into sympatry, and character displacement, where divergent evolution of body size occurs after species become sympatric (Grant and Abbott 1980; Case et al. 1983; Case and Sidell 1983; Losos 1990; Schluter 2000). In either case, different body sizes of sympatric sister lineages in warm environments indicate that body sizes diverged recently.

Indeed, the difference in body mass between sympatric compared with allopatric congeners in warm environments declined with increasing genetic distance between sister lineages (B and C—and possibly between lineages A and BC, which was significant in some top models; Table S1). The decline with genetic distance did not reflect changes in body size differences in sympatry (Fig. 3A, Table 2)—standardized differences in body mass between closely related sympatric species were consistent across the window of evolutionary time that our study encompassed (approximately 6–7 million years based on a molecular clock calibration by Weir and Schluter 2008; Fig. 3A, Table 2). Instead, the decline reflected an increased divergence in body mass within allopatric species pairs (Fig. 3A, Table 2), a pattern expected if closely related allopatric species diverged gradually over evolutionary time, perhaps adapting to different environmental selective pressures in allopatry.

In species whose ranges are in regions where the mean annual temperatures are below 25°C, body size differences within clades were similar for species pairs occurring in sympatry compared with allopatry, even at tropical latitudes (Fig. 4). This finding is consistent with either (1) weaker biotic pressures favoring the divergence of body size in cooler environments, or (2) similar biotic pressures favoring the divergence of body size across thermal environments, but with climatic pressures favoring convergence and overwhelming biotic pressures when temperatures are cooler. These alternatives may interact, especially if climate dampens biotic selective pressures by reducing population or species densities in colder environments (cf. Cardillo 2002; Olson et al. 2009; Schemske et al. 2009).

Our results are also consistent with other mechanisms, where cooler environments covary with other causal factors. For example, limited genetic variation could constrain adaptive, divergent evolution in body size in cooler environments, such as those at high latitudes (e.g., Hughes and Hughes 2007) with a history of glaciation, recolonization, and founder events. Although high latitude populations show reduced genetic variation for some genetic markers (Hughes and Hughes 2007; Eckert et al. 2008; Adams and Hadly 2013), we have not seen evidence for similar patterns in cool tropical environments (e.g., high elevation tropics; cf. Fig. 4B), suggesting that limited genetic variation is not

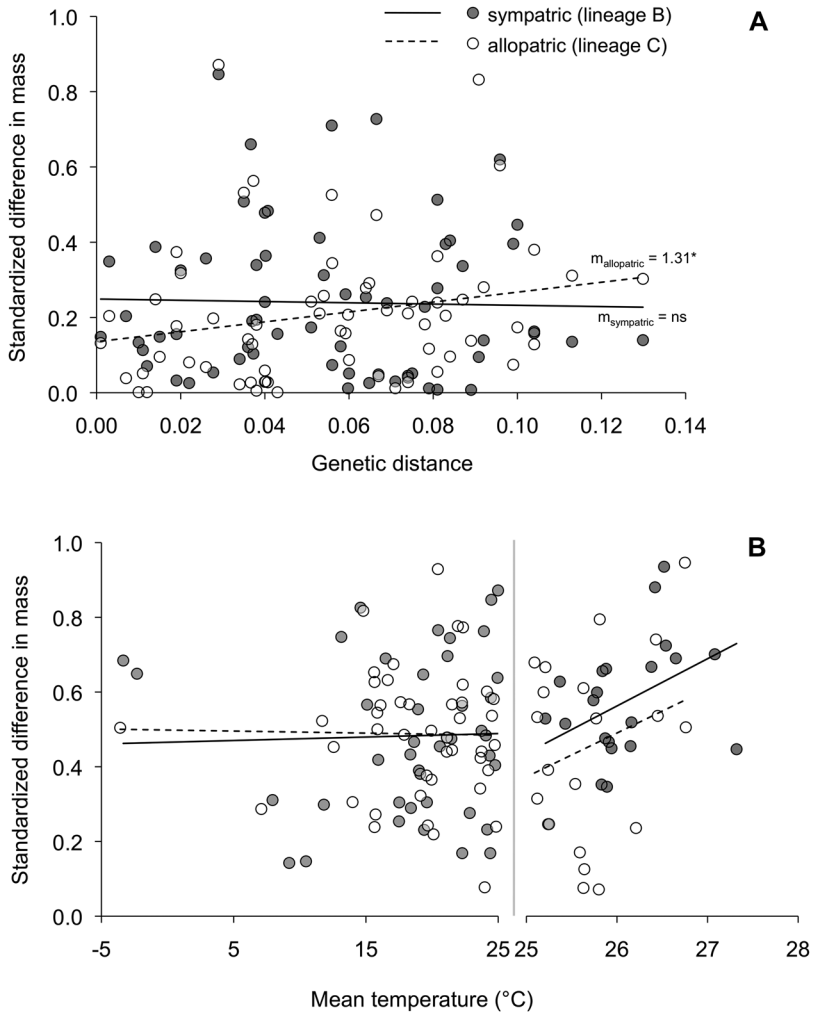


Figure 3. Changes in the relative differences in body mass between sympatric and allopatric species (Figure 2) in the same clade were primarily caused by increasing divergence in body size among allopatric lineages with increasing genetic distance (panel A; Table 2), but greater divergence among sympatric relative to allopatric lineages at warm temperatures (panel B; Table 2). *Y*-axis values are the differences in body mass (g) between sympatric lineages (A and B) or allopatric lineages (A and C), divided by the mean body mass for the clade (lineages A–C) to standardize differences across clades. In panel (A), the genetic distance is calculated between lineages B and C. A genetic distance of 0.02 represents a divergence time of approximately 1 million years before present (Weir and Schluter 2008). In panel (B), the *x*-axis is the average environmental temperature (°C) across the range of lineage B (sympatric lineage) or lineage C (allopatric lineage).

responsible for this pattern. Rates of evolution may also accelerate in warm and productive environments, even in homeotherms such as birds (Gillman et al. 2012), and this could facilitate more rapid divergence of body size in warm than in cool environments. This mechanism would predict body size divergence in sympatry to occur in cool environments, but it would take longer to achieve—a pattern that we did not find. Importantly, the DNA sequence divergence of taxa living in warm versus cold regions in our study was similar (average Tamura–Nei genetic distance of mtDNA sequence for sister lineages B and C: warm clades = 0.044, cold clades = 0.059, glm, $t = 1.78$, $df = 63{,}62$, $P = 0.08$), and these estimates of mtDNA divergence should incorporate differences in the rates of molecular evolution associated with climate (Gillman et al. 2012).

Although our results reveal some interesting patterns, we are well aware of the limitations of this study. Our sample size, for example, is relatively small, and may limit our ability to measure the effects of some of our predictor variables. Also, body mass data are scarce for many tropical species, and thus our values for tropical species could be biased by sampling error. Moreover, we have no direct evidence that the sympatric species we studied actually interact with each other, either historically or presently, although a variety of studies suggest that many do (e.g., Pierpoint 1986; Lebbin 2008; Freshwater et al. 2014). We also explored only

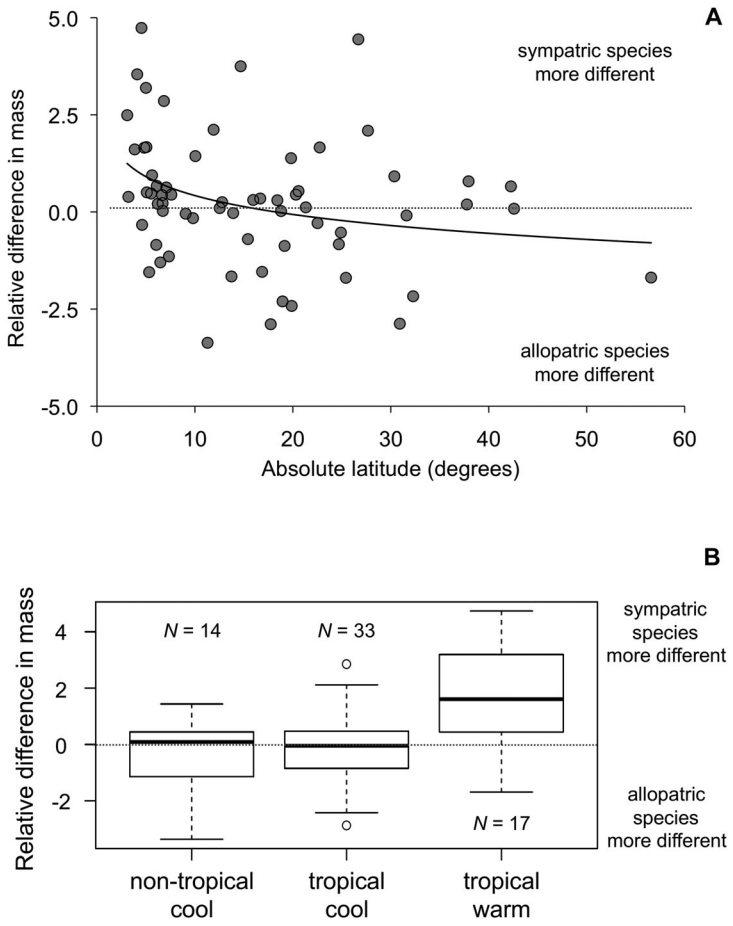


Figure 4. **The difference in body size between sympatric compared with allopatric lineages within clades declined with latitude (panel A), reflecting greater differences among sympatric compared with allopatric lineages in the warm tropics, but not the cool tropics (panel B). Once temperature was added to the best-fitting model, latitude was no longer a significant predictor (Table 1), although there was a negative relationship with latitude in some top models (ΔAICc < 2; Table S1). *Y*-axis values are ln [(absolute value of the difference in mass between sympatric lineages A and B)/(absolute value of the difference in mass between allopatric lineages A and C)]. *Y*-axis values above zero indicate greater differences between sympatric lineages, whereas values below zero indicate greater differences between allopatric lineages. Tropical clades were those whose average range centroid (average area-weighted means of the ranges of lineages A–C) fell between the Tropics of Cancer and Capricorn (about 23.4°N and S latitudes, respectively), whereas nontropical clades had average range centroids at higher latitudes. Clades in warm environments were those whose average environmental temperatures across the species' ranges (average temperatures for lineages A–C) were above 25°C, whereas clades in cool environments had average environmental temperatures below 25°C across the species' ranges. The regression line in panel (A) is in the form $y = m \times \ln(x) + b$. Box plots in panel (B) show medians (center line), the interquartile range as a box, values within 1.5 × interquartile range as whiskers, and all data that lie outside the whiskers as circles.**

one trait (body size) in our study, leaving open the possibility that other traits play more important roles in ecological divergence (e.g., Grant and Grant 2006) or thermoregulation (e.g., Tattersall et al. 2009; Greenberg et al. 2012) in different environments.

GEOGRAPHIC VARIATION IN THE IMPORTANCE OF CLIMATIC VERSUS BIOTIC SELECTIVE PRESSURES

Both Darwin (1859) and Wallace (1878) suggested that climate exerts stronger selective pressures in cold environments, whereas biotic selective pressures prevail in warm regions (see also Dobzhansky 1950). A more recent review provides further support for these broad patterns (Schemske et al. 2009). Our results are consistent with these ideas because the patterns of body size divergence that we found suggest that closely related species of birds exert a relatively stronger (biotic) selective pressure on each other in warmer environments, compared with cooler ones, at least with respect to body size. The pattern in environments above 25°C further suggests that the divergence of body sizes in sympatry relative to allopatry may increase whenever average environmental temperatures rise above 25°C (Fig. 2B).

We do not as yet understand why 25°C appears to be a threshold for divergence in body size in sympatry. Perhaps 25°C represents a threshold temperature below which body size adaptation to climate trumps adaptation to competitive interactions. Birds indeed show threshold responses to ambient temperature variation, with a plateau in metabolic energy expenditure within their thermal neutral zones, and an abrupt increase in metabolic energy expenditure above and below this zone, at the maximum (T_{uc}) and minimum (T_{lc}) critical temperatures, respectively (Peters 1983; Dawson and Whittow 2000).

All birds typically maintain their daytime body temperatures (T_b) within a narrow range (37.0–42.5°C; Dawson and Whittow 2000). The minimum critical temperature—the measure most relevant to our study—however, varies as a function of body mass, generally by the equation $T_{lc} = T_b - 34.18W^{0.199}$, where T_b is body temperature and W is mass in kilograms (Peters 1983). If we include body mass (averaged across lineages ABC) in an interaction term with environmental temperature in our best-fitting model, the model performs better (i.e., lower AICc)—body mass did not predict the difference in mass between allopatry and sympatry (calculated as the ln ratio) below 25°C, but shows a significant negative correlation above 25°C (slope = –0.56 ± 0.26 SE, $P = 0.04$) (R code, archived in Dryad, http://dx.doi.org/10.5061/dryad.v5h5f). Inserting an estimate of T_{lc} into the model, however, did not improve model performance, and the relationship with body size and T_{lc} is opposite to what we would expect if T_{lc} constrains divergence. Other hypotheses could also explain the threshold patterns with temperature that we describe here, such as interactions between diversity, productivity, and temperature.

Although the mechanism remains unknown, the dependence of body size divergence in sympatry on average environmental temperature appears to underlie both a latitudinal decline in body size divergence in sympatry (Fig. 4A) and a lack of body size divergence among sympatric tropical taxa in cooler environments, such as those in high elevation habitats (Fig. 4B). The reduced influence of species interactions on body size evolution at higher latitudes is also consistent with recent evidence showing that environmental temperature has accelerated body size divergence among closely related bird species at high compared to low latitudes (Lawson and Weir 2014).

The greater differences in body mass among sympatric congeners in warm environments that we have discovered provide new evidence for the costs of sharing similar traits in sympatry for ecologically similar species. These results are consistent with a broad array of studies documenting both greater differences in body mass among sympatric compared with allopatric species that are closely related, and greater body size divergence than expected by chance among co-occurring species that use similar resources (reviewed by Dayan and Simberloff 2005). Previous work has also documented a positive relationship between the degree of sympatry and body size divergence among sister species of mammalian carnivores, but the variation in sympatry was better explained by differences in carnassial tooth morphology (Davies et al. 2007), suggesting that selection may not have acted directly on body size in this case. The possibility remains that the body size divergence among sympatric species that we describe here is caused by selection acting on correlated traits. Nonetheless, the greater divergence in warm environments suggests that interactions among closely related species play a more important role in the evolution of traits in warm compared to cool environments, with potentially important consequences for rates of species formation, community assembly and evolution, and gradients in biodiversity (Dobzhansky 1950; Schemske 2002; 2009; Mittelbach et al. 2007; Schemske et al. 2009).

ACKNOWLEDGMENTS

We thank S. DuBay, A. Johnson, A. Naveda-Rodríguez, A. Rodriguez-Ferraro, and C. Witt for providing unpublished data on body mass, including data from specimens at the Museum of Southwestern Biology at the University of New Mexico and Museo de la Estación Biológica de Rancho Grande (Venezuela). We thank F. Bonier and C. Collins for helpful discussions, and L. Harmon and anonymous reviewers for helpful comments on the manuscript. We are also grateful for data provided by BirdLife International and NatureServe in collaboration with R. Ridgely, J. Zook, The Nature Conservancy—Migratory Bird Program, Conservation International—Center for Applied Biodiversity Science, World Wildlife Fund (United States), and Environment Canada—WILDSPACE. This work was funded by NSERC Discovery grants to PRM, RM, and SCL, and a Baillie Family Chair Endowment.

DATA ARCHIVING

The doi for our data and R code is 10.5061/dryad.v5h5f.

LITERATURE CITED

Adams, R. I., and E. A. Hadly. 2013. Genetic diversity within vertebrate species is greater at lower latitudes. Evol. Ecol. 27:133-143.

Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Global Ecol. Biogeogr. 11: 505–523.

Ashton, K. G., M. C. Tracy, and A. de Queiroz. 2000. Is Bergmann's rule valid for mammals? Am. Nat. 156:390–415.

Bartoń, K. 2015. *MuMIn*: multi-model inference. R package version 1.13.4.

Bergmann, C. 1848. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Abgedruckt aus den Göttinger Studien 1847. Vandenhoeck and Ruprecht.

BirdLife International and NatureServe. 2011. Bird species distribution maps of the world. BirdLife International, Cambridge, U.K. and NatureServe, Arlington, VA.

Blackburn, T. M., K. J. Gaston, and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. Divers. Distrib. 5:165–174.

Bonner, J. T. 2006. Why size matters. Princeton Univ. Press, Princeton, NJ.

Brown, W. L., Jr., and E. O. Wilson. 1956. Character displacement. Syst. Zool. 5:49–64.

Calder, W. A., III. 1974. Consequences of body size for avian energetics. Pp. 86–151 *in* R. A. Paynter, Jr., ed. Avian energetics. Nuttall Ornithological Club, Cambridge, MA.

Cardillo, M. 2002. Body size and latitudinal gradients in regional diversity of New World birds. Global Ecol. Biogeogr. 11:59–65.

Case, T. J., and R. Sidell. 1983. Pattern and chance in the structure of model and natural communities. Evolution 37:832–849.

Case, T. J., J. Faaborg, and R. Sidell. 1983. The role of body size in the assembly of West Indian bird communities. Evolution 37:1062–1074.

Clauss, M., M. T. Dittmann, D. W. H. Müller, C. Meloro, and D. Codron. 2013. Bergmann's rule in mammals: a cross-species interspecific pattern. Oikos 122:1465–1472.

Cornwallis, C. K., S. A. West, K. E. Davis, and A. S. Griffin. 2010. Promiscuity and the evolutionary transition to complex societies. Nature 466:969–972.

Crawley, M. J. 2013. The R book. 2nd ed. John Wiley and Sons, Chichester, U.K.

Darwin, C. R. 1859. The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, U.K.

Davies, J. T., S. Meiri, T. G. Barraclough, and J. L. Gittleman. 2007. Species co-existence and character divergence across carnivores. Ecol. Lett. 10:146–152.

Dawson, W. R., and G. C. Whittow. 2000. Regulation of body temperature. Pp. 343–390 *in* G. C. Whittow, ed. Sturkie's avian physiology. 5th ed. Academic Press, San Diego, CA.

Dayan, T., and D. Simberloff. 2005. Ecological and community-wide character displacement: the next generation. Ecol. Lett. 8:875–894.

Dial, K. P., E. Greene, and D. J. Irschick. 2008. Allometry of behavior. Trends Ecol. Evol. 23:394–401.

Dobzhansky, T. 1950. Evolution in the tropics. Am. Sci. 38:209–221.

Drummond, A. J., M. A. Suchard, D. Xie, and A. Rambaut. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol. Biol. Evol. 29:1969–1973.

Dunning, J. B., Jr. 2008. Body masses of birds of the world. 2nd ed. CRC handbook of avian body masses. Taylor and Francis Group, Boca Raton, FL.

Eckert, C. G., K. Samis, and S. C. Lougheed. 2008. Genetic variation across species' ranges: the central-marginal hypothesis and beyond. Mol. Ecol. 17:1170–1188.

Freshwater, C., C. K. Ghalambor, and P. R. Martin. 2014. Repeated patterns of trait divergence between closely related dominant and subordinate bird species. Ecology 95:2334–2345.

Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a third universal response to warming? Trends Ecol. Evol. 26:285–291.

Gelman, A., Y.-S. Su, M. Yajima, J. Hill, M. Grazia Pittau, J. Kerman, and T. Zheng. 2013. arm: data analysis using regression and multilevel/hierarchical models. R package, version 1.7-07.

Gill, F., and D. Donsker, eds. 2010–2012. IOC world bird names (versions 2.6 to 3.2). Available at http://www.worldbirdnames.org.

Gillman, L. N., L. S. C. McCowan, and S. D. Wright. 2012. The tempo of genetic evolution in birds: body mass and climate effects. J. Biogeogr. 39:1567–1572.

Grant, P. R. 1972. Convergent and divergent character displacement. Biol. J. Linn. Soc. 4:39–68.

Grant, P. R., and I. Abbott. 1980. Interspecific competition, island biogeography and null hypotheses. Evolution 34:332–341.

Grant, P. R., and B. R. Grant. 2006. Evolution of character displacement in Darwin's finches. Science 313:224–226.

Greenberg, R., V. Cadena, R. M. Danner, and G. Tattersall. 2012. Heat loss may explain bill size differences between birds occupying different habitats. PLoS One 7: e40833.

Grether, G. F., N. Losin, C. N. Anderson, and K. Okamoto. 2009. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. Biol. Rev. 84:617–635.

Hadfield, J. 2014. MCMC generalised linear mixed models. R package, version 2.21.

Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. Bioinformatics 24:129–131.

Horváthová, T., S. Nakagawa, and T. Uller. 2012. Strategic female reproductive investment in response to male attractiveness in birds. Proc. R. Soc. B Biol. Sci. 279:163–170.

Hudson, E. J., and T. D. Price. 2014. Pervasive reinforcement and the role of sexual selection in biological speciation. J. Hered. 105:821–833.

Hughes, A. L., and M. A. K. Hughes. 2007. Coding sequence polymorphism in avian mitochondrial genomes reflects population histories. Mol. Ecol. 16:1369–1376.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 93:145–159.

Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global diversity of birds in space and time. Nature 491:444–448.

Lawson, A. M., and J. T. Weir. 2014. Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. Ecol. Lett. 17:1427–1436.

Lebbin, D. J. 2008. Aggressive interactions and preliminary evidence for reversed sexual dominance in *Ramphocelus* tanagers. Ornit. Neotrop.19:329–334.

Lemoine, N. 2012. R for ecologists: putting together a piecewise regression. Available at http://www.r-bloggers.com/r-for-ecologists-putting-together-a-piecewise-regression/.

Lindsey, C. C. 1966. Body sizes of poikilotherm vertebrates at different latitudes. Evolution 20:456–465.

Lindstedt, S. L., and M. S. Boyce. 1985. Seasonality, fasting endurance and body size in mammals. Am. Nat. 125:873–878.

Losos, J. B. 1990. A phylogenetic analysis of character displacement in Caribbean *Anolis* lizards. Evolution 44:558–569.

Martin, P. R., and J. J. Tewksbury. 2008. Latitudinal variation in subspecific diversification of birds. Evolution 62:2775–2788.

Martin, P. R., R. Montgomerie, and S. C. Lougheed. 2010. Rapid sympatry explains greater color pattern divergence in high latitude birds. Evolution 64:336–347.

———. 2015. Color patterns of closely related bird species are more divergent at intermediate levels of breeding-range sympatry. Am. Nat. 185:443–451.

Meiri, S., and T. Dayan. 2003. On the validity of Bergmann's rule. J. Biogeogr. 30:331–351.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecol. Lett. 10:315–331.

New, M., D. Lister, M. Hulme, and I. Makin. 2002. A high-resolution data set of surface climate over global land areas. Clim. Res. 21:1–25.

Noor, M. A. F. 1997. How often does sympatry affect sexual isolation in *Drosophila*? Am. Nat. 149:1156–1163.

Olson, V. A., R. G. Davies, C. D. L. Orme, G. H. Thomas, S. Meiri, T. M. Blackburn, K. J. Gaston, I. P. F. Owens, and P. M. Bennett. 2009. Global biogeography and ecology of body size in birds. Ecol. Lett. 12:249–259.

Peters, R. H. 1983. The ecological implications of body size. Cambridge Univ. Press, Cambridge, U.K.

Pfennig, D. W., and K. S. Pfennig. 2012. Evolution's wedge: competition and the origins of diversity. University of California Press, Berkeley, CA.

Pierpoint, N. 1986. Interspecific aggression and the ecology of woodcreepers (Aves: Dendrocolaptidae). PhD Diss., Princeton University, Princeton, NJ.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, EISPACK authors and R-core. 2015. Linear and nonlinear mixed effects models. R package, version 3.1-120.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at http://www.R-project.org/.

Richman, A. D., and T. Price. 1992. Evolution of ecological differences in the Old World leaf warblers. Nature 355:817–821.

Schemske, D. W. 2002. Ecological and evolutionary perspectives on the origins of tropical diversity. Pp. 163–173 *in* R. L. Chazdon and T. C. Whitmore, eds. Foundations of tropical forest biology. University of Chicago Press, Chicago, IL.

———. 2009. Biotic interactions and speciation in the tropics. Pp. 219–239 *in* R. K. Butlin, J. R. Bridle, and D. Schluter, eds. Speciation and patterns of diversity. Cambridge Univ. Press, Cambridge, U.K.

Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? Ann. Rev. Ecol. Evol. Syst. 40:245–269.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford Univ. Press, Oxford, U.K.

Schmidt-Nielsen, K. 1984. Scaling: why is animal size so important? Cambridge Univ. Press, Cambridge, U.K.

Sheridan, J. A., and D. Bickford. 2011. Shrinking body size as an ecological response to climate change. Nat. Clim. Change 1:401–406.

Tattersall, G. J., D. V. Andrade, and A. S. Abe. 2009. Heat exchange from the toucan bill reveals a controllable vascular thermal radiator. Science 325:468–470.

Van Buskirk, J., R. S. Mulvihill, and R. C. Leberman. 2010. Declining body sizes in North American birds associated with climate change. Oikos 119:1047–1055.

Vézina, A. F. 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. Oecologia 67:555–565.

Violle, C., D. R. Nemergut, Z. Pu, and L. Jiang. 2011. Phylogenetic limiting similarity and competitive exclusion. Ecol. Lett. 14:782–787.

Wallace, A. R. 1878. Tropical nature and other essays. Macmillan, New York, NY.

Weir, J. T., and D. Schluter. 2008. Calibrating the avian molecular clock. Mol. Ecol. 17:2321–2328.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY.

Associate Editor: L. Harmon
Handling Editor: T. Lenormand

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Main analysis.
Table S2. Supplemental analysis.
Figure S1. Histogram showing the genetic distance between sister lineages B and C.
Figure S2. Histogram showing the genetic distance between lineages A and BC.
Figure S3. Phylogenetic relationships among the focal comparisons in our study.
Appendix S1. Detailed methods and supplementary results.

Appendix S1. Detailed methods and supplementary results.

Supplemental Methods

Phylogenies

We used the phylogenetic relationships described in these references: *Francolinus* (Forcina et al. 2012), *Lophura* (Randi et al. 2001), *Ciconia* (Slikas 1997), *Platalea* (Chesser et al. 2010), *Calidris* (Gibson and Baker 2012), *Psittacula* (Kundu et al. 2012), *Brotogeris* (Ribas et al. 2009), *Amazona* (Russello and Amato 2004), *Heliangelus* (Martin et al. 2015; see also Para et al. 2010), *Pharomachrus* (Martin et al. 2015), *Corythornis* [*Alcedo*] (Moyle et al. 2007; Melo and Fuchs 2008), *Todus* (Overton and Rhoads 2004), *Tockus* (Gonzalez et al. 2013), *Rhyticeros* (Gonzalez et al. 2013), *Bycanistes* (Gonzalez et al. 2013), *Megalaima* (den Tex and Leonard 2013), *Picoides* (Weibel and Moore 2002), *Veniliornis* (Moore et al. 2006), *Campephilus* (Fleischer et al. 2006), *Ochetorhynchus* (Chesser et al. 2007), *Cinclodes* (Freitas et al. 2012), *Dendrocincla* (Weir et al. 2009), *Dendrocolaptes* (Weir et al. 2009), *Xiphorhynchus* (Aleixo 2002), *Cercomacra* (Gómez et al. 2010), *Pteroptochos* (Chesser 1999), *Anairetes* (DuBay and Witt 2012), *Malurus* (Driskell et al. 2011), *Acanthiza* (Nicholls et al. 2000; Gardner et al. 2010), *Oriolus* (Jønsson et al. 2010), *Tachycineta* (Cerasale et al. 2012; Dor et al. 2012), *Petrochelidon* (Sheldon et al. 2005), *Acrocephalus* (Fregin et al. 2009), *Xanthomixis* [*Bernieria*] (Moyle and Marks 2006), *Orthotomus* (Sheldon et al. 2012), *Sylvia* (Voelker and Light 2011), *Regulus* (Pächert et al. 2003), *Campylorhynchus* (Barker 2007; Vázquez-Miranda et al. 2009), *Toxostoma* (Zink et al. 1999), *Mino* (Martin et al. 2015), *Lamprotornis* (Lovette and

Rubenstein 2007), *Turdus* (Voelker et al. 2007), *Monticola* (Zuccon and Ericson 2010), *Bradornis* (Sangster et al. 2010), *Chloropsis* (Moltesen et al. 2012), *Loxia* (Martin et al. 2015), *Icterus* (Jacobsen et al. 2010; Omland et al. 1999), *Quiscalus* (Powell et al. 2008), *Peucaea* (DaCosta et al. 2009), *Melozone* [*Pipilo*] (DaCosta et al. 2009), *Paroaria* (Sedano and Burns 2010; we did not follow Dávalos and Porzecanski 2009 because they incorporated phenotypic characters), *Ramphocelus* (Burns and Racicot 2009), *Chlorochrysa* (Sedano and Burns 2010), *Tangara* (Sedano and Burns 2010), *Cyanerpes* (Martin et al. 2015), *Diglossa* (Mauck and Burns 2009), *Cardinalis* (Figs. 1 and 2 in Klicka et al. 2007).

Mass

We compiled data on body mass from Dunning (2008) and various articles, handbooks, and online databases and museum collections. We preferentially used masses that were collected in areas of sympatry (lineages A and B) or allopatry (lineage C). If we could not find these data from preferred areas of sympatry or allopatry, we used data that were collected as close as possible to the desired areas. We took the average mass of males and females for use in analyses; for species with no sex-specific data, we took the average of all masses available.

Genetic Distance

We calculated the genetic distance between (i) lineages B and C, and (ii) lineages A and BC (Figure 1) using mitochondrial DNA sequences obtained from Genbank (accession numbers below). We preferentially used cytochrome-*b* sequences (52

comparisons) because this gene had previously been used for clock calibrations in birds (Weir and Schluter 2008). When the cytochrome-*b* sequence was not available (12 comparisons), we used ND2 (9 comparisons), COI (2 comparisons), and COII (1 comparison). We aligned sequences with the homologous gene from the chicken (*Gallus*; Desjardins and Morais 1990) using Clustal X (v. 2.0.10; Larkin et al. 2007), visually inspected them using MacClade (v. 4.08; Maddison and Maddison 2005), removed sequences that did not readily align with the relevant gene from the chicken, and measured genetic distance using MEGA (v. 5.0; Tamura et al. 2011). We calculated between-group mean Tamura-Nei genetic distances (B-C and A-BC) because this measure corrects for multiple substitutions at one site, incorporates differences in substitution rates between nucleotides, and does not assume equal nucleotide frequencies (Tamura and Nei 1993). We included transitions and transversions as well as all codon positions, assumed uniform rates among sites and homogeneous patterns among lineages, and used pairwise deletion to address gaps or missing data (Tamura et al. 2011).

The Genbank accession numbers for sequences used to calculate genetic distance in our study are: *Francolinus* (cytb; FR691632, EU165707, NC_011817, AF013762), *Lophura* (cytb; AF314644, AF314640, AF314638, AF534558, AF534557, NC_012895, AF314643, EU417810), *Ciconia* (cytb; NC_002196, NC_002197, DQ485896, AY567910, AY567909, U70822, AB026193, AB026818), *Platalea* (cytb; GU346979, GU346980, GU346984, GU346985, GU346986, GU346987), *Calidris* (cytb; FJ499023, EF373131, EF373143, AY156160), *Psittacula* (cytb; GQ996495, GQ996496, GQ996502, KC439289, KC876665, KC876664, KC876663, KC876662,

KC876661, GQ996500, GQ996510, AY220107, AY220109, GQ996508, GQ996501), *Brotogeris* (cytb; 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* (cytb; AY283456, AY283455, AY283453, AY283452, AY283451, AY283461); *Amazona vinacea-pretrei-tucumana* (COI; AY301459, AY301457, AY301462), *Amazona agilis-collaria-leucocephala/ventralis/ vittata* (cytb; 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* (cytb; AF441615, AF441616, AF441617, AF441618, AF441619, AF441620, AF441621, AF441622, AF441623, AF441624, AF441625, AF441626, AF441627, AF441628, AF441629, U89186, AF407450), *Tockus* (cytb; KC754875, AF346931, AF346930, AF346933, AF346932, KC754885), *Rhyticeros* (cytb; GU257914, KC754858, KC754856, KC754854, KC754851, KC754852, KC754861, KC754859, GU257915), *Bycanistes* (cytb; KC754809, KC754810, KC754806, KC754812, AF346923, AF346922, AF346921, AF346920, AF346919), *Megalaima* (sequence was not available from

Genbank - genetic distance was estimated from den Tex and Leonard 2013), *Picoides* (cytb; AF389305, AF389304, AF425070, AF425067, AF425064, AF425058, AF425055, AF425052, AF425049, AF425046, AF389331, AF389330, AY863147, AY701066), *Veniliornis* (cytb; AY927220, AY927219, AY927209, AY942893, AF389337), *Campephilus* (cytb; DQ521895, DQ521894, AY940798), *Ochetorhynchus* (cytb; GQ140082, GQ140078, GQ140074), *Cinclodes* (ND2; JF975144, JF975145, JF975154), *Dendrocincla* (cytb; GU215186, GU215182, GU215181, GU215184, GU215180, GU215179, GU215178, GU215177, AY442986, AY442985, AY065713), *Dendrocolaptes* (cytb; GU215187, JF276383, JF276381, JF276384, JF276382, JF276385, AY442991, AY089817, EF212896, EF212895), *Xiphorhynchus* (cytb; AY504924, AY504912, AY504891, AY504880, AY089804, AY089820, EF190607, AY089831), *Cercomacra* (cytb; HM637182, DQ294490, HM637188, GU215217, HM637187, HM637186, EF639940, EF639941, GU215216, GU215218, GU215219, GU215220), *Pteroptochos* (COII; AF111826, AF111825, AF111824, AF111821, AF111820, AF111819, AF111818), *Anairetes* (cytb; JX273112, JX273111, JX273110, JX273109, JX273108, JX273107, JX273106, JX273115, JX273114), *Malurus* (ND2; GU825874, EU144238, EF621357, AY488326, JF967669), *Acanthiza* (cytb; AF129236, AF129235, AF129234, AF129233, AF129232), *Oriolus* (ND2; GQ901764, GQ901767, GQ901775), *Tachycineta* (cytb; GU460236, AY052451, AY052449, AY052450), *Petrochelidon* (cytb; AY825985, AY825983, AY825984), *Acrocephalus* (cytb; AJ004244, AJ004243, AJ004242, AJ004291, AJ004290, AJ004292, HQ608855, AJ004258, AJ004257), *Xanthomixis* [*Bernieria*] (cytb; AF199388, AF199389, AF199391, HQ706181), *Orthotomus* (ND2; JX006125, JN826602, HQ011062,

HQ011061, HQ011060, HQ011059, DQ871379, JX006112, JX006111, JX006133, JX006132, JX006131), *Sylvia* (cytb; AJ534533, AJ534531, AJ534532), *Regulus* (cytb; AY894876, AY894877, AY894878, AY894882, AY894883, AY894884, AY894886, AY894887, AY894888), *Campylorhynchus* (cytb; DQ004889, DQ004888, DQ004884, DQ004882), *Toxostoma* (cytb; AF130235, AF130237, DQ241266, DQ241262, DQ241251), *Mino* (ND2; DQ466868, DQ469044, DQ469045, DQ469047, DQ469048, DQ469049, DQ469050, EF468160, EF468161, DQ469046), *Lamprotornis* (ND2; EF468238, EF468240, EF468124, EF468122, EF468121, AY329425), *Turdus* (cytb; EU154627, DQ910956, EU154623, DQ910951, EU154634, DQ910960, EU154628, DQ910957, EU154616, DQ910945, DQ910949, EU154620, EU154625, DQ910954, EU154604, DQ910936, EU154659, EU154658, DQ910984), *Monticola* (cytb; GU237084, GU237083, EF434526, EF434525, GU237099, EF434509, EF434508, EF434527), *Bradornis* (cytb; AY329450, AY329463, HM633325, HM633395), *Chloropsis* (cytb; JX445233, JX445234, JX445235, JX445236, JX445202, JX445201, JX445200, JX445199, JX445198, JX445228, JX445227, JX445226), *Loxia* (cytb; AF171660, AF171661, AF171655, AF342878, AF171663, AF171662, AF171658, AF171657, AY495386), *Icterus* (cytb; AF089033, AF099301, AF099300, AF089030, AF310064, AF099304), *Quiscalus* (cytb; AF089056, GU215210, FJ389570, AF089054, GU215209, GU215208, GU215211, FJ389558), *Peucaea* (cytb; FJ547265, FJ547264, FJ547263, FJ547266), *Melozone* (cytb; AF314644, EU325776, FJ547262, EF529937), *Paroaria* (cytb; EU647990, EU647989, EU647988, FJ715681, FJ715672, FJ715671, FJ715670, FJ715664, FJ715663, FJ715662), *Ramphocelus* (cytb; FJ799881, EF529964, U15721, U15723, GU215320, AF310048), *Chlorochrysa* (cytb; AY383094,

AY383095, EU647981), *Tangara* (cytb; AY383156, AY383145, AY383144, AY383121, AY383125), *Cyanerpes* (cytb; GU215303, GU215298, GU215296, AF006225, AY190167, GU215302), *Diglossa* (cytb; EU647907, EU647906, EU647901, EU647899, EU647896, EU647895, EU647893, AF310050), *Cardinalis* (cytb; EU325777, EF530009, EF530008, EF530007).

Overlapping Non-focal Congeners

Our study tests the importance of sympatry among closely related lineages for the evolution of body size. However, other non-focal and closely related species may overlap the ranges of our focal lineages, thus influencing their patterns of evolution and potentially obscuring the interactions between focal lineages (e.g., Martin et al. 2015). The potential bias of non-focal, closely related species should be particularly acute when these species differentially overlap either lineage B or C. Closely related species that overlap lineage A should cause A to diverge from both B and C, and thus not overly bias our results. Similarly, closely related species that overlap both B and C, or A, B and C could cause these lineages to evolve, but should not overly bias our results.

We considered a non-focal congener to be sympatric with B or C if: [(geographic area of overlap of the ranges of the non-focal species and lineage B, in km^2)/(geographic range size of lineage B, in km^2)] > 0.50, or if [(geographic area of overlap of the ranges of the non-focal species and lineage C, in km^2)/(geographic range size of lineage C, in km^2)] > 0.50. We summed the number of non-focal congeners that were sympatric with either B or C 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 = 3. In a supplementary analysis, we also tested if separating the number of non-focal congeners that were sympatric with lineage B versus C affected our main result (see Statistical Methods below for details, and Table S2 for results).

Degree of Sympatry

We measured the degree of range overlap between A and B from the perspective of both lineage A and lineage B, and included both of these measures as predictors in our statistical models. We predicted that an increase in overlap of lineage B on lineage A would cause lineage A to diverge from both lineage B and C, thus reducing the likelihood of divergence between B and C. We predicted that an increase in overlap of lineage A on lineage B would increase the potential for divergent evolution in lineage B because more populations of lineage B would be subject to selection by lineage A. Overlap of lineage A was measured as: [(geographic area of overlap of the ranges of lineages A and B, in km^2)/(geographic range size of lineage A, in km^2)]. Overlap of species B was measured as: [(geographic area of overlap of the ranges of lineages A and B, in km^2)/(geographic range size of lineage B, in km^2)]. For lineages with different breeding and wintering ranges (as defined by BirdLife International and NatureServe 2011), we calculated overlap for breeding and wintering ranges separately, and then took the average for use as a predictor in our statistical models.

Mean Latitude

We measured the mean centroid (area-weighted mean) latitude of the ranges of lineages A, B and C using ArcGIS 10.1. We then calculated the average latitude of lineages A, B and C for each phylogenetically independent comparison, and used this value as a predictor in our statistical models. We calculated the mean latitude as: average{[absolute value (latitude of lineage A)], [absolute value (latitude of lineage B)], [absolute value (latitude of lineage C)]}. For lineages with different breeding and wintering ranges, we calculated the average latitude of the breeding and wintering ranges of lineages A, B and C separately, and then took the average latitude of the breeding and wintering ranges. We included latitude in our models to test if the influence of sympatry varied with latitude.

Continent

We tested for an effect of geographic variation by recording the continent that held the majority of the breeding range of lineage B, and including continent as a predictor in our statistical models. We focused on lineage B because this lineage was most likely to evolve due to interactions in sympatry (with lineage A), and thus was most informative for the assessment of geographic variation. We lumped Central America and the Caribbean with North America, and considered Europe and Asia together, following Martin and Tewksbury (2008). Sample sizes (number of phylogenetically independent comparisons) for the various continents were: Africa (n = 7), Australia (n = 5), Eurasia (n = 14), North America (n = 13), South America (n = 25).

Temperature

We estimated environmental temperatures for focal clades using high-resolution (10 minute latitude x 10 minute longitude) terrestrial climate data (New et al. 2002). In ArcGIS (v. 10.1), we intersected the ranges of each focal lineage with average monthly temperature data from New et al. (2002). We then calculated the average temperature across all 10 x 10 minute blocks that overlapped the focal ranges across all 12 months of the year. For migratory species with distinct breeding and wintering ranges (11 of 211 species), we calculated the mean temperatures on the breeding and wintering ranges only for the months typically spent on those ranges. We then calculated the mean temperature for the lineage as the mean of the breeding and wintering range temperatures. For migratory species that had part of their range used for both breeding and wintering (i.e., occupied all year round; 14 of 211 species), we first calculated the mean temperature across all 12 months for areas of the range occupied year round. We then calculated the temperature for the exclusive breeding range as: [(temperature for the breeding-only range x area of the breeding-only range)+(temperature of the range occupied all year x area of the range occupied all year)]/[(area of the breeding-only range) + (area of the range occupied all year)]. We calculated the temperature for the wintering range as: [(temperature for the wintering-only range x area of the wintering-only range)+(temperature of the range occupied all year x area of the range occupied all year)]/[(area of the wintering-only range) + (area of the range occupied all year)].

We then took the average of temperatures for breeding and wintering as in the other migratory species.

We estimated the months during which breeding and wintering ranges were occupied by each lineage using Poole (2013), the online Handbook of the Birds of the World (http://www.hbw.com), Higgins et al. (2006), and Cramp (1977, 1983, 1992). For migratory species, we calculated an alternative measure for environmental temperature that weighted the temperatures for the breeding and wintering ranges by the number of months that these ranges were occupied. We used these values in the analysis to test whether these different measures of temperature influenced our results (see Supplemental Results below). Once we had calculated the average temperature for each lineage, we averaged the temperatures across lineages A, B and C for each phylogenetically independent comparison for use in our statistical models.

We also calculated the relative difference in temperatures for sympatric lineages (A versus B) compared with allopatric lineages (A versus C) as: ln {[absolute value (temperature of lineage A – temperature of lineage B)]/[absolute value (temperature of lineage A – temperature of lineage C)]}. We included the relative difference in temperatures between sympatric and allopatric clades in our analysis because a greater difference in temperature could have resulted in a greater divergence in body size among lineages.

Geographic Distance among Allopatric Lineages

We estimated the distance between the (allopatric) ranges of lineages C and A by measuring the distance (in km) between their centroids (latitude, longitude), using an online calculator (http://www.csgnetwork.com/gpsdistcalc.html). For lineages with different breeding and wintering ranges, we took the average of the distances between the centroids of their breeding and wintering ranges.

Statistical Methods

We transformed variables that were significantly different from normal, as appropriate. We converted highly skewed variables from continuous to categorical if transformations failed to improve their distributions. We then plotted the response variables against each of the predictor variables to identify the nature of each relationship (e.g., linear, logarithmic). After transformations, eight of our predictor variables were continuous, but no pairs of variables were highly correlated: the average of the absolute values of r from Pearson correlations was 0.17 (N= 28 pairwise comparisons), while the maximum value was 0.62 between the genetic distance of lineages B and C, and the genetic distance of lineages A and BC. The relationship between environmental temperature and the response variable suggested a threshold response, with distinct patterns above and below 24-26°C. Thus, we ran a piecewise regression analysis following Lemoine (2012) and Crawley (2013) (R code for this analysis is archived in Dryad, http://dx.doi.org/10.5061/dryad.v5h5f). The piecewise regression analysis identified 25.34˚C as the breakpoint, so we converted temperature into a categorical variable (warm > 25°C, cold < 25°C). We then standardized our continuous predictor

variables by subtracting the mean and dividing by two standard deviations, using the R package *arm* version 1.7-07 (Gelman et al. 2014). Standardization allowed us to compare the effects of predictor variables that were measured on different scales.

We ran initial generalized least squares models using the *nlme* package (v. 3.1-120; Pinheiro et al. 2015) including all predictor variables but no interaction terms. We did not include interactions because we did not have *a priori* hypotheses about how these factors would interact to influence differences in body mass in sympatry relative to allopatry. We examined the performance of the full model by plotting standardized residuals against fitted values and all predictors, by testing for differences in the variance of residuals for each predictor using Bartlett's tests, and by testing if the distribution of residuals differed from normality using a Shapiro-Wilk test (see Zuur et al. 2009 for details). Different continents showed significantly different variances, so we compared our model with a model that specified heterogeneity in variance structure for different continents, following Zuur et al. (2009). The new model did not perform as well (assessed using AIC scores) as the simpler model without specified variance structures, so we report results from the simpler model.

We tested all possible combinations of predictor variables in a generalized linear model using the *dredge* command in the R package *MuMIn* (v. 1.13.4; Bartoń 2015), and ranked these models using AIC adjusted for small sample sizes (AICc). We identified the best-fitting model as the model with the lowest AICc, and top models as all models with delta AICc < 2. We then checked the performance of the best-fitting model the same way that we checked the performance of the full model,

but also examined normal quantile-quantile plots, predicted values versus the square root of the standard deviance residuals, and Cook's distances. All Cook's distances were less than 0.5, suggesting that no datum was particularly influential on our results (Zuur et al. 2009). We report results from our best-fitting model (lowest AICc score; Table 1), and from all of our top models (delta AICc < 2; Table S1). The R code for these analyses is archived along with the dataset in Dryad, http://dx.doi.org/10.5061/dryad.v5h5f.

We also ran additional analyses to test whether different ways of measuring our predictor variables had any influence on our main results. Specifically, we tested if separating the number of non-focal congeners that were sympatric with lineage B versus C, and if weighting temperatures by time spent on the breeding versus wintering grounds for migratory species, affected our main result. The results of these analyses are presented in the Supplemental Results below.

After running our main analysis, we ran another linear mixed-effects model using the R package *nlme* (v. 3.1-120; Pinheiro et al. 2015) to assess the contribution of changes in allopatric versus sympatric lineages to the significant relationships from our main analysis (where temperature and genetic distance between lineages B and C were important in our best-fitting model). We included the environmental temperature of lineage B or C as the predictor variable, as opposed to the average temperature of lineages A, B and C (in the main analysis), to allow us to assess the importance of temperature of allopatric and sympatric lineages separately. We checked and transformed variables as in the main analysis, and then ran our full model, with sympatry (yes or no), temperature (warm > 25°C, or cold < 25°C), and

genetic distance between lineages B and C as predictors, and Sympatry*temperature and Sympatry*genetic distance of BC as interactions, corresponding to our main analysis. We compared models with different random effects using AIC, and selected the best model as the model with the lowest AIC value. The linear mixed-effects model with 'comparison' as a random factor performed best given the data. Once we had selected the best model with respect to random effects, we checked the model fit to the data using the same methods as for the main analysis. We report the effects of genetic distance between lineages B and C and temperature for sympatric and allopatric lineages separately. The R code for these analyses is archived along with the dataset in Dryad, http://dx.doi.org/10.5061/dryad.v5h5f.

Supplemental Results

We report the results of all of our top models (ΔAICc <2) from our main analysis in Table S1. We also report the results of all of our top models (ΔAICc <2) from an additional analysis that separated the number of nonfocal congeners that overlapped either lineage B or C in the analysis (Table S2). The supplemental analysis that used average environmental temperatures for migratory birds weighted by the number of months they spent in breeding versus wintering ranges yielded identical results to the main analysis (Tables 1, S1; R code archived in Dryad, http://dx.doi.org/10.5061/dryad.v5h5f). The relationship between average environmental temperature and body mass divergence again showed a threshold response at the same breakpoint (25.34°C), and our comparisons separated into the

same "warm" and "cold" groups as in the analysis with non-weighted temperatures. The weighted relative difference in temperature between sympatric and allopatric lineages was not present in any of the top models (ΔAICc<2), as in the original analysis.

Without temperature in the best-fitting model (Table 1), the pseudo R^2 value dropped from 0.305 to 0.107, the intercept was no longer significant (effect size = 0.25±0.20 SE, P=0.21), and the effect of genetic distance of lineages B and C remained (effect size = -1.11±0.41 SE, P=0.008).

Supplementary Results

Table S1. Main analysis. Comparison of predictor variables in our top models[1] (delta AICc < 2). Blanks indicate predictor variables that were not important in the model. Four predictor variables are not included in this table because they were not important in any of the top models: Overlap by nonfocal congeners, Overlap of lineage A, Continent of lineage B, Difference in temperature between AB/AC. *N* = 64 phylogenetically independent comparisons.

Model ranking	Intercept[2]	Genetic distance between lineages A & BC[3]	Genetic distance between lineages B & C[3]	Overlap of lineage B	Absolute latitude of lineage ABC	Average temperature of lineage ABC[4]	Geographic distance b/t lineage A & C	df	logLik	AICc	delta AICc	weight	Pseudo[5] R^2
1	1.536		−0.770			−1.746		4	−112.66	234.0	0.00	0.184	0.305
2	1.325		−0.696		−0.581	−1.457		5	−111.62	234.3	0.27	0.161	0.328
3	1.307		−0.758		−0.752	−1.433	0.519	6	−110.63	234.7	0.74	0.127	0.348
4	1.377	−0.597			−0.672	−1.529		5	−112.02	235.1	1.07	0.108	0.319
5	1.637	−0.612				−1.882		4	−113.41	235.5	1.50	0.087	0.289
6	1.363	−0.670			−0.852	−1.510	0.527	6	−111.02	235.5	1.52	0.086	0.340
7	1.409				−0.689	−1.573		4	−113.42	235.5	1.52	0.086	0.289
8	1.564		−0.822			−1.783	0.322	5	−112.27	235.6	1.57	0.084	0.314
9	1.624		−0.710	−0.306		−1.865		5	−112.34	235.7	1.71	0.078	0.312

[1] response variable = ln[(absolute value (mass of lineage A − mass of lineage B))/(absolute value (mass of lineage A − mass of lineage C))]

[2] intercept > 0 indicates larger differences in body mass among sympatric, compared with allopatric, lineages at warm temperatures (above 25°C)

[3] Tamura-Nei genetic distances for mitochondrial sequence

[4] categorical (warm > 25°C, cold < 25°C); estimates are for cold temperatures relative to warm temperatures

[5] pseudo R^2 = 1 − (sum((y−predict(model))^2)/sum((y−mean(y))^2))

2

Table S2. Supplemental analysis. Comparison of predictor variables in our top models[1] (delta AICc < 2) when the number of non-focal congeners that were sympatric with lineage B versus C were separated in the model. Blanks indicate predictor variables that were not important in the model. Four predictor variables are not included in this table because they were not important in any of the top models: Overlap of B by nonfocal congeners, Overlap of lineage A, Continent of lineage B, Difference in temperature between AB/AC. *N* = 64 phylogenetically independent comparisons.

Model ranking	Intercept[2]	Genetic distance between lineages A & BC[3]	Genetic distance between lineages B & C[3]	Overlap of C by nonfocal congeners[4]	Overlap of lineage B	Absolute latitude of lineage ABC	Average temperature of lineage ABC[5]	Geographic distance b/t lineage A & C	df	logLik	AICc	delta AICc	weight
1	1.536		−0.770				−1.746		4	−112.66	234.0	0.00	0.159
2	1.325		−0.696			−0.581	−1.457		5	−111.62	234.3	0.27	0.139
3	1.307		−0.758			−0.752	−1.433	0.519	6	−110.63	234.7	0.74	0.109
4	1.377	−0.597				−0.672	−1.529		5	−112.02	235.1	1.07	0.093
5	1.637	−0.612					−1.882		4	−113.41	235.5	1.50	0.075
6	1.363	−0.670				−0.852	−1.510	0.527	6	−111.02	235.5	1.52	0.074
7	1.409					−0.689	−1.573		4	−113.42	235.5	1.52	0.074
8	1.564		−0.822				−1.783	0.322	5	−112.27	235.6	1.57	0.072
9	1.601		−0.762	−0.357			−1.727		5	−112.31	235.7	1.65	0.069
10	1.386		−0.682	−0.421		−0.621	−1.416		6	−111.11	235.7	1.70	0.068
11	1.624		−0.710		−0.306		−1.865		5	−112.34	235.7	1.71	0.068

[1] response variable = ln[(absolute value (mass of lineage A − mass of lineage B))/(absolute value (mass of lineage A − mass of lineage C))]

[2] intercept > 0 indicates larger differences in body mass among sympatric, compared with allopatric, lineages at warm temperatures (above 25°C)

[3] Tamura-Nei genetic distances for mitochondrial sequence

[4] categorical (yes or no); estimates are for overlap of nonfocal congeners relative to no overlap of nonfocal congeners

[4] categorical (warm > 25°C, cold < 25°C); estimates are for cold temperatures relative to warm temperatures

3

Figure S1. Histogram showing the genetic distance between sister lineages B and C. A genetic distance of 0.02 represents a divergence time of approximately 1 million years before present (Weir and Schluter 2008).

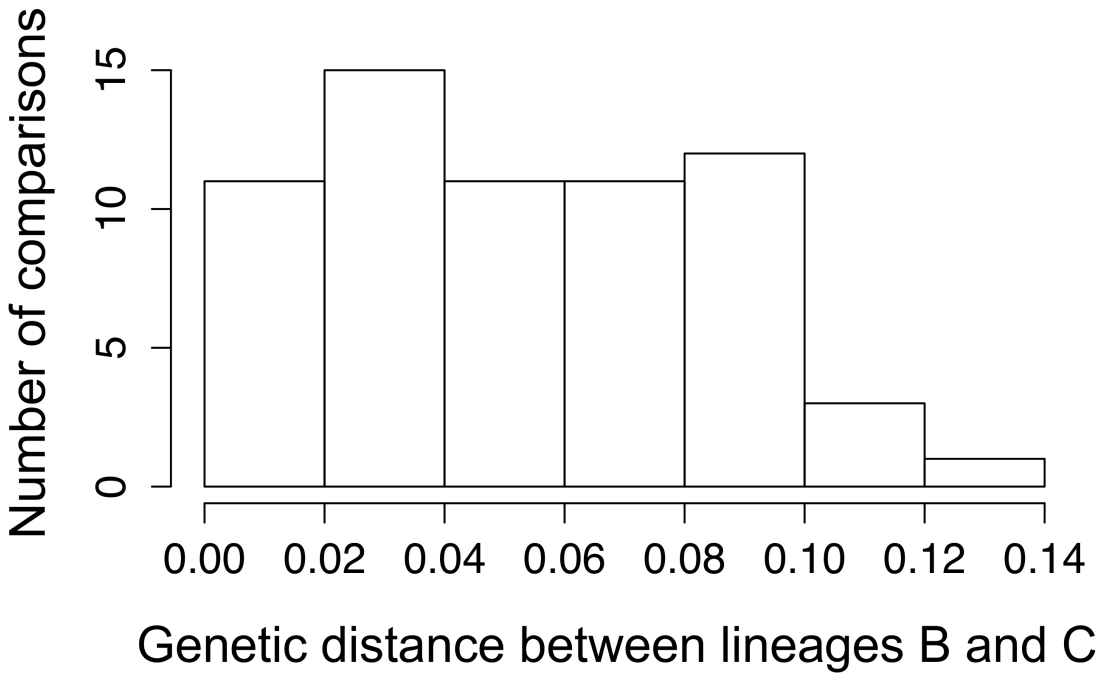


Figure S2. Histogram showing the genetic distance values between lineages A and BC. A genetic distance of 0.02 represents a divergence time of approximately 1 million years before present (Weir and Schluter 2008).

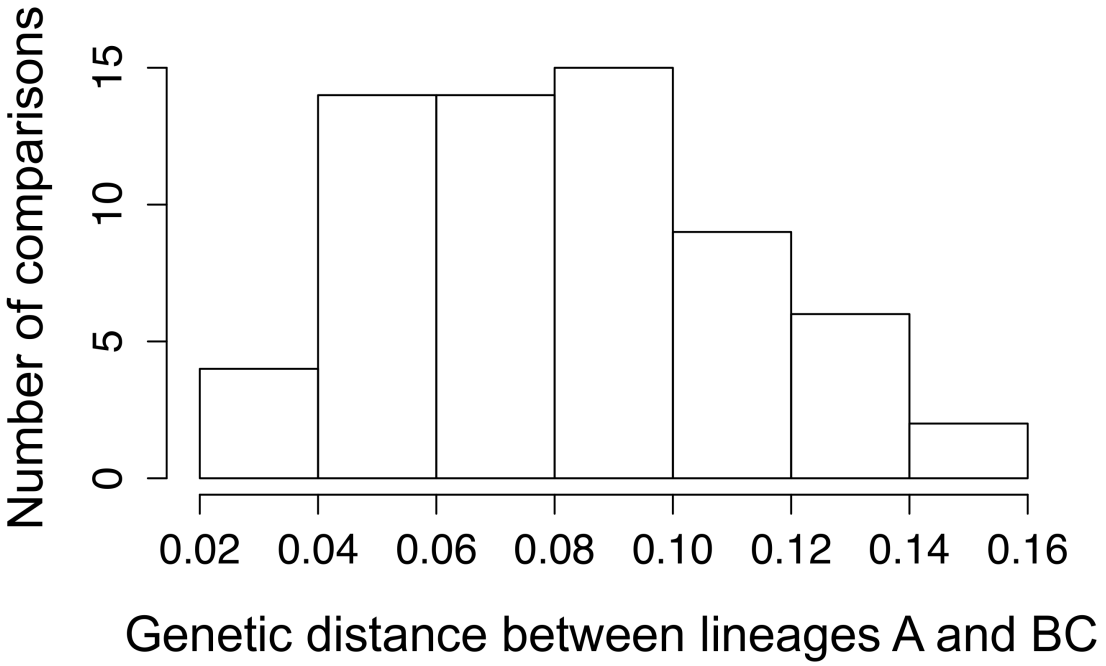
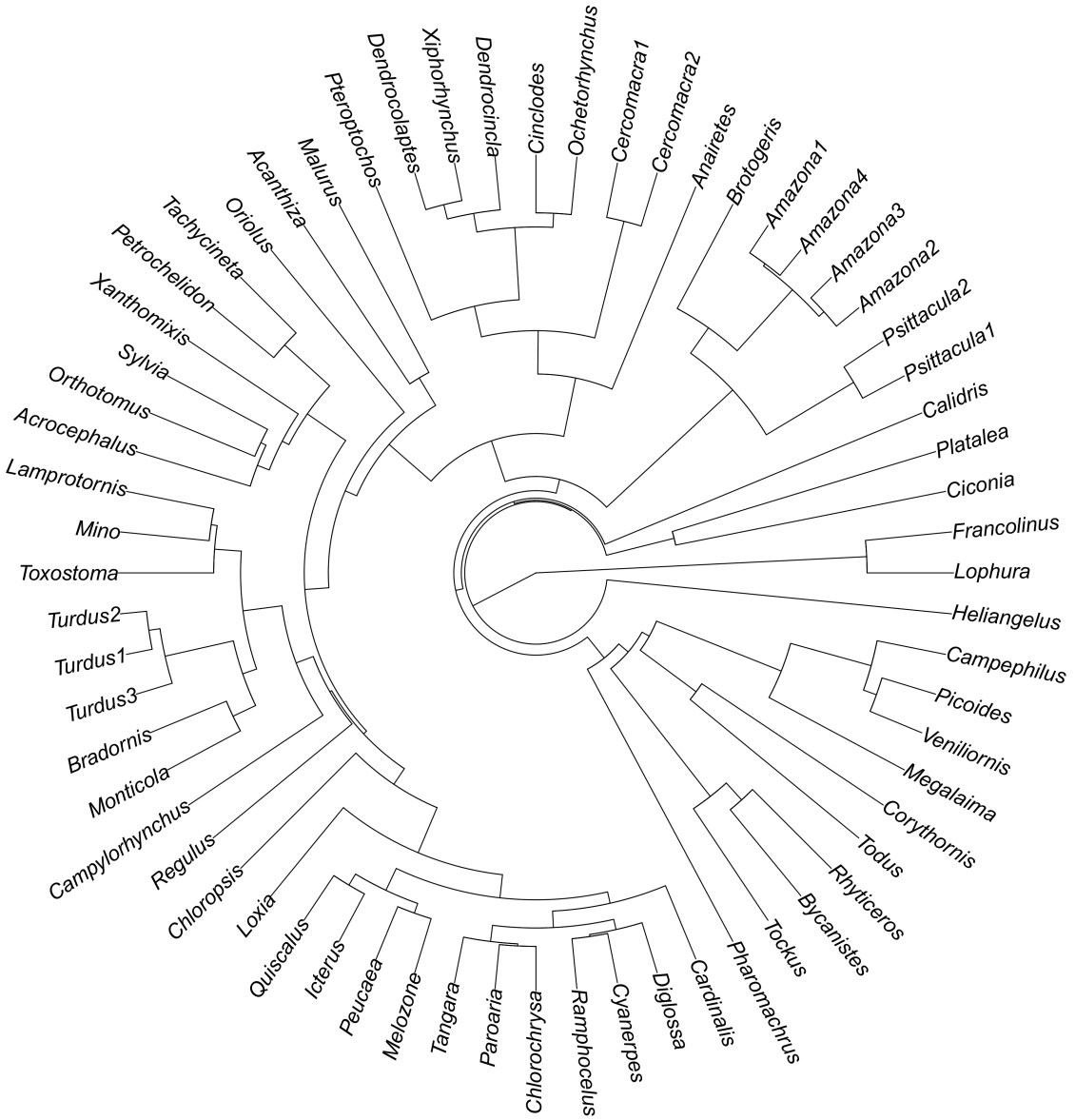


Figure S3. Phylogenetic relationships among the focal comparisons in our study. The tree represents a maximum clade credibility tree from 1,000 trees from Jetz et al. 2012 (http://birdtree.org). See Methods for details and R code for Newick format.



References (Appendix S1)

Aleixo, A. 2002. Molecular systematics and the role of the "várzea" – "terra–firme" ecotone in the diversification of *Xiphorhynchus* woodcreepers (Aves: Dendrocolaptidae). Auk 119:621–640.

Barker, F. K. 2007. Avifaunal interchange across the Panamanian Isthmus: insights from *Campylorhynchus* wrens. Biol. J. Linnean Soc. 90:687–702.

Bartoń, K. 2015. *MuMIn*: Multi–model inference. R package version 1.13.4.

BirdLife International and NatureServe. 2011. Bird species distribution maps of the world. BirdLife International, Cambridge, UK and NatureServe, Arlington, VA.

Burns, K. J., and R. A. Racicot. 2009. Molecular phylogenetics of a clade of lowland tanagers: implications for avian participation in the Great American Interchange. Auk 126:635-648.

Cerasale, D. J., R. Dor, D. W. Winkler, and I. J. Lovette. 2012. Phylogeny of the *Tachycineta* genus of New World swallows: insights from complete mitochondrial genomes. Mol. Phylogenet. Evol. 63:64-71.

Chesser, R. T. 1999. Molecular systematics of the rhinocryptid genus *Pteroptochos*. Condor 101:439-446.

Chesser, R. T., F. K. Barker, and R. T. Brumfield. 2007. Fourfold polyphyly of the genus formerly known as *Upucerthia*, with notes on the systematics and evolution of the avian subfamily Furnariinae. Mol. Phylogenet. Evol. 44:1320-1332.

Chesser, R. T., C. K. L. Yeung, C.-T. Yao, X.-H. Tian, and S.-H. Li. 2010. Molecular phylogeny of the spoonbills (Aves: Threskiornithidae) based on mitochondrial DNA. Zootaxa 2603:53-60.

Cramp, S., ed. 1977. Handbook of the birds of the Middle East and north Africa. The birds of the Western Palearctic. Volume I. Ostrich to ducks. Oxford University Press, Oxford, UK.

Cramp, S., ed. 1983. Handbook of the birds of the Middle East and north Africa. The birds of the Western Palearctic. Volume III. Waders to gulls. Oxford University Press, Oxford, UK.

Cramp, S., ed. 1992. Handbook of the birds of the Middle East and north Africa. The birds of the Western Palearctic. Volume VI. Warblers. Oxford University Press, Oxford, UK.

Crawley, M. J. 2013. The R book. Second edition. John Wiley and Sons, Chichester, UK.

DaCosta, J. M., G. M. Spellman, P. Escalante, and J. Klicka. 2009. A molecular systematic revision of two historically problematic songbird clades: *Aimophila* and *Pipilo*. J. Avian Biol. 40:206-216.

Dávalos, L. M., and A. L. Porzecanski. 2009. Accounting for molecular stochasticity in systematics revisions: species limits and phylogeny of *Paroaria*. Mol. Phylogenet. Evol. 53:234-248.

den Tex, R.-J., and J. A. Leonard. 2013. A molecular phylogeny of Asian barbets: speciation and extinction in the tropics. Mol. Phylogenet. Evol. 68:1-13.

Desjardins, P., and R. Morais. 1990. Sequence and gene organization of the chicken mitochondrial genome. J. Mol. Biol. 212:599-634.

66 Dor, R., M. D. Carling, I. J. Lovette, F. H. Sheldon, and D. W. Winkler. 2012. Species
67 trees for the tree swallows (Genus *Tachycineta*): an alternative phylogenetic
68 hypothesis to the mitochondrial gene tree. Mol. Phylogenet. Evol. 65:317-322.
69 Driskell, A. C., J. A. Norman, S. Pruett-Jones, E. Mangall, S. Sonsthagen, and L.
70 Christidis. 2011. A multigene phylogeny examining evolutionary and ecological
71 relationships in the Australo-papuan wrens of the subfamily Malurinae (Aves).
72 Mol. Phylogenet. Evol. 60:480-485.
73 DuBay, S. G., and C. C. Witt. 2012. An improved phylogeny of the Andean tit-tyrants
74 (Aves, Tyrannidae): more characters trump sophisticated analyses. Mol.
75 Phylogenet. Evol. 64:285-296.
76 Dunning, J. B., Jr. 2008. Body masses of birds of the world. CRC handbook of avian
77 body masses, second edition. Taylor and Francis Group, Boca Raton, FL.
78 Fleischer, R. C., J. J. Kirchman, J. P. Dumbacher, L. Bevier, C. Dove, N. C. Rotzel, S. V.
79 Edwards, M. Lammertink, K. J. Miglia, and W. S. Moore. 2006. Mid-Pleistocene
80 divergence of Cuban and North American Ivory-billed Woodpeckers. Biol. Lett.
81 2:466-469.
82 Forcina, G., P. Panayides, M. Guerrini, F. Nardi, B. K. Gupta, E. Mori, O. F. Al-Sheikhly, J.
83 Mansoori, I. Khaliq, D. N. Rank, B. M. Parasharya, A. A. Khan, P. Hadjigerou, and
84 F. Barbanera. 2012. Molecular evolution of the Asian francolins (*Francolinus*,
85 Galliformes): a modern reappraisal of a classic study in speciation. Mol.
86 Phylogenet. Evol. 65:523-534.

87 Fregin, S., M. Haase, U. Olsson, and P. Alström. 2009. Multi-locus phylogeny of the
88 family Acrocephalidae (Aves: Passeriformes) – the traditional taxonomy
89 overthrown. Mol. Phylogenet. Evol. 52:866-878.
90 Freitas, G. H. S., A. V. Chaves, L. M. Costa, F. R. Santos, and M. Rodrigues. 2012. A new
91 species of *Cinclodes* from the Espinhaço Range, southeastern Brazil: insights
92 into the biogeographical history of the South American highlands. Ibis
93 154:738-755.
94 Gardner, J. L., J. W. H. Trueman, D. Ebert, L. Joseph, and R. D. Magrath. 2010.
95 Phylogeny and evolution of the Meliphagoidea, the largest radiation of
96 Australasian songbirds. Mol. Phylogenet. Evol. 55:1087-1102.
97 Gelman, A., Y.-S. Su, M. Yajima, J. Hill, M. Grazia Pittau, J. Kerman, and T. Zheng. 2014.
98 *arm*: data analysis using regression and multilevel/hierarchical models. R
99 package version 1.7-07.
100 Gibson, R., and A. Baker. 2012. Multiple gene sequences resolve phylogenetic
101 relationships in the shorebird suborder Scolopaci (Aves: Charadriiformes).
102 Mol. Phylogenet. Evol. 64:66-72.
103 Gómez, J. P., G. A. Bravo, R. T. Brumfield, J. G. Tello, and C. D. Cadena. 2010. A
104 phylogenetic approach to disentangling the role of competition and habitat
105 filtering in community assembly of Neotropical forest birds. J. Anim. Ecol.
106 79:1181-1192.
107 Gonzalez, J.-C., B. C. Sheldon, N. J. Collar, and J. A. Tobias. 2013. A comprehensive
108 molecular phylogeny for the hornbills (Aves: Bucerotidae). Mol. Phylogenet.
109 Evol. 67:468-483.

110 Higgins, P. J., J. M. Peter, and S. J. Cowling, eds. 2006. Handbook of Australian, New
111 Zealand and Antarctic birds. Volume 7. Boatbill to starlings. Oxford University
112 Press, Oxford, UK.
113 Jacobsen, F., N. R. Friedman, and K. E. Omland. 2010. Congruence between nuclear
114 and mitochondrial DNA: combination of multiple nuclear introns resolves a
115 well-supported phylogeny of New World orioles (*Icterus*). Mol. Phylogenet.
116 Evol. 56:419-427.
117 Jetz, W., G. H. Thomas, J. B. Joy, K. Hartmann, and A. O. Mooers. 2012. The global
118 diversity of birds in space and time. Nature 491: 444-448.
119 Jønsson, K. A., R. C. K. Bowie, R. G. Moyle, M. Irestedt, L. Christidis, J. A. Norman, and J.
120 Fjeldså. 2010. Phylogeny and biogeography of Oriolidae (Aves: Passeriformes).
121 Ecography 33:232-241.
122 Klicka, J., K. Burns, and G. M. Spellman. 2007. Defining a monophyletic Cardinalini: a
123 molecular perspective. Mol. Phylogenet. Evol. 45:1014-1032.
124 Kundu, S., C. G. Jones, R. P. Prys-Jones, and J. J. Groombridge. 2012. The evolution of
125 the Indian Ocean parrots (Psittaciformes): extinction, adaptive radiation and
126 eustacy. Mol. Phylogenet. Evol. 62:296-305.
127 Larkin, M. A., G. Blackshields, N. P. Brown, R. Chenna, P. A. McGettigan, H. McWilliam,
128 F. Valentin, I. M. Wallace, A. Wilm, R. Lopez, J. E. Thompson, T. J. Gibson, and D.
129 G. Higgins. 2007. Clustal W and Clustal X version 2.0. Bioinformatics 23:2947-
130 2948.

131 Lemoine, N. 2012. R for ecologists: putting together a piecewise regression.
132 http://www.r-bloggers.com/r-for-ecologists-putting-together-a-piecewise-
133 regression/
134 Lovette, I. J., and D. R. Rubenstein. 2007. A comprehensive molecular phylogeny of
135 the starlings (Aves: Sturnidae) and mockingbirds (Aves: Mimidae): congruent
136 mtDNA and nuclear trees for a cosmopolitan avian radiation. Mol. Phylogenet.
137 Evol. 44:1031-1056.
138 Maddison, D. R., and W. P. Maddison. 2005. MacClade, version 4.08. Sinauer
139 Associates, Sunderland, MA.
140 Martin, P. R., R. Montgomerie, and S. C. Lougheed. 2015. Color patterns of closely
141 related bird species are more divergent at intermediate levels of breeding-
142 range sympatry. Am. Nat., in press.
143 Martin, P. R., and J. J. Tewksbury. 2008. Latitudinal variation in subspecific
144 diversification of birds. Evolution 62:2775-2788.
145 Mauck, W. M., III, and K. J. Burns. 2009. Phylogeny, biogeography, and recurrent
146 evolution of divergent bill types in the nectar-stealing flowerpiercers
147 (Thraupini: *Diglossa* and *Diglossopis*). Biol. J. Linnean Soc. 98:14-28.
148 Melo, M., and J. Fuchs. 2008. Phylogenetic relationships of the Gulf of Guinea *Alcedo*
149 kingfishers. Ibis 150:633-639.
150 Moltesen, M., M. Irestedt, J. Fjeldså, P. G. P. Ericson, and K. A. Jønsson. 2012.
151 Molecular phylogeny of Chloropseidae and Irenidae - cryptic species and
152 biogeography. Mol. Phylogenet. Evol. 65:903-914.

153 Moore, W. S., A. C. Weibel, and A. Agius. 2006. Mitochondrial DNA phylogeny of the
154 woodpecker genus *Veniliornis* (Picidae, Picinae) and related genera implies
155 convergent evolution of plumage patterns. Biol. J. Linnean Soc. 87:611-624.
156 Moyle, R. G., J. Fuchs, E. Pasquet, and B. D. Marks. 2007. Feeding behavior, toe count,
157 and the phylogenetic relationships among alcedinine kingfishers (Alcedininae).
158 J. Avian Biol. 38:317-326.
159 Moyle, R. G., and B. D. Marks. 2006. Phylogenetic relationships of the bulbuls (Aves:
160 Pycnonotidae) based on mitochondrial and nuclear DNA sequence data. Mol.
161 Phylogenet. Evol. 40:687-695.
162 New, M., D. Lister, M. Hulme, and I. Makin. 2002. A high-resolution data set of surface
163 climate over global land areas. Clim. Res. 21:1-25.
164 Nicholls, J. A., M. C. Double, D. M. Rowell, and R. D. Magrath. 2000. The evolution of
165 cooperative and pair breeding in thornbills *Acanthiza* (Pardalotidae). J. Avian
166 Biol. 31:165-176.
167 Omland, K. E., S. M. Lanyon, and S. J. Fritz. 1999. A molecular phylogeny of the New
168 World orioles (*Icterus*): the importance of dense taxon sampling. Mol.
169 Phylogenet. Evol. 12:224-239.
170 Overton, L. C., and D. D. Rhoads. 2004. Molecular phylogenetic relationships based
171 on mitochondrial and nuclear gene sequences for the todies (*Todus*, Todidae)
172 of the Caribbean. Mol. Phylogenet. Evol. 32:524-538.
173 Pächert, M., J. Martens, J. Kosuch, A. A. Nazarenko, and M. Veith. 2003. Phylogenetic
174 signal in the song of crests and kinglets (Aves: *Regulus*). Evolution 57:616-629.

175 Para, J. L., J. A. McGuire, and C. H. Graham. 2010. Incorporating clade identity in
176 analyses of phylogenetic community structure: an example with
177 hummingbirds. Am. Nat. 176:573-587.
178 Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and the R Core team. 2015. *nlme*: Linear
179 and nonlinear mixed effects models. R package version 3.1-120.
180 Poole, A., ed. 2013. The Birds of North America Online. Cornell Lab of Ornithology,
181 Ithaca, NY; Retrieved from the Birds of North America Online:
182 http://bna.birds.cornell.edu/bna/
183 Powell, A. F. L. A., F. K. Barker, and S. M. Lanyon. 2008. A complete species-level
184 phylogeny of the grackles (*Quiscalus* spp.), including the extinct Slender-billed
185 Grackle, inferred from mitochondrial DNA. Condor 110:718-728.
186 Randi, E., V. Lucchini, A. Hennache, R. T. Kimball, E. L. Braun, and J. D. Ligon. 2001.
187 Evolution of the mitochrondrial DNA control region and cytochrome b genes
188 and the inference of phylogenetic relationships in the avian genus *Lophura*
189 (Galliformes). Mol. Phylogenet. Evol. 19:187-201.
190 Ribas, C. C., C. Y. Miyaki, and J. Cracraft. 2009. Phylogenetic relationships,
191 diversification and biogeography in Neotropical *Brotogeris* parakeets. J.
192 Biogeogr. 36:1712-1729.
193 Russello, M. A., and G. Amato. 2004. A molecular phylogeny of *Amazona*:
194 implications for Neotropical parrot biogeography, taxonomy, and conservation.
195 Mol. Phylogenet. Evol. 30:421-437.
196 Sangster, G., P. Alström, E. Forsmark, and U. Olsson. 2010. Multi-locus phylogenetic
197 analysis of Old World chats and flycatchers reveals extensive paraphyly at

family, subfamily and genus level (Aves: Muscicapidae). Mol. Phylogenet. Evol. 57:380-392.

Sedano, R. E., and K. J. Burns. 2010. Are the northern Andes a species pump for Neotropical birds? Phylogenetics and biogeography of a clade of Neotropical tanagers (Aves: Thraupini). J. Biogeogr. 37:325-343.

Sheldon, F. H., C. H. Oliveros, S. S. Taylor, B. McKay, H. Chuan Lim, M. A. Rahman, H. Mays, and R. G. Moyle. 2012. Molecular phylogeny and insular biogeography of the lowland tailorbirds of southeast Asia (Cisticollidae: *Orthotomus*). Mol. Phylogenet. Evol. 65:54-63.

Sheldon, F. H., L. A. Whittingham, R. G. Moyle, B. Slikas, and D. W. Winkler. 2005. Phylogeny of swallows (Aves: Hirundinidae) estimated from nuclear and mitochondrial DNA sequences. Mol. Phylogenet. Evol. 35:254-270.

Slikas, B. 1997. Phylogeny of the avian family Ciconiidae (storks) based on cytochrome b sequences and DNA-DNA hybridization distances. Mol. Phylogenet. Evol. 8:275-300.

Tamura, K., and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol. Biol. Evol. 10:512-526.

Tamura, K., D. Peterson, N. Peterson, G. Stecher, M. Nei, and S. Kumar. 2011. MEGA5: Molecular Evolutionary Genetics Analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol. Biol. Evol. 28:2731-2739.

220 Vázquez-Miranda, H., A. G. Navarro-Sigüenza, and K. E. Omland. 2009.
221 Phylogeography of the Rufous-naped Wren (*Campylorhynchus rufinucha*):
222 speciation and hybridization in Mesoamerica. Auk 126:765-778.
223 Voelker, G., and J. E. Light. 2011. Palaeoclimatic events, dispersal and migratory
224 losses along the Afro-European axis as drivers of biogeographic distribution in
225 *Sylvia* warblers. BMC Evol. Biol. 11:163.
226 Voelker, G., S. Rohwer, R. C. K. Bowie, and D. C. Outlaw. 2007. Molecular systematics
227 of a speciose, cosmopolitan songbird genus: defining the limits of, and
228 relationships among, the *Turdus* thrushes. Mol. Phylogenet. Evol. 42:422-434.
229 Weibel, A. C., and W. S. Moore. 2002. Molecular phylogeny of a cosmopolitan group
230 of woodpeckers (genus *Picoides*) based on COI and cyt b mitochondrial gene
231 sequences. Mol. Phylogenet. Evol. 22:65-75.
232 Weir, J. T., E. Bermingham, and D. Schluter. 2009. The Great American Biotic
233 Interchange in birds. Proc. Natl. Acad. Sci. USA 106:21737-21742.
234 Weir, J. T., and D. Schluter. 2008. Calibrating the avian molecular clock. Mol. Ecol.
235 17:2321-2328.
236 Zink, R. M., D. L. Dittmann, J. Klicka, and R. C. Blackwell-Rago. 1999. Evolutionary
237 patterns of morphometrics, allozymes, and mitochondrial DNA in thrashers
238 (genus *Toxostoma*). Auk 116:1021-1038.
239 Zuccon, D., and P. G. P. Ericson. 2010. The *Monticola* rock-thrushes: phylogeny and
240 biogeography revisited. Mol. Phylogenet. Evol. 55:901-910.
241 Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects
242 models and extensions in ecology with R. Springer, New York, NY.