Phenotypic responses to climate change are significantly dampened in big-brained birds

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Abstract

Anthropogenic climate change is rapidly altering local environments and threatening biodiversity throughout the world. Although many wildlife responses to this phenomenon appear largely idiosyncratic, a wealth of basic research on this topic is enabling the identification of general patterns across taxa. Here we expand those efforts by investigating how avian responses to climate change are affected by the ability to cope with ecological variation through behavioral flexibility (as measured by relative brain size). After accounting for the effects of phylogenetic uncertainty and interspecific variation in adaptive potential, we confirm that although climate warming is generally correlated with major body size reductions in North American migrants, these responses are significantly weaker in species with larger relative brain sizes. Our findings suggest that cognition can play an important role in organismal responses to climate change by actively buffering individuals from the effects of global change.

Introduction

Anthropogenic climate change is resulting in rapid global warming and increasingly variable and unpredictable weather (Trenberth *et al.* 2015; National Academies of Sciences 2016; Ummenhofer & Meehl 2017). Faced with these ecological threats, wildlife populations are either revealing new extremes in their phenotypic plasticity (Andrew *et al.* 2017; Møller *et al.* 2018), shifting their geographic distributions (Tingley *et al.* 2009) and phenologies (Miller-Rushing *et al.* 2008; Horton *et al.* 2020), or evolving new phenotypes (Weeks *et al.* 2020b). Although theoretical models have identified some of the reasons why different species have responded so differently to similar environmental phenomena (e.g., Botero *et al.* 2015; Haaland & Botero 2019), newly documented effects continue to appear largely idiosyncratic (Radchuk *et al.* 2019; Siepielski *et al.* 2019) and highly dependent on natural history. A better understanding of the factors that modulate phenotypic responses to climate change will therefore be critical for setting effective conservation priorities and, particularly, for assessing the relative vulnerability of species in communities at risk (Williams *et al.* 2008; Bateman *et al.* 2020).

Behavioral flexibility is likely to reduce vulnerability to climate change because changes in the phenology or availability of food can often be accommodated by shifts in diet or foraging behavior. It is therefore expected that species that possess a greater potential for behavioral flexibility should be buffered from climate-driven selection and may even be able to cope with, at least initially, major environmental changes without significantly altering their phenotype ("cognitive buffer hypothesis" Allman *et al.* 1993). In birds, behavioral flexibility can be reasonably approximated by the size of the brain relative to the body (Lefebvre *et al.* 2004). Specifically, avian relative brain size is a good indicator of learning ability (Rensch 1956), memory (Roth *et al.* 2012), neuron numbers (Olkowicz *et al.* 2016), and the size of areas that

deal with decision making, associative learning, foraging innovation, and tool use (Sayol *et al.* 2016). Additionally, avian relative brain size is associated with reduced mortality rates (Sol *et al.* 2007), longer lifespans (Minias & Podlaszczuk 2017; Jiménez-Ortega *et al.* 2020), increased capacities to thrive in human-altered environments (Shultz *et al.* 2005; Maklakov *et al.* 2011), and more stable population dynamics in variable and unpredictable climates (Fristoe *et al.* 2017). Here we test the hypothesis that phenotypic responses to climate change are buffered by increased capacities for behavioral flexibility in North American migratory birds.

Recent global warming has consistently led to body size reductions in a variety of taxa (Gardner *et al.* 2011; Teplitsky & Millien 2014), including birds (Weeks *et al.* 2020b). This seemingly universal response provides a unique comparative opportunity to investigate how behavioral flexibility modulates phenotypic responses to climate change. We envision at least two possible mechanisms through which adaptive and plastic responses to this phenomenon may be weakened in species with greater behavioral flexibility (Fig 1). First, cognitive buffering could broaden fitness curves, leading to smaller fitness differentials and weaker incentives to alter the phenotype when climates change (Fig. 1a). Second, behavioral flexibility could alter the balance of opposing forces in stabilizing selection and could thereby result in smaller peak shifts with climate change (Fig. 1b). For example, while warmer temperatures select for smaller bodies, intra- and interspecific competition tend to select for larger ones (Leyequién *et al.* 2007). Thus, if behavioral flexibility is more effective at buffering the effect of temperature than that of competition, then the expected shift in peak fitness under warmer temperatures should be smaller (all other things being equal) and fitness differentials should be further reduced under climate change.

Because some of the observed recent changes in avian body size may be driven by natural selection, our analyses controlled for the effects of two well-known correlates of evolutionary rates: mutation rate (Uchimura *et al.* 2015) and generation time (Latta *et al.* 2013), respectively estimated as neutral substitution rate (Kimura 1987) and either longevity (de Magalhães *et al.* 2010) or generation time (Bird *et al.* 2020).

Methods

Data and Data Sources

Tarsus length is considered one of the most accurate measurements of intraspecific variation in body size in passerines (Rising & Somers 1989; Senar & Pascual 1997; Weeks *et al.* 2020b). Accordingly, we extracted tarsus length measurements for 25,727 adult specimens belonging to 49 different species of North American perching birds in Weeks *et al.* (2020a) and followed their methods to estimate the extent to which temperature, precipitation, and productivity on the breeding and wintering grounds affect this metric. Our sample is restricted to the Passerifomes in recognition of potential order-level differences in the allometric scaling of the brain among birds (Logan *et al.* 2018). The specimens in Weeks *et al.* (2020b) were collected from window collisions during migration, meaning that their actual breeding localities are unknown. As a result, environmental predictors in our analyses were estimated for each specimen in our dataset from the mean environmental values for the entire breeding range of their corresponding species (Birdlife International 2018) during the year of sample. Environmental parameters included data from NASA's GISS Surface Temperature Analysis, GISTEMP v4 (Lenssen *et al.* 2019; GISS Team 2020), the Climate Prediction Center's Merged Analysis of Precipitation, CMAP (Xie &

106 Arkin 1997), and NASA's Normalized Difference Vegetation Index dataset (NDVI3g) from the
107 'gimms' R package (Pinzon & Tucker 2014; Detsch 2021). Following Week's *et al.* (2020a), we
108 selected June climate data from the breeding grounds and December climate data from the
109 wintering grounds and calculated each species' climate values for each year separately (the
110 "time-lag 0" approach in Weeks *et al.* 2020b). The R code used to obtain and process yearly
111 climate data is available in Appendix S1, section 1.

112 We then collated brain size and body mass estimates from previous studies (Fristoe *et al.*
113 2017; Sayol *et al.* 2018, 2020) and added new brain size measurements for 27 species. When
114 brain size data were available from multiple sources (N = 10 species), we used sample-based
115 weighted averages. New brain volumes were estimated similarly to previous studies (Lefebvre *et*
116 *al.* 2004) by filling the brain cavity of museum specimens with 1 mm glass microballoons (GB
117 01, Conservation Resources UK Ltd.), weighing these microballoons on a digital scale with 0.01
118 gram precision, and converting their weights to volume given their known density. Our entire
119 dataset of brain sizes (49 species) is available in Data S1. Maximum lifespan data (1,049 species
120 total) were collated from the literature (Wasser & Sherman 2010; Minias & Podlaszczuk 2017;
121 USGS 2020; Data S2). We also recorded the provenance of lifespan estimates (wild or captive
122 animal) for downstream analyses.

123 As a proxy for mutation rate, we computed substitution rates for intron 5 of the
124 transforming growth factor beta-2 (tgfb2) gene, a putative neutral marker available in GenBank
125 (Sayers *et al.* 2021) for most of the species included in this study. Sequences were obtained by
126 BLASTing (BLASTN, Zhang *et al.* 2000) a complete sequence of the intron against the NCBI
127 database (nucleotide collection), restricting the search to genera in our sample. Our BLAST
128 search relied on an expected threshold of 0.05, a word size of 28, and a match and mismatch

score of 1 and -2. We then downloaded the fragments that aligned with our query sequence and selected the largest sequence per species. The resulting 96 sequences were aligned with MAFFT v7 (Katoh *et al.* 2002, https://mafft.cbrc.jp/alignment/server/) using an "auto" strategy, which was further processed with Gblocks 0.91b (Castresana 2000) to remove poorly aligned positions (not allowing any gap positions). Last, we integrated phylogenetic relationships and their uncertainty into our analyses by running each step in our models over a sample of 100 trees of the posterior tree distribution generated from a recent version (2016) of the global bird phylogeny (Global Phylogeny of Birds; Jetz *et al.* 2012) using the Hackett backbone (Hackett *et al.* 2008).

Statistical Analyses

Because brain size and longevity scale allometrically (Iwaniuk & Nelson 2003; Wasser & Sherman 2010), we began our analysis by separately evaluating their values relative to body size (Figs. S1-S3), computed as the residuals in log-log regressions with Pagel's lambda fitted in 'sensiPhy' (Paterno *et al.* 2018). When estimating relative lifespan, our regression model accounted for both body size and provenance (i.e., wild or captive animal) because lifespan is generally longer in captive animals (Stark *et al.* 2020). Given that 'sensiPhy' can handle only one predictor at a time, we modified the 'tree_phylolm()' function from that package to handle multiple predictors and calculated the posterior median residuals across all phylogenetic trees for use in downstream analyses (code in Appendix S2). We note that during the course of this study, direct information on generation length became available (Bird *et al.* 2020). As expected, relative lifespan (our original predictor) and generation time were strongly correlated (Pearson's

151 correlation coefficient: 0.742, $p < 0.0001$), and the models including either lifespan or generation
152 time yield qualitatively identical results (Appendix S2, section 4).

153 We assessed the neutrality of the tgfb2 sequence alignment by computing Tajima's D
154 (Tajima 1989) and testing whether it differed significantly from zero with the tajima.test function
155 in the R package pegas (Paradis 2010). We used BEAST2 v2.5.2 (Bouckaert *et al.* 2014) to
156 compute branch-specific relative substitution rates under an uncorrelated exponential molecular
157 clock and Yule tree prior. We set a TN substitution model with empirical base frequencies and a
158 Gamma distribution with four categories (the best supported model using ModelFinder as
159 implemented in the server W-IQ-TREE, http://iqtree.cibiv.univie.ac.at/, Trifinopoulos *et al.*
160 2016; Kalyaanamoorthy *et al.* 2017). Our final analysis of substitution rates relied on two
161 independent MCMC chains that ran for 10^7 generations with a thinning interval of 1,000. After
162 discarding the initial 10% of the generations as "burn in" we computed a summary tree with the
163 software TreeAnnotator (included in the package BEAST2) using the "maximum credibility
164 tree" as our target tree type (we also used this approach to compute a summary tree from the set
165 of trees downloaded from the Global Bird Phylogeny, hereafter "summary tree"). Moreover, we
166 obtained a sample of 1,000 trees from the posterior distribution to assess uncertainty in
167 substitution rates. After observing satisfactory convergence with Tracer v1.7.1 (ESS values all >
168 100; Rambaut *et al.* 2018) and confirming that branch-specific substitution rates showed
169 overlapping and unimodal peaks, we calculated their posterior medians and used these as taxon-
170 specific estimates of substitution rates. These posterior medians (Fig. S4) covered 31 of the 49
171 passerine species from Weeks *et al.* (2020b) and are available in Data S3.

172 We used Bayesian phylogenetic generalized linear mixed models in MCMCglmm
173 (Hadfield 2010) to investigate the role of relative brain size in modulating phenotypic change.

The unit of observation in these analyses was the individual (i.e., N = 25,727 specimens from the Weeks *et al.* (2020b) dataset), which allowed us to maximize the power of our tests. Because individuals within our sample are grouped into species, we specified the random effects in MCMCglmm as "~phylo+species" to explicitly account for two kinds of non-independence (i.e., repeated measures within species and differential relatedness among species; see Sandvig *et al.* 2019; Lemaître *et al.* 2020). We nevertheless note that a simpler analysis based on species level averages (i.e., N=49 species) also indicates that body size reduction has been significantly slower in North American migrants with larger relative brain sizes (see Appendix S3). In both approaches we used a variance-covariance matrix derived from the summary tree of the Global Bird Phylogeny.

The dependent variable in our phylogenetic generalized linear mixed models was adult tarsus length, and the list of potential predictors included variables sampled at the individual (i.e., sex, season, year, breeding temperature anomaly, wintering temperature anomaly, breeding precipitation average, wintering precipitation average, breeding average NDVI, wintering average NDVI) and the species level (i.e., relative brain size, relative lifespan, and mutation rate). Environmental parameters were sampled at the same year of collection of each specimen (Table S1). The fully parameterized model also included interactions between residual lifespan and year (to account for the possibility that species with shorter lifespan may potentially decrease their body size at faster rates), and between relative brain size and breeding temperature anomaly (to account for the possibility that species with greater capacity for behavioral flexibility may respond differently to temperature change; see Weeks *et al.* (2020b). All continuous variables were transformed to Z-scores before model fitting. We simplified the model through stepwise elimination of non-significant predictors (largest pMCMC values first) until a reduced set of only

197 significant predictors remained (pMCMC < 0.05). Upon identifying the fully reduced model, we
198 used it to jointly evaluate support for an interaction between neutral substitution rates and year
199 on tarsus length (again, to account for the possibility that species with faster mutation rates could
200 enable faster body size evolution). We assessed the significance of this term only after model
201 reduction because data for neutral substitution rates were lacking for many species leading to
202 significant data reduction ($N_{specimens}$ = 12,385, $N_{species}$= 31). This interaction was nevertheless
203 found not to be significant, so we report findings of the reduced model without it (N = 25,727
204 specimens from 49 species).

205 To account for the effects of phylogenetic uncertainty in our analyses, we fitted two
206 models (the log-log regression of brain mass on body mass and the fully reduced phylogenetic
207 generalized linear mixed model) on a sample of 100 randomly selected trees from the posterior
208 tree distribution with the Hackett backbone (Hackett *et al.* 2008; Jetz *et al.* 2012). Specifically,
209 we computed residual brain sizes with a given tree and used them in the model of tarsus length
210 while accounting for phylogenetic non-independence with the same tree. The 100 resulting
211 models were then assembled into a pseudoposterior and summarized to obtain final coefficient
212 estimates. We fitted four chains for each of these regression models with the 'mcmcglmm'
213 package in R (Hadfield 2010). Convergence was assessed with multichain convergence
214 diagnostics (Gelman-Rubin statistics < 1.1), confirming high estimated sample sizes, and
215 visualization of trace plots. Each mcmcglmm chain was run for 13,000 iterations, including a
216 "burn in" of 3,000 and a thinning interval of 10. We used recommended vague priors on the
217 random effects by choosing inverse Wishart distributions with $\psi = 1$ and $\nu = 0.02$ (Hadfield
218 2010).

219 *Accounting for potential temporal variation in relative brain size*

It is possible that the size of brains and bodies are changing at different rates in response to climate change (i.e., that allometric scaling itself is changing over time). To investigate the extent to which this issue could affect our findings, we began by asking if absolute brain size has changed over time. Because the number of available skull specimens per species was small (51 skulls from 27 species; 1.89 ± 0.32 per species) and power was low, it is not surprising that these analyses did not detect significant changes through time in absolute brain size ($p = 0.734$; Appendix S2, section 2.2). Thus, as an alternative, we proceeded to compare temporal variation within-species (brain specimens were typically collected in different years) with observed brain size variation among-species, discovering that variation among species was substantially greater than variation within them (one sample t-test: $t = -19.96$, $df = 22$, $p < 0.0001$; see Appendix S2, section 2.2). Based on these findings we are reasonably confident that the effects of any potential within-species changes in allometric scaling over time are minor and that, if they indeed exist, they are unlikely to affect the interspecific comparisons reported below.

We nevertheless note that if brain size has indeed remained invariant as bodies become smaller, then estimates of relative brain size could be inflated by comparing older brain specimens against contemporary body sizes. This issue could be ideally addressed by sampling body and brain size from the same specimens, but this was not possible here because specimen IDs were not available for all brain sizes collated from literature and because some of the museum skulls we measured had not been archived with their corresponding bodies. As a result, we addressed this issue instead by performing a robustness analysis (Appendix S2, section 2.3) in which we matched our collected brain volumes with time-specific estimates of body size. Specifically, we recomputed all species-specific equations for tarsus length change over time in Weeks *et al.* (2020b) and used them to calculate the expected body size of the corresponding

species at the year of each sample (Data S4). We note that each of these equations was parameterized from thousands of empirical records, making them one of the best estimators of body size available for our analyses. Although this analysis was done with only the 27 species for which we collected brain size estimates ourselves and involved a separate model simplification process, its results were qualitatively identical to the ones reported in the main text (see Table S2).

Results

Estimating mutation rates. Our analyses of intron 5 of tgfb2 confirm that this marker evolves in a nearly neutral manner and that its substitution rates are therefore a reasonable proxy for variation in mutation rates (Kimura 1987). The recovered Tajima's D (D = -1.70) was not significantly different from 0 under the assumption of a normal (p = 0.09) or a beta distribution (p = 0.07; Fig S5). Additionally, the summary tree derived from the alignment of tgfb2 was consistent with both the Global Bird Phylogeny (Fig. 6) and previous phylogenetic studies based on multiple markers (Barker *et al.* 2015; Fig. S7-S8). Neutral substitution rates extracted from the sample of 1,000 trees ranged from 0.246 to 2.179 and showed significant variation among clades (Fig. S4).

Comparing responses to climate change. Our regression results corroborated the findings of Weeks *et al.* (2020b). Namely, increases in temperature and precipitation levels within breeding grounds are linked to significant body size reductions in North American migratory birds. Reassuringly, we found no evidence that these reductions were significantly constrained by mutation rate (neutral substitution rate x Year: 0.001, 95% CI: -0.006-0.026, pMCMC =

0.250; Table 1) or relative lifespan (relative lifespan x year: -0.0004, 95% CI: -0.010-0.011, pMCMC = 0.970; Table 1). In support of the cognitive buffer hypothesis, we also found that the negative effects of breeding temperature were significantly weakened by relative brain size (final model: relative brain size x breeding ground temperature: 0.012; 95% CI 0.002-0.022, pMCMC = 0.024; Table 1). We note that the individual effects of warmer breeding temperatures in our model appear relatively small (Table 1), perhaps because these body size changes have been measured across only four decades and because interspecific variation is much larger than intraspecific variation in our sample. Nevertheless, we also note that when considering solely the relative magnitude of these effects (Fig. 2a), the buffering effect of large relative brain sizes on phenotypic change is truly staggering. For example, the expected effect of breeding temperature on a species with a brain size equivalent to the largest relative brain size in our dataset (i.e., Song Sparrow, *Melospiza melodia*: relative brain size = 0.334; range of predicted tarsus length over the standardized range of breeding temperatures: 23.90-23.84; Fig. 2b) is only 30% of the expected effect in a species with a brain size equivalent to the smallest brain in our sample (i.e., Swainson's Thrush, *Catharus ustulatus*, Turdidae, Relative Brain Size = -0.276; range of predicted tarsus length = 22.33-22.13; Fig. 2c). When relative brain size was redefined to account for temporal variation in allometric scaling, we obtained qualitatively identical results (Appendix S2, Section 2.3; Table S2).

Brain size is known to be positively correlated with migration distance (Vincze 2016), raising the possibility that the effects we report here are ultimately a reflection of migratory constraints rather than differences in cognitive ability. To explicitly test this hypothesis, we recomputed our models after replacing relative brain size with migratory distance (Appendix S1, section 2; Appendix S2 section 5) and found that this alternative model set exhibits generally

weaker measures of fit. Additionally, we estimated models including both relative brain size and migratory distance after verifying that variance inflation was not a major problem. In this latter model set, we found that migration distance was not a significant predictor and that it dropped out early in the model selection process (Appendix S2, section 5). We therefore conclude that the observed effects of brain size on body size reduction are unlikely to be an epiphenomenon, a conclusion that is further supported by earlier studies based on this same dataset, which found that migration distance was not a predictor of phenotypic change (Zimova *et al.* 2021).

Discussion

We have shown here that previously reported temperature-related reductions in avian body size have been dramatically dampened in migratory North American passerines with larger relative brain size. This finding confirms, for the first time, that cognitive capacity can shape animal responses to anthropogenic climate change. Specifically, it supports the notion that an increased potential for behavioral flexibility (Mikhalevich *et al.* 2017) can facilitate a species' ability to withstand warmer local temperatures, just as it facilitates dealing with other forms of climatic variability (Fristoe *et al.* 2017).

The change in avian body sizes over the last four decades could be the product of either contemporary evolution (Gardner *et al.* 2011; Weeks *et al.* 2020b) or differential expression of already existing norms of reaction (i.e., plasticity; see Mariette & Buchanan 2016; Andrew *et al.* 2017). In both scenarios we see a clear role for cognition because rates of body size evolution were found to be significantly slower in species with larger relative brain size. Specifically, the cognitive buffer hypothesis (Allman *et al.* 1993) suggests that an increased capacity for

behavioral flexibility can buffer the fitness consequences of environmental change. In the selection scenario, the cognitive buffer hypothesis therefore predicts that bigger brains should lead to increased survival (Sol *et al.* 2007) and weakened selection gradients as temperatures change. In the plasticity scenario, it predicts instead that bigger brains should have favored the evolution of shallower norms of reaction long before the onset of anthropogenic climate change. Thus, we conclude that our findings are consistent with the cognitive buffer hypothesis, even if some or all the body size changes reported here are the result of underlying phenotypic plasticity.

Perhaps one of the most important questions that remains is whether the cognitive buffering effects reported here are biologically meaningful. In that context, we note that body size reductions in migratory North American passerines with the smallest brains in our dataset were about three times as large as those with largest brains (Fig. 2B). Because small changes in body size can dramatically affect an individual's ability to dissipate heat (Bergmann 1847), we conclude that these differences suggest a very strong buffering effect for behavioral flexibility. In fact, we note that the magnitude of this cognitive buffering may be even stronger given that the range of relative brain sizes in our sample is relatively small. Specifically, while the ratio between the smallest and largest brain in our sample is only 2.21, the ratio between an average parrot (Psittaciformes) and an average chicken-like bird is greater than five (Galliformes; cf. Fristoe *et al.* 2017). Thus, it is possible that differences in buffering intensities across a broader taxonomic range of "small-brained" and "large-brained" birds may be even more pronounced.

It is also possible that migratory birds (i.e., the subset of species included in this study) are particularly prone to climate-driven body size reduction because temperate summers have become consistently warmer and migration represents a major demographic bottleneck (Marra *et al.* 2015; Sergio *et al.* 2019) that selects for increased flight efficiency (Bowlin & Wikelski 2008;

Gray 2019). Additionally, it is likely that selection for smaller body size is being reinforced during the non-breeding season among birds in our sample because many of these neotropical migrants winter in montane tropical forests (Gómez *et al.* 2014; Céspedes & Bayly 2019) that are also undergoing rapid warming (Krishnaswamy *et al.* 2014). In sharp contrast, resident North American species are experiencing increasingly variable winters with more frequent and more extreme cold temperatures (Trenberth *et al.* 2015; National Academies of Sciences 2016; Ummenhofer & Meehl 2017), a phenomenon that selects for larger bodies and may therefore hinder overall body size reductions in the first place (Gardner *et al.* 2011). Thus, although our findings demonstrate that avian responses to climate change can be significantly dampened by cognitive buffering (*sensu* Allman 1993), they also remind us that the strength of these effects is likely to depend on how climate has changed across the entire annual cycle of each species of interest.

In conclusion, we have presented evidence that cognitive capacity has modulated the phenotypic responses of migratory North American birds to recent climate changes in a manner that is consistent with existing theory and physiological expectation. This finding confirms a long-standing prediction of the cognitive buffer hypothesis (Allman *et al.* 1993), namely, that an increased capacity for behavioral flexibility can reduce gradients of selection in evolution. Our findings also have practical implications for conservation (see Foden *et al.* 2019; Bateman *et al.* 2020), as they suggest that the ultimate effect of climate change on the composition of biological communities may be partially determined by the range and frequency distribution of relative brain sizes within the species that currently inhabit them (Fristoe & Botero 2019).

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559 Table 1

560 Coefficient table from MCMCglmm model selection

Parameter	**Posterior Mean**	**LL-95% CI**	**UL-95% CI**	**pMCMC**
Intercept	23.235	18.629	27.800	0.001
Year	-0.146	-0.158	-0.135	0.001
Breeding Temperature	-0.034	-0.045	-0.023	0.001
Breeding Precipitation	-0.061	-0.080	-0.044	0.001
Breeding NDVI *	0.018	-0.010	0.045	0.212
Wintering Temperature	0.030	0.019	0.040	0.001
Wintering Precipitation *	0.014	-0.006	0.035	0.216
Wintering NDVI *	0.015	-0.044	0.083	0.606
Sex	0.473	0.454	0.491	0.001
Season	0.026	0.004	0.049	0.028
Relative Lifespan x Year *	-0.0004	-0.010	0.011	0.970

Neutral Substitution Rate x Year	*	0.001	-0.006	0.026	0.250
Relative Brain Size		0.472	-0.644	1.583	0.404
Relative Brain Size x Breeding Temperature		0.012	0.002	0.022	0.024

561

562 * Denotes effect estimate is from last time the effect featured in a model before elimination
563 during model selection

564

Fig 1. Alternative mechanisms by which behavioral flexibility may alter selection gradients and weaken phenotypic responses to climate change. (**A**) Behavioral flexibility could broaden fitness curves through cognitive buffering (see main text), leading to a reduced fitness differential with climate change. Additionally, (**B**) behavioral flexibility could alter the balance of opposing forces in stabilizing selection, leading to smaller peak shifts and even weaker fitness differentials under climate change. Vertical dashed lines show the predicted decrease in relative fitness for species with smaller (thin) and larger (thick lines) capacity for behavioral flexibility.

Fig 2. Body size reduction with warming breeding temperatures is modulated by relative brain size. Fitted lines show the predicted body size decrease for the species with the largest and smallest relative brain sizes in our study (Song Sparrow, *Melospiza melodia*, Passerellidae, Relative Brain Size = 0.334 in panel **B** in red and Swainson's Thrush, *Catharus ustulatus*, Turdidae, Relative Brain Size = -0.276 in panel **C** in blue). The fitted lines in (**A**) look almost flat to the eye because the magnitude of these changes is relatively small compared to the range of body sizes in our sample. To better showcase the effect of relative brain size in our model, we plot these fitted lines again in (**B and C**). Dashed lines show constant body size and vertical hinges depict the predicted reduction in body size over the observed change in breeding temperatures (scaled) over the previous four decades.

Fig S1. Brain and body mass scale allometrically. Relative brain size was measured by the median residuals from a log-log regression using phylogenetic regression using Pagel's model of evolution (lambda = 0.764 ± 0.018) and phylogenetic uncertainty.

Fig S2. Maximum lifespan and body mass scale allometrically. Relative lifespan was measured by the median residuals from a log-log regression using phylogenetic regression using Pagel's

model of evolution (lambda = 0.464 ± 0.021) and phylogenetic uncertainty. Dashed line illustrates predicted captive-origin lifespans.

Fig S3. Relative lifespan estimates varied across the tree. Highlighted clades contain species that were used in downstream regressions.

Fig. S4. Neutral substitution rates varied across the tgfb2 tree. Text color indicates whether species were used in estimating the neutral substitution rates and tgfb2 tree only (grey) or also used in downstream regression analyses (black).

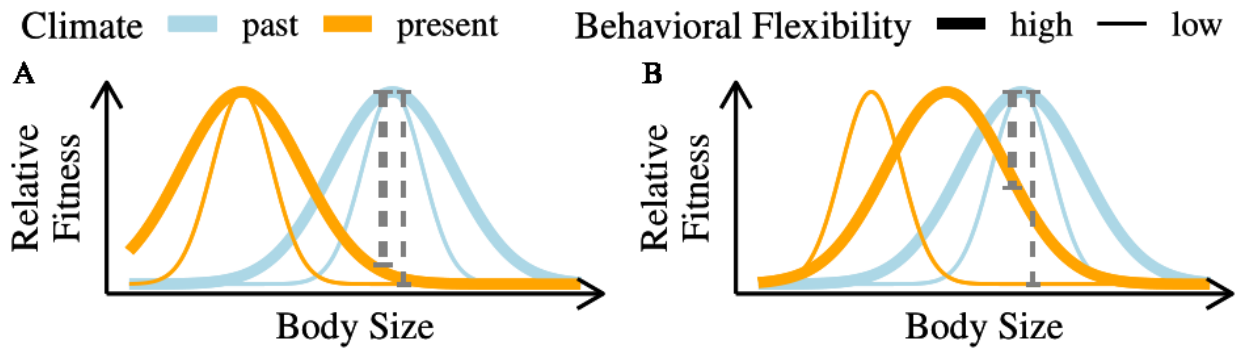
Fig S5. The alignment of the intron 5 of tgfb2 gene yielded Tajima's D values (dashed lines) that were not significantly different from 0 assuming Normal (**A**) or Beta (**B**) distributions. Shaded portions of distributions and colored text show exact p-values.

Fig S6. The summary trees from the Global Bird and phylogenetic analysis based on the intron tgfb2 show widespread agreement.

Fig. S7. Summary tree from Barker et al.'s (2015) concatenated analysis shows widespread agreement of major groups with tgfb2 tree in Emberizoidea.

Fig. S8. Species tree from Barker et al.'s (2015) shows widespread agreement of major groups with tgfb2 tree in Emberizoidea.

604 Fig 1



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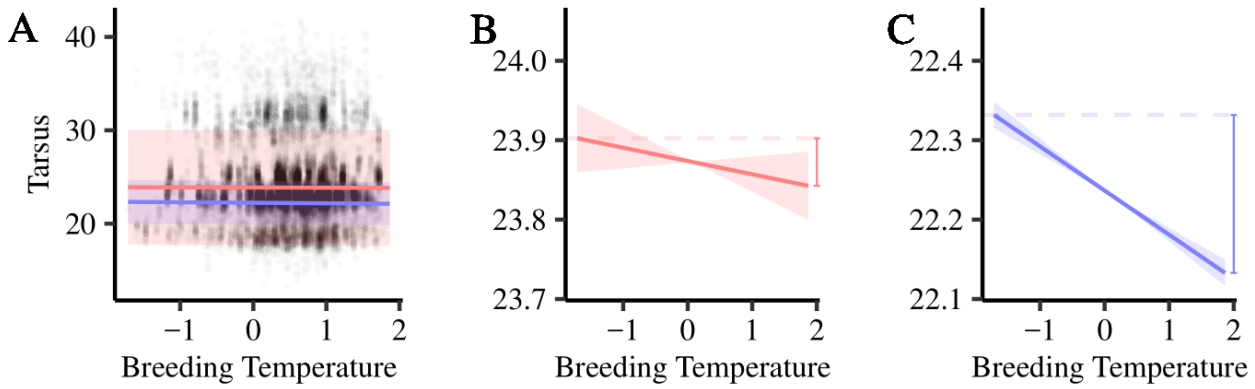
607 Fig 2



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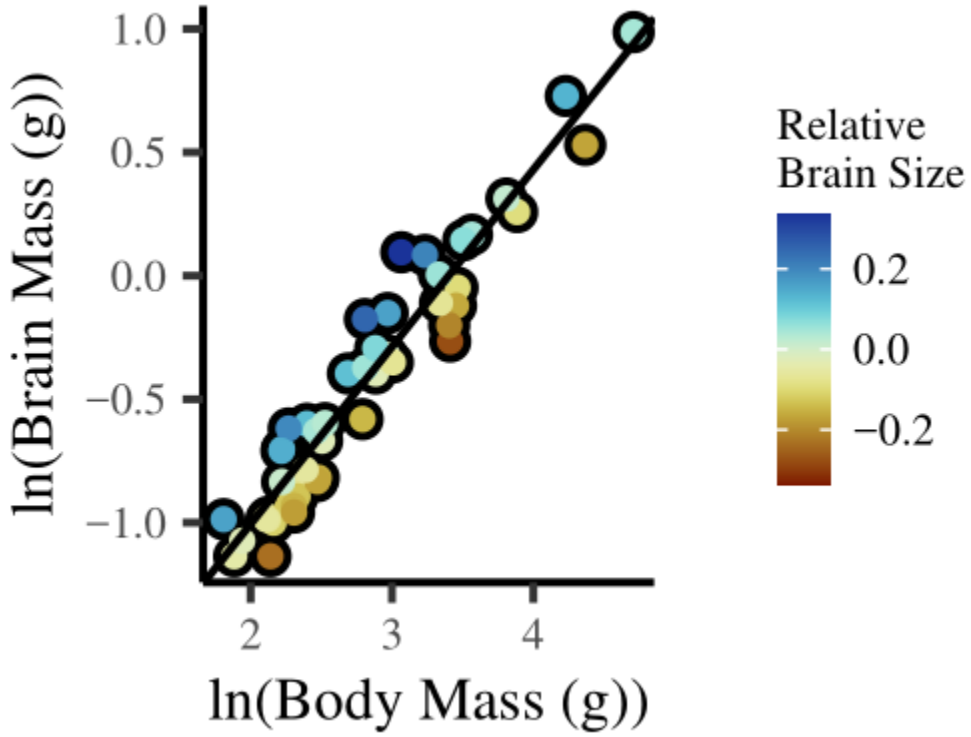
610 Fig S1



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613 Fig S2

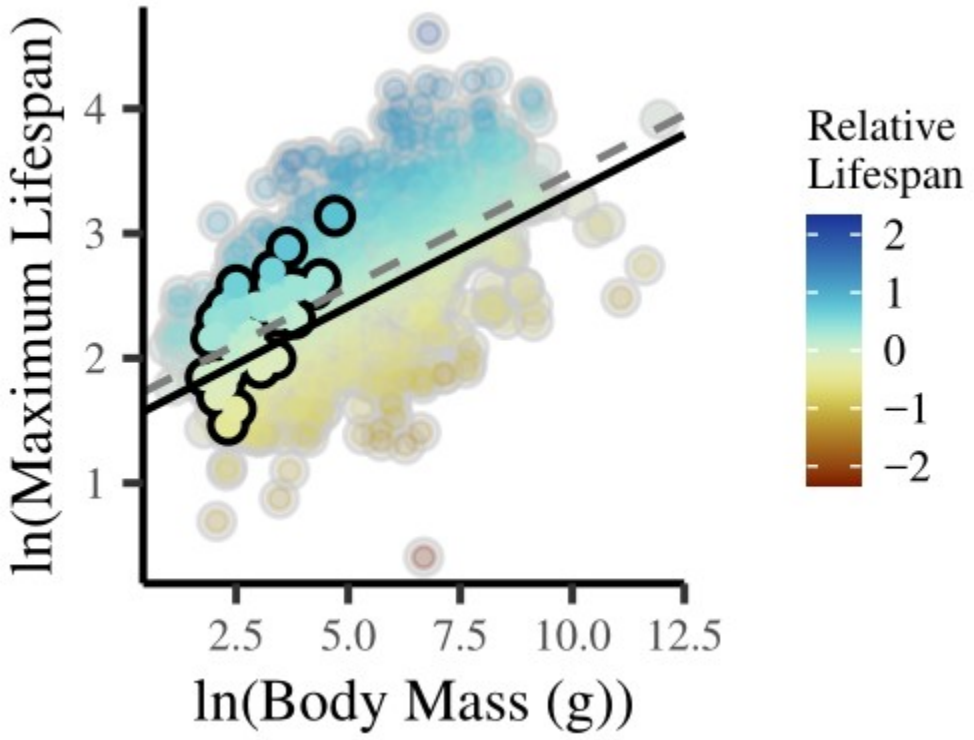

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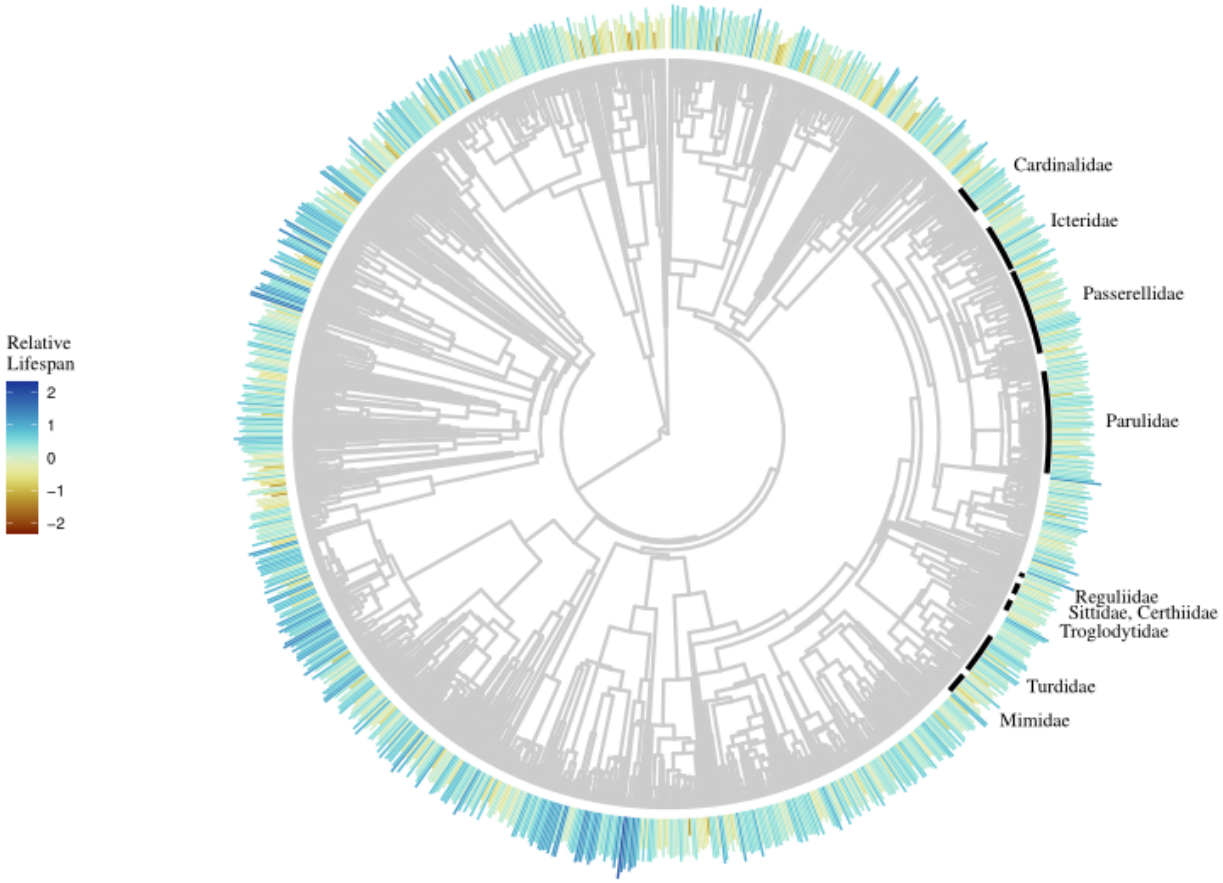
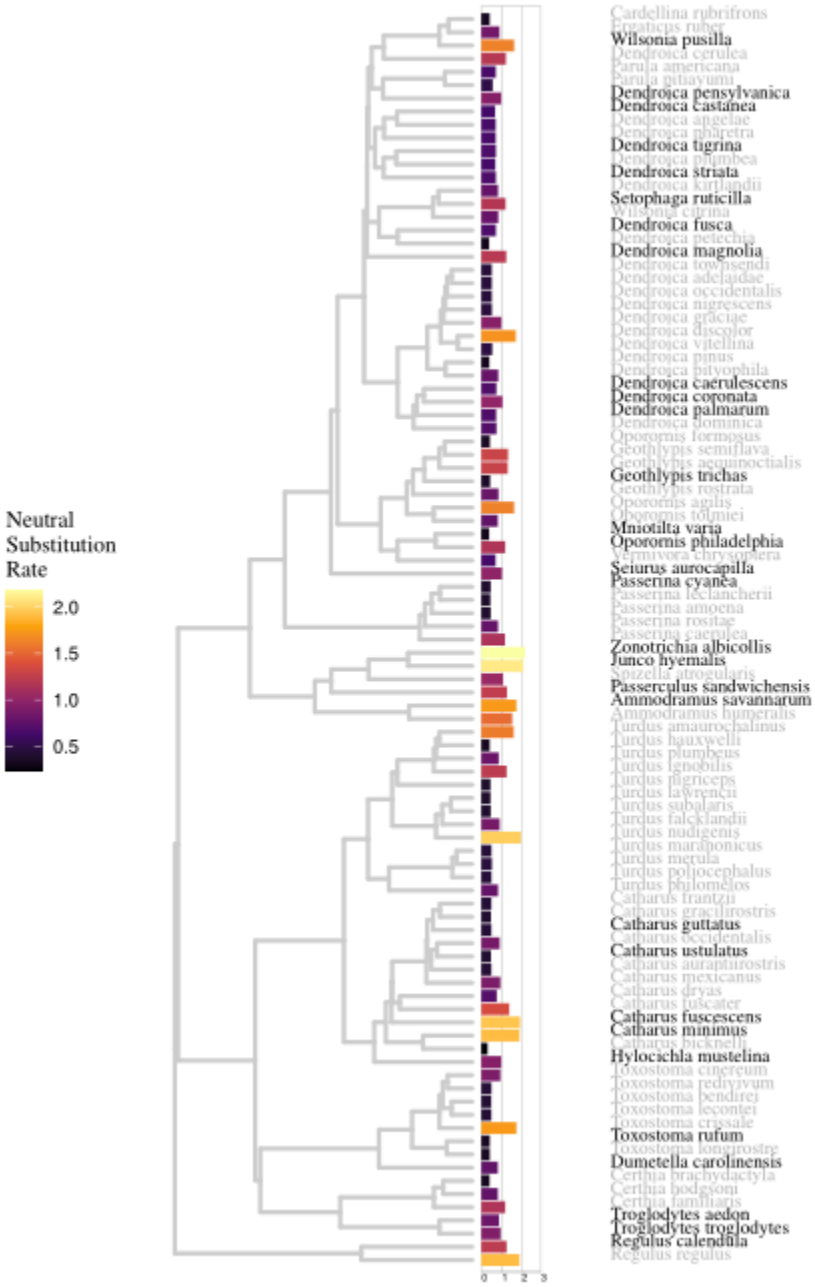
Fig S3


Relative
Lifespan
2
1
0
−1
−2
Cardinalidae
Icteridae
Passerellidae
Parulidae
Reguliidae
Sittidae, Certhiidae
Troglodytidae
Turdidae
Mimidae

619 Fig S4



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622 Fig S5

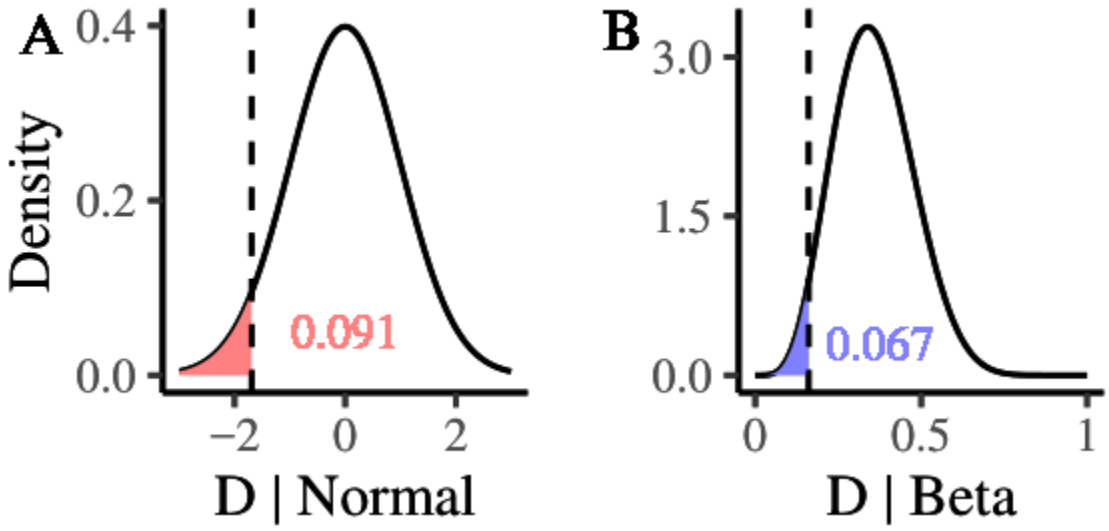

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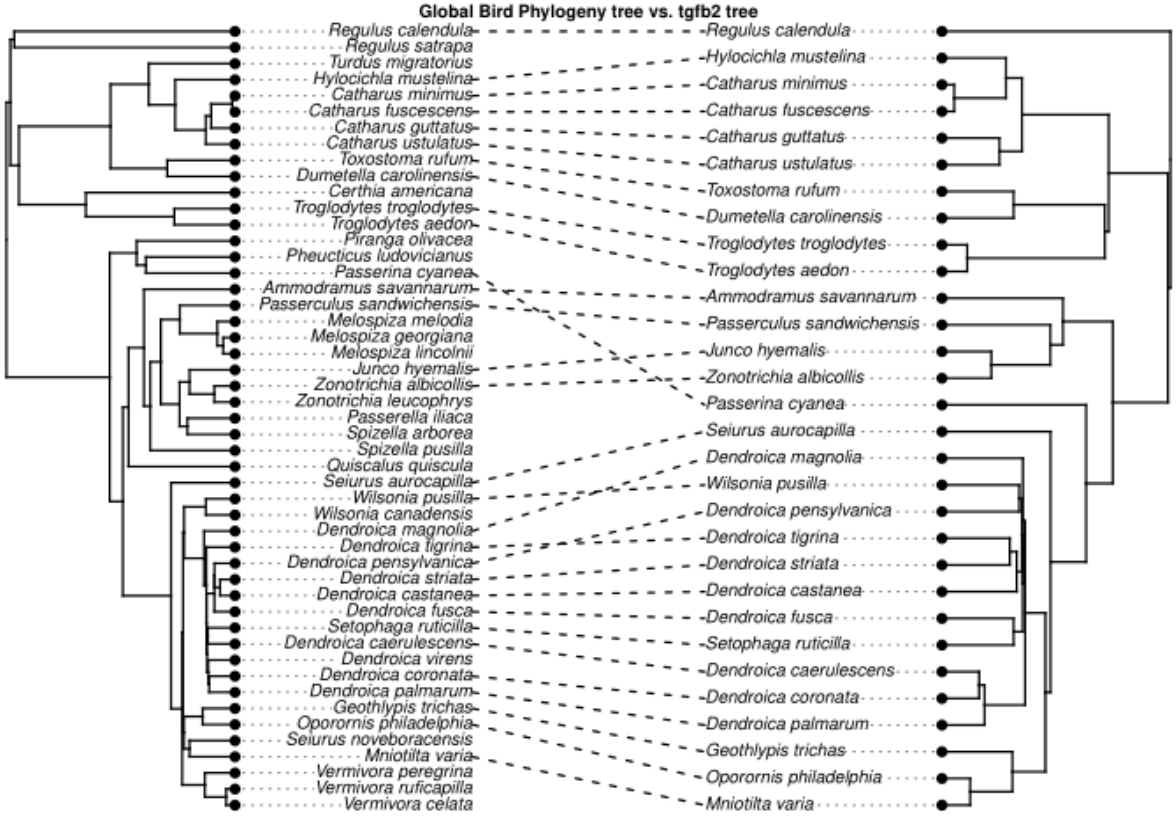
Fig S6


Global Bird Phylogeny tree vs. tgfb2 tree
Regulus calendula
Regulus satrapa
Turdus migratorius
Hylocichla mustelina
Catharus minimus
Catharus fuscescens
Catharus guttatus
Catharus ustulatus
Toxostoma rufum
Dumetella carolinensis
Certhia americana
Troglodytes troglodytes
Troglodytes aedon
Piranga olivacea
Pheucticus ludovicianus
Passerina cyanea
Ammodramus savannarum
Passerculus sandwichensis
Melospiza melodia
Melospiza georgiana
Melospiza lincolnii
Junco hyemalis
Zonotrichia albicollis
Zonotrichia leucophrys
Passerella iliaca
Spizella arborea
Spizella pusilla
Quiscalus quiscula
Seiurus aurocapilla
Wilsonia pusilla
Wilsonia canadensis
Dendroica magnolia
Dendroica tigrina
Dendroica pensylvanica
Dendroica striata
Dendroica castanea
Dendroica fusca
Setophaga ruticilla
Dendroica caerulescens
Dendroica virens
Dendroica coronata
Dendroica palmarum
Geothlypis trichas
Oporornis philadelphia
Seiurus noveboracensis
Mniotilta varia
Vermivora peregrina
Vermivora ruficapilla
Vermivora celata
Regulus calendula
Hylocichla mustelina
Catharus minimus
Catharus fuscescens
Catharus guttatus
Catharus ustulatus
Toxostoma rufum
Dumetella carolinensis
Troglodytes troglodytes
Troglodytes aedon
Ammodramus savannarum
Passerculus sandwichensis
Junco hyemalis
Zonotrichia albicollis
Passerina cyanea
Seiurus aurocapilla
Dendroica magnolia
Wilsonia pusilla
Dendroica pensylvanica
Dendroica tigrina
Dendroica striata
Dendroica castanea
Dendroica fusca
Setophaga ruticilla
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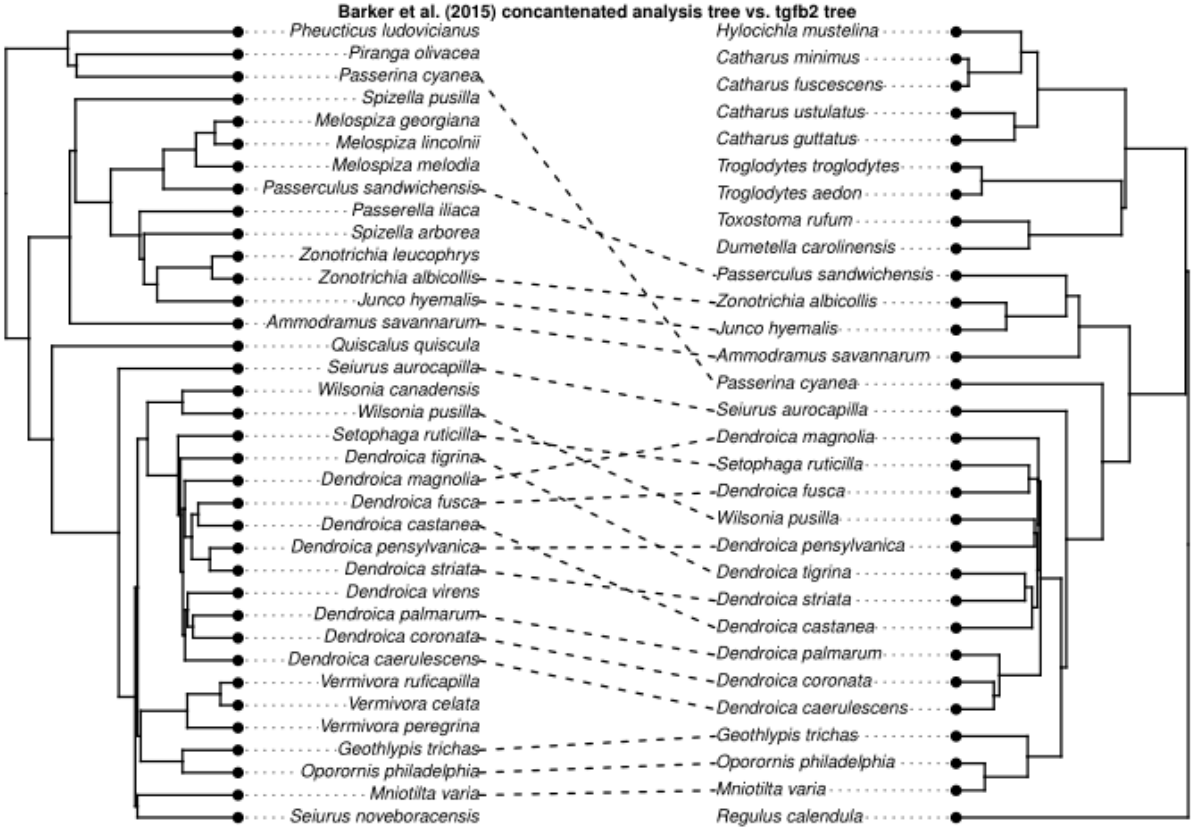
Dendroica coronata
Dendroica palmarum
Geothlypis trichas
Oporornis philadelphia
Mniotilta varia

Fig S7


Barker et al. (2015) concantenated analysis tree vs. tgfb2 tree
Pheucticus ludovicianus
Piranga olivacea
Passerina cyanea
Spizella pusilla
Melospiza georgiana
Melospiza lincolnii
Melospiza melodia
Passerculus sandwichensis
Passerella iliaca
Spizella arborea
Zonotrichia leucophrys
Zonotrichia albicollis
Junco hyemalis
Ammodramus savannarum
Quiscalus quiscula
Seiurus aurocapilla
Wilsonia canadensis
Wilsonia pusilla
Setophaga ruticilla
Dendroica tigrina
Dendroica magnolia
Dendroica fusca
Dendroica castanea
Dendroica pensylvanica
Dendroica striata
Dendroica virens
Dendroica palmarum
Dendroica coronata
Dendroica caerulescens
Vermivora ruficapilla
Vermivora celata
Vermivora peregrina
Geothlypis trichas
Oporornis philadelphia
Mniotilta varia
Seiurus noveboracensis
Hylocichla mustelina
Catharus minimus
Catharus fuscescens
Catharus ustulatus
Catharus guttatus
Troglodytes troglodytes
Troglodytes aedon
Toxostoma rufum
Dumetella carolinensis
Passerculus sandwichensis
Zonotrichia albicollis
Junco hyemalis
Ammodramus savannarum
Passerina cyanea
Seiurus aurocapilla
Dendroica magnolia
Setophaga ruticilla
Dendroica fusca
Wilsonia pusilla
Dendroica pensylvanica
Dendroica tigrina
Dendroica striata
Dendroica castanea
Dendroica palmarum
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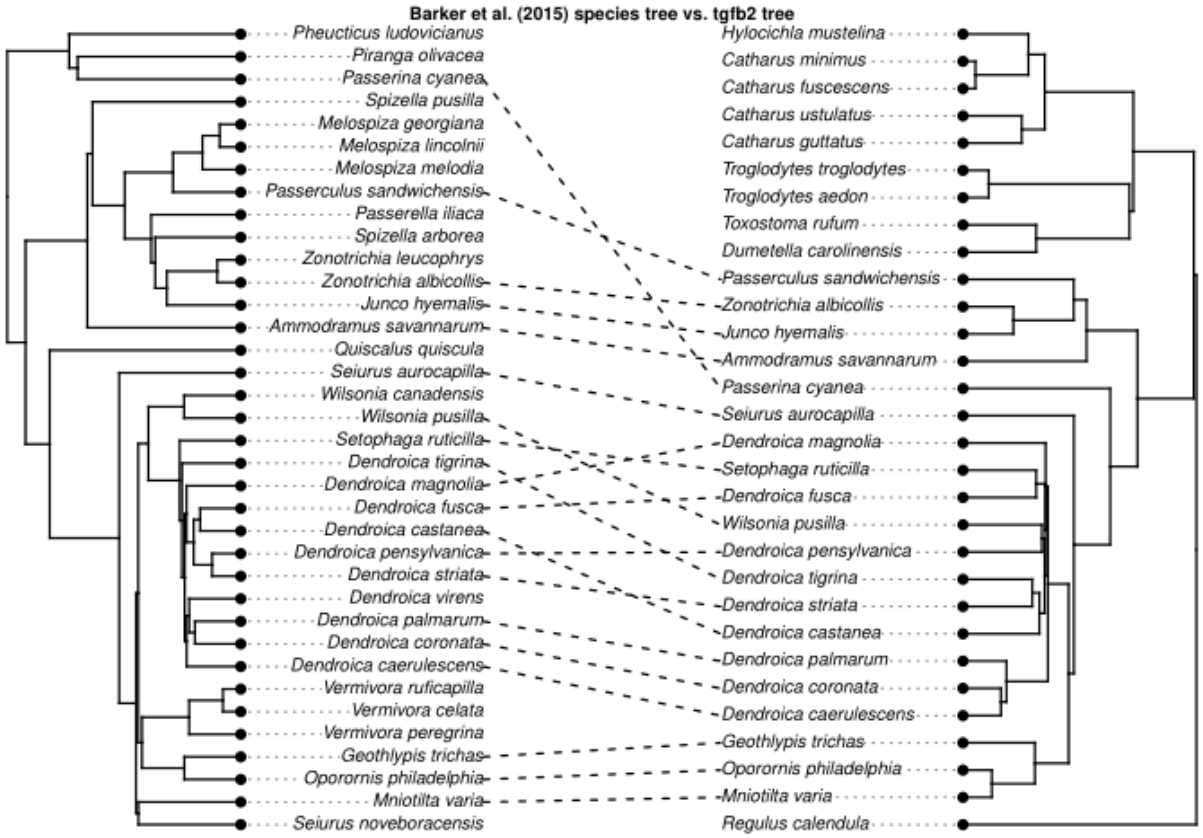
Dendroica caerulescens
Geothlypis trichas
Oporornis philadelphia
Mniotilta varia
Regulus calendula

631 Fig S8



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Appendix S3: Species level analysis of avian responses to climate change

In the main text we recreate Weeks *et al.*'s (2020) analysis, adding new variables and finding support for the idea that species with larger relative brain sizes have responded more slowly to the recent warming of their breeding grounds. Our main analyses maximize power by using individuals as the unit of observation while accounting statistically for phylogenetic non-independence among species and repeated measures within them. Here we present an alternative approach for the analysis of the same dataset, where every variable is summarized at the species level (N = 49).

Our species-level analysis involved two steps. First, we estimated the effect of breeding temperature on tarsus length in a mixed model with species-specific, random slopes for the effect of breeding temperature on tarsus length using "lmerTest" in R (Kuznetsova *et al.* 2017). The model also accounted for the main effects uncovered by Weeks *et al.* (2020) in their analyses (i.e., season, sex, and year) and was formulated as:

```
lmer(Tarsus~ year_scaled + breeding_temp_scaled+Sex + season +
(1+breeding_temp_scaled|phylo),data=full_data)
```

We then extracted the species-level random slopes from this first model and regressed them onto the species-level averages of relative brain size using phylogenetic regressions (Revell 2012). In this second step, we also considered the effects of the additional species-level covariates included in the main text: neutral substitution rate and relative lifespan. Multicollinearity among predictor variables was negligible as variance inflation factors were below 10.

Table 1

Coefficient table from model selection in second step

Parameter	Estimate	SE	t-value	P-value
Intercept	-0.018	0.005	-3.348	0.002
Neutral substitution rate	0.01	0.006	1.71	0.094
Relative brain size	0.02	0.007	2.846	0.007
Relative brain size x neutral substitution rate	0.029	0.009	3.135	0.003
Relative brain size x relative lifespan *	0.001	0.007	0.167	0.869
Relative brain size x relative lifespan x neutral substitution rate *	-0.001	0.009	-0.068	0.946
Relative lifespan	-0.009	0.006	-1.634	0.11
Relative lifespan x neutral substitution rate	-0.024	0.008	-2.947	0.005

* Denotes estimated effect the last time a parameter was included in a model before elimination during model selection

The new analyses confirm our findings in the main text: species with higher relative brain sizes have reduced their body sizes more slowly in response to warming temperatures on their breeding grounds (Estimate = 0.02 ± 0.007, t-value = 2.846, P-value = 0.007; Figure 1; Table 1). In this case, our model also detected a significant interaction between relative brain size and the neutral substitution rate (Estimate = 0.029 ± 0.009, t-value = 3.135, P-value = 0.003; Table 1),

indicating that the buffering effects of cognition on body size reduction are stronger in species with faster background rates of evolution.

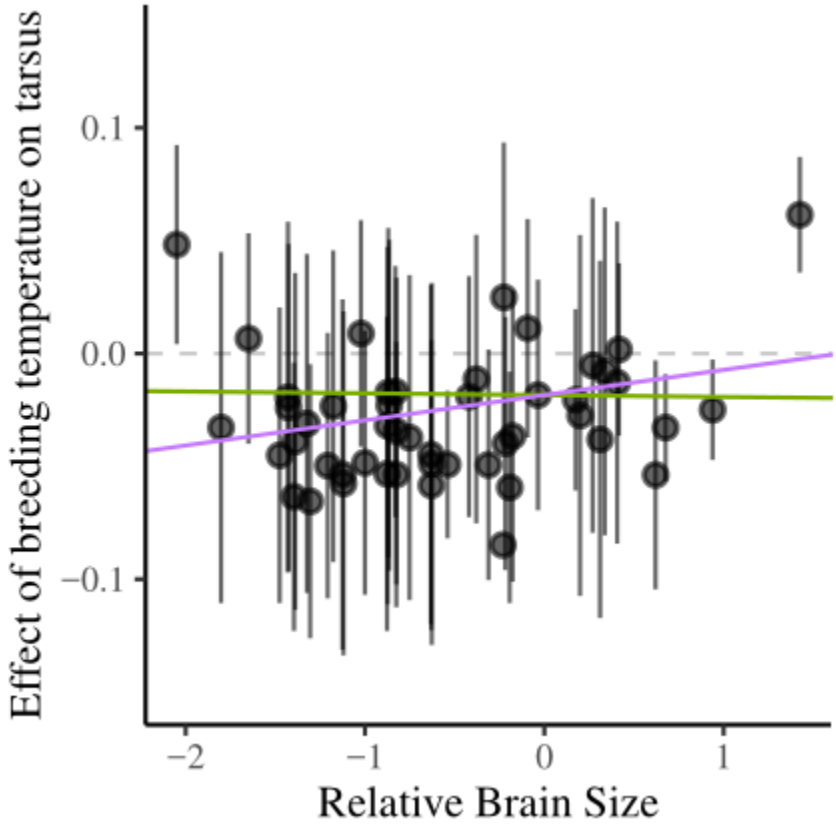

Figure 1. Effect of breeding temperature on body size as a function of relative brain size and neutral substitution rates. Model predictions for species with different levels of neutral substitution rates are depicted in purple (75th quartile) and green (25th quartile). Points depict species-specific slope estimates and vertical bars depict their 95% confidence intervals.

673 **References**

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