

## LETTER

# 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 behavioural 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 global change by actively buffering individuals from the environmental effects of warming temperatures.

**KEYWORDS**

birds, body size, brain size, climate change, cognitive buffer

**INTRODUCTION**

Anthropogenic climate change is resulting in rapid global warming and increasingly variable and unpredictable weather (National Academies of Sciences, 2016; Trenberth et al., 2015; 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 (Horton et al., 2020; Miller-Rushing et al., 2008) 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 (Bateman et al., 2020; Williams et al., 2008).

Behavioural 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 behaviour. It is, therefore, expected that species that possess a greater potential for behavioural 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, behavioural 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 (Jiménez-Ortega et al., 2020; Minias & Podlaszczuk, 2017), increased capacities to thrive in human-altered environments (Maklakov et al., 2011; Shultz et al., 2005) 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 behavioural 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 behavioural 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 behavioural flexibility (Figure 1). First, cognitive buffering could broaden fitness curves, leading to smaller fitness differentials and weaker incentives to alter the phenotype when climates change (Figure 1a). Second, behavioural flexibility could alter the balance of opposing forces in stabilizing selection and could thereby result in smaller peak shifts with climate change (Figure 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 behavioural 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.

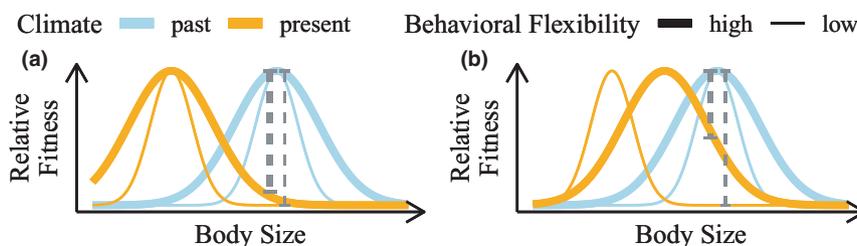
Because some of the observed recent changes in avian body size may be driven by natural selection, our analyses controlled for the effects of two well-known correlates of evolutionary rates: mutation rate (Uchimura et al., 2015) and generation time (Latta et al., 2013), respectively, estimated as neutral 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 Passeriformes 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 data set 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 & Arkin, 1997) and NASA's Normalized Difference Vegetation Index data set (NDVI3g) from the 'gimms' R package (Detsch, 2021; Pinzon & Tucker, 2014). Following Week's et al. (2020a), we selected June climate data from the breeding grounds and December climate data from the wintering grounds and calculated each species' climate values for each year separately (the 'time-lag 0' approach in Weeks et al., 2020b). The R code used to obtain and process yearly climate data is available in Appendix S1, section 1.



**FIGURE 1** Alternative mechanisms by which behavioural flexibility may alter selection gradients and weaken phenotypic responses to climate change. (a) Behavioural flexibility could broaden fitness curves through cognitive buffering (see main text), leading to a reduced fitness differential with climate change. Additionally, (b) behavioural 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 behavioural flexibility

We then collated brain size and body mass estimates from previous studies (Fristoe et al., 2017; Sayol et al., 2018, 2020) and added new brain size measurements for 27 species. When brain size data were available from multiple sources ( $N = 10$  species), we used sample-based weighted averages. New brain volumes were estimated similarly to previous studies (Lefebvre et al., 2004) by filling the brain cavity of museum specimens with 1-mm glass microballoons (GB 01, Conservation Resources UK Ltd.), weighing these microballoons on a digital scale with 0.01 gram precision, and converting their weights to volume given their known density. Our entire data set of brain sizes (49 species) is available in Data S1. Maximum lifespan data (1049 species total) were collated from the literature (Wasser & Sherman, 2010; Minias & Podlaszczuk, 2017; USGS, 2020; Data S2). We also recorded the provenance of lifespan estimates (wild or captive animal) for downstream analyses.

As a proxy for mutation rate, we computed substitution rates for intron 5 of the transforming growth factor beta-2 (*tgfb2*) gene, a putative neutral marker available in GenBank (Sayers et al., 2021) for most of the species included in this study. Sequences were obtained by BLASTing (BLASTN, Zhang et al., 2000) a complete sequence of the intron against the NCBI database (nucleotide collection), restricting the search to genera in our sample. Our BLAST 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 (Figures 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\_phyloIml()' 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 correlation coefficient: 0.742,  $p < 0.0001$ ), and the models including either lifespan or generation time yield qualitatively identical results (Appendix S2, section 4).

We assessed the neutrality of the *tgfb2* sequence alignment by computing Tajima's D (Tajima, 1989) and testing whether it differed significantly from zero with the *tajima.test* function in the R package *pegas* (Paradis, 2010). We used BEAST2 v2.5.2 (Bouckaert et al., 2014) to compute branch-specific relative substitution rates under an uncorrelated exponential molecular clock and Yule tree prior. We set a TN substitution model with empirical base frequencies and a Gamma distribution with four categories (the best supported model using ModelFinder as implemented in the server W-IQ-TREE, <http://iqtree.cibiv.univie.ac.at/>; Kalyaanamoorthy et al., 2017; Trifinopoulos et al., 2016). Our final analysis of substitution rates relied on two independent MCMC chains that ran for  $10^7$  generations with a thinning interval of 1000. After discarding the initial 10% of the generations as 'burn in' we computed a summary tree with the software TreeAnnotator (included in the package BEAST2) using the 'maximum credibility tree' as our target tree type (we also used this approach to compute a summary tree from the set of trees downloaded from the Global Bird Phylogeny, hereafter 'summary tree'). Moreover, we obtained a sample of 1000 trees from the posterior distribution to assess uncertainty in substitution rates. After observing satisfactory convergence with Tracer v1.7.1 (ESS values all  $>100$ ; Rambaut et al., 2018) and confirming that branch-specific substitution rates showed overlapping and unimodal peaks, we calculated their posterior medians and used these as taxon-specific estimates of substitution rates. These posterior medians (Figure S4) covered 31 of the 49 passerine species from Weeks et al. (2020b) and are available in Data S3.

We used Bayesian phylogenetic generalized linear mixed models in MCMCglmm (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) data set), 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; Lemaitre 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 behavioural 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 significant predictors remained (pMCMC < 0.05). On identifying the fully reduced model, we used it to jointly evaluate support for an interaction between neutral substitution rates and year on tarsus length (again, to account for the possibility that species with faster mutation rates could enable faster body size evolution). We assessed the significance of this term only after model reduction because data for neutral substitution rates were lacking for many species leading to significant data reduction ( $N_{\text{specimens}} = 12,385$ ,  $N_{\text{species}} = 31$ ). This interaction was nevertheless found not to be significant, so we report findings of the reduced model without it ( $N = 25,727$  specimens from 49 species).

To account for the effects of phylogenetic uncertainty in our analyses, we fitted two models (the log-log regression of brain mass on body mass and the fully reduced phylogenetic generalized linear mixed model) on a sample of 100 randomly selected trees from the posterior tree distribution with the Hackett backbone (Hackett et al., 2008; Jetz et al., 2012). Specifically, we computed residual brain sizes with a given tree and used them in the model of tarsus length while accounting for phylogenetic non-independence with the same tree. The 100 resulting models were then assembled into a pseudoposterior and summarized to obtain final coefficient estimates. We fitted four chains for each of these regression models with the ‘mcmcglmm’ package in R (Hadfield, 2010). Convergence was assessed with multichain convergence diagnostics (Gelman-Rubin statistics <1.1), confirming

high estimated sample sizes, and visualization of trace plots. Each mcmcglmm chain was run for 13,000 iterations, including a ‘burn in’ of 3000 and a thinning interval of 10. We used recommended vague priors on the random effects by choosing inverse Wishart distributions with  $\psi = 1$  and  $\nu = 0.02$  (Hadfield, 2010).

### 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;  $1.89 \pm 0.32$  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 ( $p = 0.07$ ; Figure S5). Additionally, the summary tree derived from the alignment of *tgfb2* was consistent with both the Global Bird Phylogeny (Figure S6) and previous phylogenetic studies based on multiple markers (Barker et al., 2015; Figures S7, S8). Neutral substitution rates extracted from the sample of 1000 trees ranged from 0.246 to 2.179 and showed significant variation among clades (Figure 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%

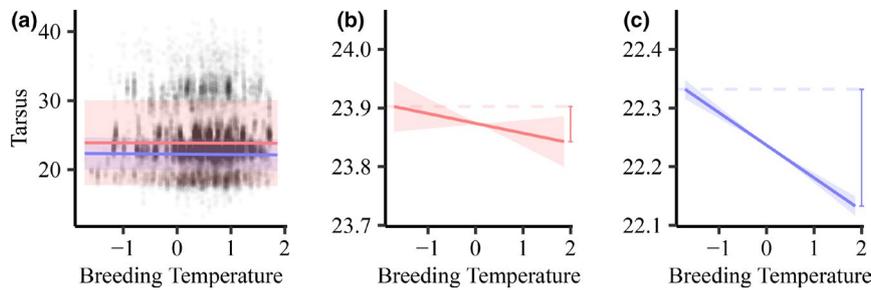
CI:  $-0.006$ – $0.026$ , pMCMC = 0.250; Table 1) or relative lifespan (relative lifespan x year:  $-0.0004$ , 95% CI:  $-0.010$ – $0.011$ , pMCMC = 0.970; Table 1). In support of the cognitive buffer hypothesis, we also found that the negative effects of breeding temperature were significantly weakened 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 (Figure 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 data set (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; Figure 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; Figure 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

**TABLE 1** 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 <sup>a</sup>	0.018	–0.010	0.045	0.212
Wintering temperature	0.030	0.019	0.040	0.001
Wintering precipitation <sup>a</sup>	0.014	–0.006	0.035	0.216
Wintering NDVI <sup>a</sup>	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 <sup>a</sup>	–0.0004	–0.010	0.011	0.970
Neutral substitution rate x year <sup>a</sup>	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

<sup>a</sup>Denotes effect estimate is from last time the effect featured in a model before elimination during model selection.



**FIGURE 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

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 data set, 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 behavioural 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 Andrew et al., 2017; Mariette & Buchanan, 2016). 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 behavioural 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 favoured 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 data set were about three times as large as those with largest brains (Figure 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 behavioural 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, although 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 5 (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 (Céspedes & Bayly, 2019; Gómez et al., 2014) 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 (National Academies of Sciences, 2016; Trenberth et al., 2015; 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 behavioural flexibility can reduce gradients of selection in evolution. Our findings also have practical implications for conservation (see Bateman et al., 2020; Foden et al., 2019), 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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## AUTHOR CONTRIBUTIONS

JWB conceived the study. All authors contributed to study design. JWB and JGP performed analyses. JGP

collected new brain size data and worked with sequence data. JWB wrote the first draft of the manuscript and all authors contributed substantially to revisions.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13971>.

## DATA AVAILABILITY STATEMENT

All data and code are provided as supporting information and are archived on Zenodo. <https://doi.org/10.5281/zenodo.5834578>.

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