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No evidence that warmer temperatures are associated with selection for smaller body sizes

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Reductions in animal body size over recent decades are often interpreted as an adaptive evolutionary response to climate warming. However, for reductions in size to reflect adaptive evolution, directional selection on body size within populations must have become negative, or, where already negative, more so, as temperatures increased. To test this hypothesis, we performed a meta-analysis of the association between annual estimates of directional selection on body size from wild populations and annual mean temperatures in 39 studies. We found no evidence that warmer environments were associated with selection for smaller size. Instead, selection consistently favoured larger individuals, and was invariant to temperature. These patterns were similar in ectotherms and endotherms. An analysis using year rather than temperature revealed similar patterns, suggesting no evidence that selection has changed over time, and also indicating that the lack of association with annual temperature was not an artefact of choosing an erroneous time window for aggregating the temperature data. Although phenotypic trends in size will be driven by a combination of genetic and environmental factors, our results suggest little evidence for a necessary ingredient—negative directional selection—for declines in body size to be considered an adaptive evolutionary response to changing selection pressures.

1. Introduction

It has been suggested that reductions in adult animal body size may be a general response of animal populations to global warming [1–3], and hence that ‘shrinking’ body size may be considered a third general response to climate change equivalent to changes in species distributions and phenology [4,5]. Although the evidence for consistent declines is not unequivocal [1,6], and other analyses have suggested no such general pattern exists [7,8], declines in body size have been reported in both ectotherms and endotherms, and across aquatic and terrestrial systems [1,2]. These declines in size are also apparent over both contemporary (recent decades [1,2]) and longer time scales (past tens of thousands of years; [9]).

Whether or not declines in body size are a general phenomenon, declines in size with warmer temperatures are often interpreted as an adaptive evolutionary response to a warming climate, presumably generated by changing selection pressures [6,10]. This inference typically stems from extension of the

64 biogeographic pattern known as Bergmann's rule [11], by
65 which, within a given clade, smaller species tend to be
66 found in warmer climates. For endotherms that maintain a
67 constant body temperature, this pattern may be an energeti-
68 cally based adaptive response to temperature because
69 smaller size results in a higher surface area to volume ratio,
70 improving heat loss in warmer conditions [11]. However,
71 the coupling of body size and temperature associated with
72 Bergmann's rule has been described for ectotherms as well
73 as endotherms [1,3]. Furthermore, numerous studies of
74 ectotherms have demonstrated genetic differentiation in
75 adult size among populations or congeneric species along
76 latitudinal and elevational gradients [12–16], suggesting
77 that the pattern may be the result of adaptive evolution for
78 ectotherms as well.

79 Phenotypic plasticity may also contribute to the bioge-
80 graphic pattern of smaller body sizes being found at
81 warmer temperatures. In ectotherms, for example, higher
82 temperatures during development typically lead to smaller
83 adult body size, an empirical pattern known as the tempera-
84 ture–size rule [17]. Recent work has also found that warmer
85 temperatures during development can lead to smaller body
86 size in endotherms, suggesting that temperature-dependent
87 developmental plasticity may be a general response to
88 warmer temperatures (e.g. [18]). The reasons for the observed
89 thermal plasticity in size, and its potential adaptive value,
90 remain poorly understood [19–23]. However, if smaller
91 body size has fitness advantages at higher temperatures,
92 temperature–size plasticity may represent adaptive variation
93 [22,24–28]. As a result, in general, it follows that for both
94 endotherms and ectotherms that thermal plasticity in body
95 size may be adaptive if smaller size is favoured at warmer
96 temperatures.

97 Any observed declines in adult size during recent climate
98 warming could therefore be due to adaptive evolution, to
99 adaptive or non-adaptive phenotypic plasticity or to a combi-
100 nation thereof, but the contributions of these mechanisms to
101 observed trends are currently unknown [6,10,29]. One diffi-
102 culty in invoking adaptive evolution as an explanation is
103 that few studies have both estimated selection and document-
104 ed that changes in body size through time are genetically
105 based [6,30,31]. Critically, however, if adaptive evolution in
106 response to warming environmental temperature is the mech-
107 anism resulting in reductions in body size, selection on body
108 size must become negative, or, where already negative, it
109 must have become more negative with increased tempera-
110 tures. The general applicability of this explanation can be
111 tested by comparing selection analyses across many popu-
112 lations. This test is now possible due to the availability of
113 numerous estimates of natural selection in the wild from con-
114 temporary populations [32–34], and the hard work of
115 quantifying selection and reporting these data in a standar-
116 dized format has made possible attempts at generalizing
117 patterns of selection [35–37]. Previous synthetic analyses
118 have shown that larger body size is associated with higher fit-
119 ness components in many organisms [38,39], but did not
120 consider whether environmental factors modulated this
121 relationship. Another analysis investigated whether climate
122 could explain spatial and temporal variation in selection
123 and found that while precipitation consistently explained
124 most variation in selection, variation in temperature did
125 explain variation in selection for some organisms, particu-
126 larly invertebrates [40]. However, that analysis did not

investigate the specific predictions concerning selection on
body size and temperature as outlined above.

Here, we tested the hypothesis that the direction and
magnitude of selection on body size in a population has
changed consistently with the temperature experienced by
that population. Specifically, we examined whether warmer
temperatures are associated with selection for smaller
body sizes, which would constitute a necessary—if far from
sufficient—component of the argument that adaptive evol-
utionary responses underlie declines in body size. We also
considered whether this relationship differs between
endothermic and ectothermic animals, and whether selection
on body size has simply changed over time, by considering
the relationship between estimates of selection and year.
We did so by combining published databases of estimates
of selection in the wild collated from longitudinal studies
where selection has been measured across two or more
years within a population, with annual temperature data
(as detailed in [38]). From these datasets, we built a meta-
analytical model that estimated the association between
temperature and selection on body size, while controlling
for the effects of sampling error and variation among species
and different studies.

2. Methods

(a) Selection database

We used a previously assembled database of temporally repli-
cated studies of phenotypic selection on quantitative traits from
wild populations, using studies where two or more annual esti-
mates of selection were available from a given population. Full
methods describing how the database was assembled are avail-
able in [40] and we refer the reader to that paper for additional
details. In brief, this database is from an exhaustive literature
review using a key-word search to identify studies (published
up until December 2012) that reported temporally replicated esti-
mates of natural selection from wild populations. We then
supplemented this database with results from a literature
search, using the same methodologies employed before, for
additional studies meeting the above criteria published up
until December 2018. No evidence of publication bias was
detected through inspection of funnel plots (electronic
supplementary material, figure S1).

The database consists of standardized measures of selection
coefficients: gradients and differentials. Selection gradients iden-
tify the strength and direction of direct selection acting on body
size after accounting for indirect selection via trait correlations,
whereas selection differentials reflect total selection (direct and
indirect). We do note that although selection gradients in prin-
ciple reflect the direct targets of selection, this is only the case
when all relevant traits have been included in the original anal-
yses. Thus, there is still likely an indirect component of
selection that exists in the estimated selection gradients, and
hence, the extent to which they predict the evolution of body
size. These standardized selection coefficients represent selection
on size in terms of the relationship between relative fitness and
variation in size measured in standard deviation units, and are
desirable because they allow for cross-study comparisons,
irrespective of study organism or fitness measure [32,41].

In order to test the implications of changing temperature for
patterns of selection on size, we only considered directional
selection. Thus, we only included those studies that quantified
selection on size-based traits, which included selection on overall
body size or mass, but also on components of size such as prin-
cipal component scores. These estimates came from studies

conducted between 1965 and 2016, the majority of which involve long-term studies of endotherms, particularly birds and mammals, and resulted in a total of 1595 estimates of selection gradients (from 23 studies) and 1181 estimates of selection differentials (from 16 studies; table 1) from a total of 32 species (electronic supplementary material, table S1).

(b) Temperature database

To relate the annual estimates of selection to temperature in the same year in the same geographical location for each study, we used a previously assembled climate database [40]. This climate database was subsequently updated to include temperature data for the additional selection studies uncovered in the new literature search. In brief, assembly of this database involved obtaining local temperature data at a resolution of $0.5 \times 0.5^\circ$ cells from the CRU-TS 3.1 (CRU-TS 4.02 for updated studies) Climate Database [42]. This is one of the finest scale climate databases available at a global scale and has been used for similar analyses [43,44]. From these data, we generated grid files containing annual mean temperature. To obtain appropriate temporal climatic information for each study location, we performed a spatial overlay of study site coordinates over each climatic grid using the function *over* in the R package *sp* [45]. We acknowledge that there may be very fine-scale local temperature variation within a 0.5° grid cell [46,47], but given the scale of the geographical and temporal variation in our datasets, these 0.5° grid cell annual estimates provide a manageable means of testing for broad-scale general patterns which will be relevant even if only indirectly linked [48]; we return to this point in the Discussion. All analyses used temperature values that were mean-centred within each study, so as to assess the impact of relative changes in temperature at each site.

We first verified that there was an increase in annual mean temperature over time within populations. We assessed this by using a mixed model, regressing temperature on year

$$t_{ij} = C + Dy_{ij} + c_j + d_j y_{ij} + e_{ij}, \quad (2.1)$$

where t_{ij} was the (mean-centred) temperature in interval i of study j . C and D are the fixed effect intercept and slope of the regression of temperature on year, y_{ij} is the year for interval i of study j , centred on the year 1990 (an arbitrarily defined mid-time point over the period of study in the database), c_j and d_j are study-specific random effects for the intercept and slope, respectively, and e_{ij} are residuals. This model estimates the variances of, and covariances between, the c_j and d_j terms, as well as the residual variance.

Results from this model showed that across studies reporting selection gradients, temperature has increased by $0.043^\circ\text{C yr}^{-1}$ (95% CI: 0.031, 0.057), and for studies reporting differentials, temperature has increased by $0.022^\circ\text{C yr}^{-1}$ (95% CI: 0.016, 0.027). Both the temporal and spatial span of studies presenting gradients or differentials differ, which we suspect explains the observed differences in the slopes. Regardless, annual mean temperature of the specific study sites associated with our selection estimates has increased through time, matching global patterns [49,50].

(c) Meta-analytical model

Though we also implemented a phylogenetically informed approach (see below and electronic supplementary material), we started with the simpler approach taken in [38], using a random effects hierarchical meta-analysis to estimate an overall slope of the relationship between the estimated selection coefficients and the respective temperature measure for each site at each time point, taking into account sampling error, and variation between species, between studies and within studies (as random effects). We also included a random regression term of

Table 1. Characteristics of the data analysed: number of datasets and number of estimates; mean and standard deviation (std.); median and range of the duration of studies; and the number of datasets, studies, species and number of estimates of selection coefficients for different taxonomic groups. (Note that a 'dataset' is defined as the set of selection estimates for a given phenotypic trait and fitness component for a given study, so a study may contain multiple datasets.) See also electronic supplementary material, table S1.

	selection gradients	selection differentials
number of datasets (total # estimates)	109 (1595)	83 (1181)
mean (std. dev.) of study duration, in years	13.6 (9.5)	13.9 (9.9)
median (range) of study duration, in years	12 (2–33)	12 (2–36)
taxonomic groups: # of datasets, studies, species and estimates		
amphibian	1, 1, 1, 3	1, 1, 1, 3
bird	59, 7, 7, 1333	43, 6, 6, 979
fish	12, 5, 4, 56	10, 3, 3, 54
insect	11, 3, 3, 39	15, 3, 3, 63
mammal	10, 4, 3, 124	10, 2, 2, 74
reptile	17, 4, 4, 40	4, 1, 1, 8

temperature within each study to model any variation between populations in the effect of temperature. This hierarchical model separates the observation process (i.e. modelling statistical noise in inference of individual selection coefficients stemming from sampling error) from a process model (i.e. modelling variation in the underlying (latent) selection coefficients in response to temperature, which is the biological process in which we are ultimately interested). Because sampling error can lead to erroneous inferences regarding variation in selection [35,36], we used only those estimates from the database that had associated standard errors. Additionally, even though the overall regressions in which we are interested are not strictly biased if sampling error is not accounted for [36], such regressions could be very sensitive to influential outliers [51]. Indeed, such outliers are common in databases of selection estimates (including those in the present analyses; cf. figures 1–3; electronic supplementary material, figures S2–S4), and it is almost always the case that outliers result from extremely low-powered studies (e.g. where n is especially small).

We modelled the distribution of estimated selection coefficients (linear gradients and differentials) according to

$$\beta_{ijk} = A + B.t_{ijk} + a_j + b_j.t_{ijk} + s_k + \epsilon_{ijk} + e_{ijk}, \quad (2.2)$$

where β_{ijk} is the i th selection gradient estimate for dataset j (that is, a given combination of phenotypic trait and/or fitness component and/or species, etc. for a given study; hereafter 'dataset') in species k . A and B are the fixed effect intercept and slope, respectively, of the regression of selection coefficients on (dataset centred) annual temperature values, t_{ijk} (note that these are the same as t_{ij} in equation (2.1), but for completeness here, we also index by k).

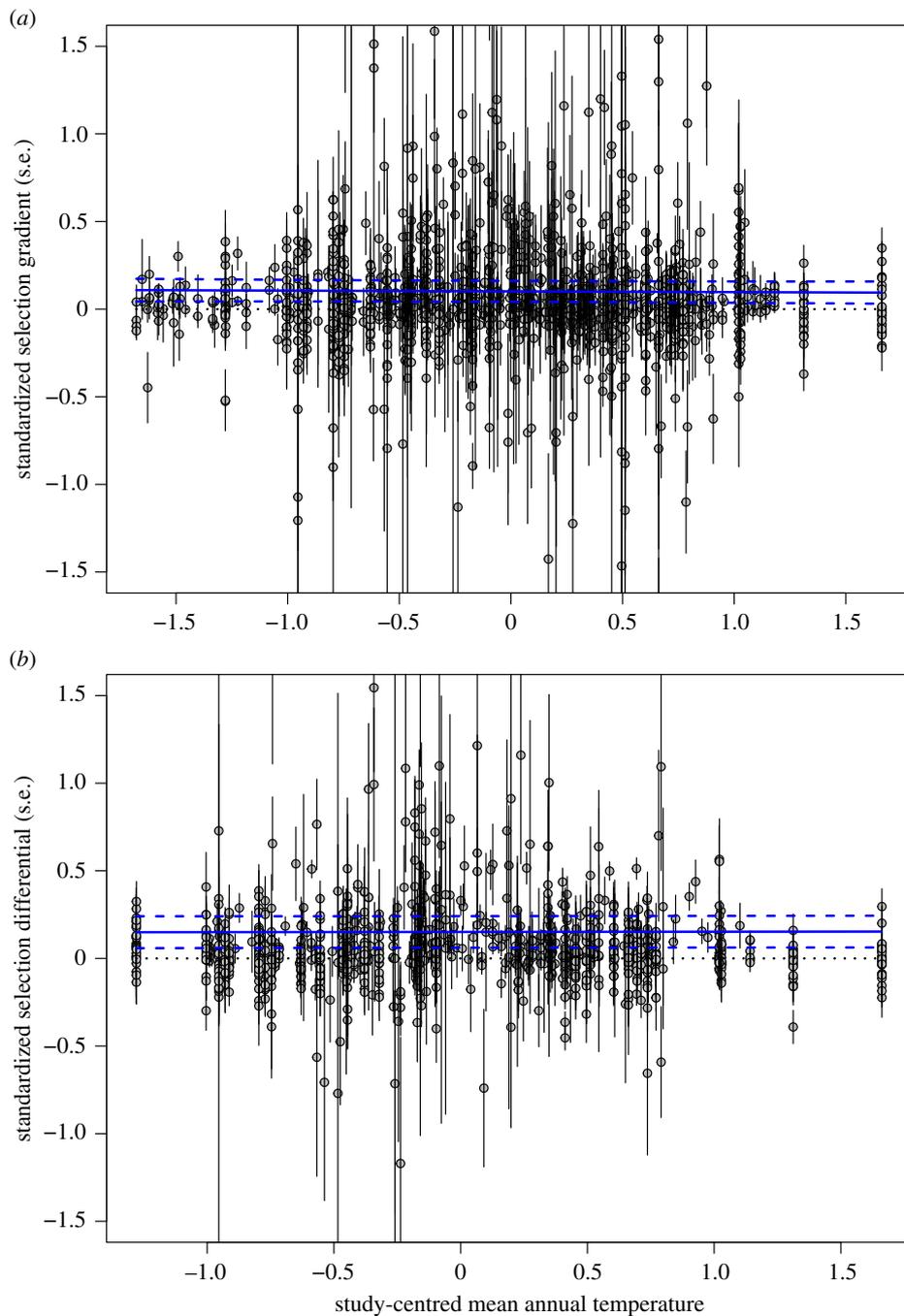


Figure 1. Warmer temperatures are not associated with selection for smaller body size in animals. The figure shows the relationship between standardized selection (a) gradients or (b) differentials (with error bars of s.e. for each estimate) on animal body size and study-centred annual mean temperature. The blue lines show the overall regression (solid blue line) from models 1 and 2 in table 2 along with the 95% prediction interval (dotted blue lines). The panels do not show outliers (estimated selection coefficients greater than 3.0, which were included in the analysis), which affects the scale on the figure; but see electronic supplementary material, figure S2 for the equivalent figure with all the data (note that all analyses used the full dataset). (Online version in colour.)

Q1

The model in (2.2) is a random effects meta-analytic model, but with a greatly elaborated treatment of heterogeneity, including a random effects structure to allow for variation among datasets in the relationship between selection coefficients and temperature. Thus, a_j is the intercept of dataset j and b_j the slope of the effect of temperature within dataset j , with variances and covariance modelled according to

$$\begin{bmatrix} a_j \\ b_j \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_a^2 & \sigma_{a,b} \\ \sigma_{a,b} & \sigma_b^2 \end{bmatrix}\right)$$

s_k are species-specific random intercepts distributed according to $s_k \sim N(0, \sigma_s^2)$, ϵ_{ijk} are measurement errors, with variances described by the reported standard errors for each estimate), $\epsilon_{ijk} \sim N(0, \text{s.e.}_{ijk}^2)$, and e_{ijk} are residuals distributed as

$e_{ijk} \sim N(0, \sigma_e^2)$. Note that the variances of measurement errors are defined by the published standard errors of the estimates, while the variances (σ_a^2 , σ_b^2) and covariance ($\sigma_{a,b}$) associated with the random slopes and intercepts, as well as the variances of species effects (σ_s^2) and residuals (σ_e^2), are estimated by the model.

This model structure is closely related to that used in [40], though the parameters of direct interest here are the fixed effects, and in particular, the overall regression coefficient B , and the model is presented in a more standard mixed-model framework. The models were fitted to different subsets of the database using the R package MCMCglmm [52], using diffuse Gaussian priors for fixed effects, diffuse inverse gamma priors for σ_c^2 and σ_e^2 and parameter expanded priors [53,54] for the covariances in the random regression component of the model. All statistics

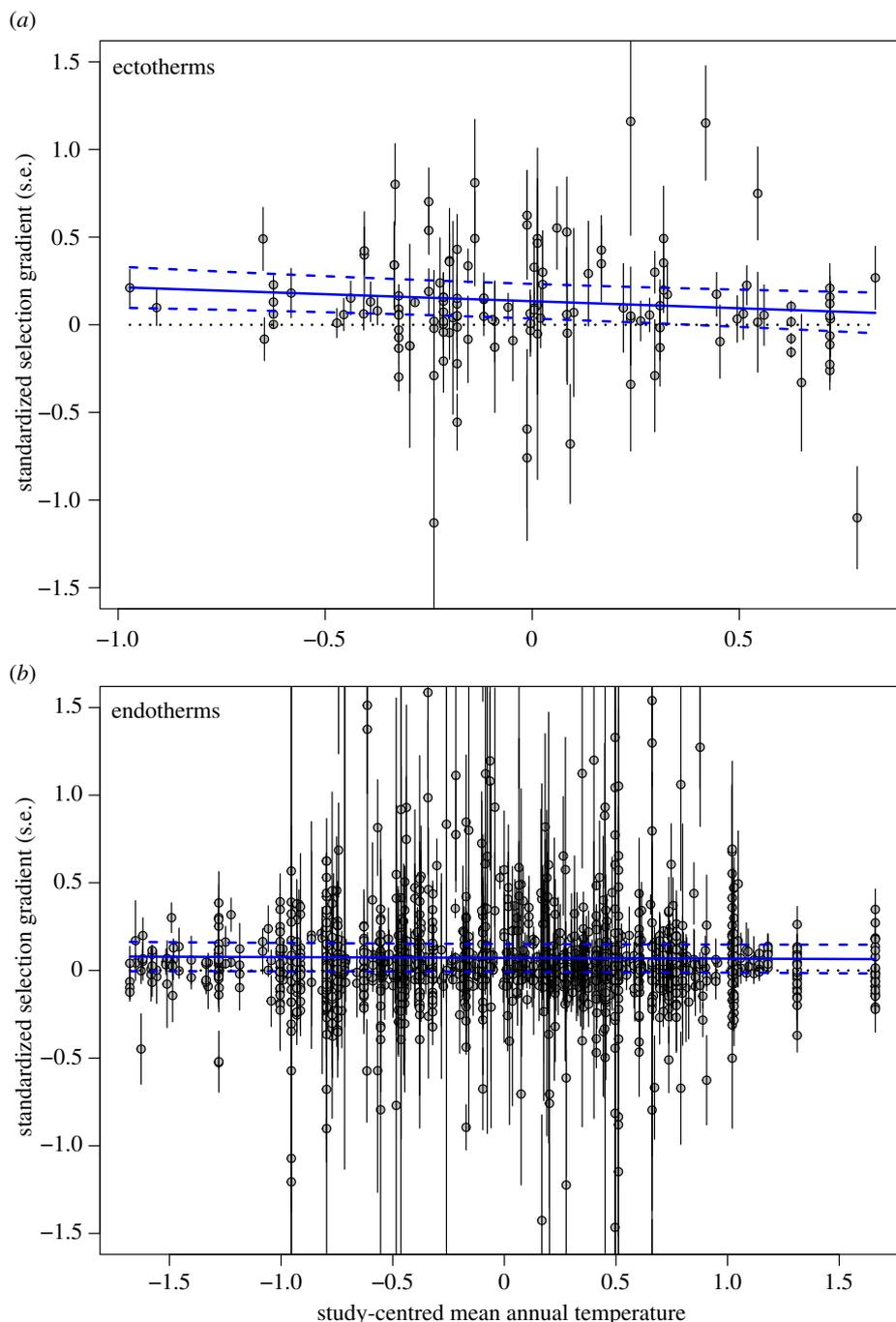


Figure 2. Warmer temperatures are not associated with selection for smaller body size in either (a) ectotherm or (b) endotherm animals. The figure shows the relationship between standardized selection gradients for (a) ectotherms or (b) endotherms (with error bars of s.e. for each estimate) and study-centred annual mean temperature. The blue lines show the overall regression (solid blue line) from models 3 and 4 in table 2 along with the 95% prediction interval (dotted blue lines). The panels do not show outliers (estimated selection coefficients greater than 3.0, which were included in the analysis), which affects the scale on the figure; but see Q1 electronic supplementary material, figure S3 for the equivalent figure with all the data (note that all analyses used the full dataset). (Online version in colour.)

reported are means of the posterior distribution, with associated 95% credible intervals (CIs). We note that considering modes rather than means gave identical conclusions. The models were run on the dataset of gradients (model 1 in Results) and differentials (model 2 in Results). As an index of heterogeneity, the variance components associated with the random effect terms are presented in electronic supplementary material, table S2.

In addition, for this main analysis of interest, we also performed a full phylogenetic random regression meta-analytical model (see electronic supplementary material). Because we did not detect a phylogenetic signal in either the intercepts or slopes from these models, we present the simpler models in the main text and place these more complicated phylogenetically informed models in the electronic supplementary material

table S3. The conclusions regarding the fixed effects remained the same across all models.

To explore potential differences in selection between ectotherms and endotherms, we also built models (models 3 and 4) that evaluated whether or not there were differences in the mean selection coefficients in the two groups, and in their relationship with temperature. We did so by including a two-level factor for group (endotherm versus ectotherm), and its interaction with the effect of mean-centred temperature in model 1. We restricted this analysis to selection gradients, because sample sizes of selection differentials for endotherms were insufficient.

Finally, the above analyses modelled the relationship between estimates of directional selection on size and annual

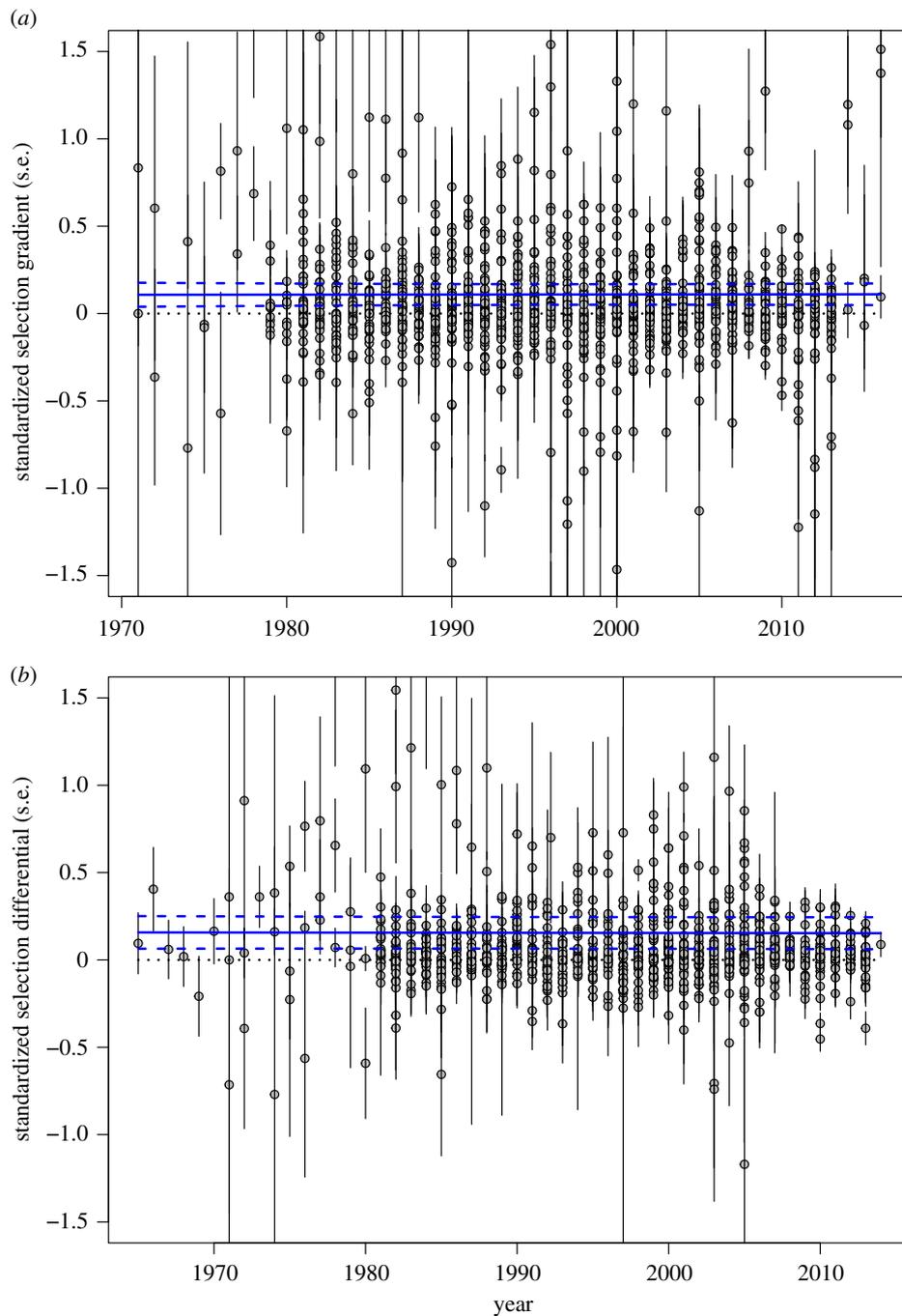


Figure 3. Directional selection on body size did not consistently change over the 46-year period of record. The figures show the relationship between standardized selection (a) gradients or (b) differentials (with error bars of s.e. for each estimate) and the year selection was estimated. The blue lines show the overall regression (solid blue line) from models 5 and 6 in table 2 along with the 95% prediction interval (dotted blue lines). The fixed slope in this random regression model simply reflects the average within-study slope, and thus reflects a hypothetical study spanning the entire time range. The panels do not show outliers (estimated selection coefficients greater than 3.0, which were included in the analysis), which affects the scale on the figure; but see electronic supplementary material, figure S4 for the Q1 equivalent figure with all the data (note that all analyses used the full dataset). (Online version in colour.)

mean temperature in their respective year, and as such represent the most general test of selection–temperature relationships. However, it is plausible that annual mean temperature may not be the most critical thermal window shaping selection, assuming such a window exists. For example, an intra-annual component of temperature, such as variance in temperature, or a measure of extremes such as mean daily maximum temperature, may be more relevant (although our previous analyses show that annual mean temperature and maximal temperature are positively correlated across the study sites [40]). Because of these issues, we also performed an analysis that tested for evidence that selection simply changes over time. This was accomplished by investigating the relationship between estimates of selection and year of study (models 5 and 6). We fit models using the

year of the study rather than temperature in models 1 and 2 outlined above (i.e. we replace t_{ijk} with year terms y_{ijk} where year values were mean-centred on an arbitrary time point of 1990). Of course, any of a number of factors that might drive selection could vary with time in such an analysis. However, this analysis should be able to detect whether selective regimes have changed over time, regardless of the relevant thermal window.

3. Results

Our meta-analysis of patterns of selection on body size showed overall positive directional selection on body size, both for selection gradients (figure 1a) and selection

Table 2. Results from the meta-analytical models relating annual selection coefficients to temperature or year. Shown are the posterior means for the intercepts (*A*) and slopes (*B*) and their 95% credible intervals when selection on body size was regressed on mean annual temperature (models 1–4) or year (models 5 and 6). Separate models for temperature–selection gradient relationships are presented for ectotherms (model 3) and endotherms (model 4). Details of the variance components for models 1 and 2 are given in electronic supplementary material, table S2.

model	intercept		slope	
	<i>A</i>	95% CI	<i>B</i>	95% CI
<i>temperature as predictor</i>				
model 1: gradients	0.108	0.051, 0.168	−0.004	−0.020, 0.009
model 2: differentials	0.156	0.073, 0.254	−0.0002	−0.009, 0.008
model 3: gradients, ectotherms	0.147	0.044, 0.238	−0.060	−0.130, 0.011
model 4: gradients, endotherms	0.070	−0.005, 0.152	−0.0008	−0.014, 0.013
<i>year as predictor</i>				
model 5: gradients	0.108	0.04, 0.17	0.00007	−0.0011, 0.0011
model 6: differentials	0.157	0.072, 0.247	−0.0002	−0.0008, 0.0005

differentials (figure 1*b*). There was no evidence for change in either selection gradients or selection differentials with increasing temperature (figure 1 and table 2: models 1 and 2, respectively; electronic supplementary material, table S2), and in particular no indication that selection favoured smaller body sizes at higher temperatures (i.e. no evidence that selection became negative or more negative; figure 1). Including phylogeny in this model did not qualitatively change these findings: there was no indication of an effect of temperature on selection coefficients in the phylogenetic models, nor was there support for a phylogenetic component to the species effect (electronic supplementary material, table S3).

We next considered a model that allowed different intercepts and slopes for ectothermic and endothermic taxonomic groups to the basic model specified by equation (2.2). The average selection gradient did not differ between ectotherms and endotherms (endotherm intercept – ectotherm intercept = −0.083, 95% CI: −0.192, 0.026), and there was no difference between the two groups in the slope of the relationship between selection gradients and temperature (endotherm slope – ectotherm slope: 0.064; 95% CI: −0.018, 0.131). For completeness, we subsequently ran two separate models for ectotherms and endotherms (table 2: models 3 and 4, respectively), to generate group-specific slopes and intercepts, rather than contrasts, and again detected no relationship between selection on size and temperature among ectotherms (figure 2*a*) or endotherms (figure 2*b* and table 2).

Finally, we found no evidence of any association between directional selection on body size and year for either selection gradients (figure 3*a* and table 2: model 5) or selection differentials (figure 3*b* and table 2: model 6). That is, there was no evidence that the strength or direction of selection on body size changed over time.

4. Discussion

Our analyses of contemporary patterns of selection on animal body size documented over the past several decades showed no evidence of any association between temperature increases and selection for reductions in body size. In fact, selection on

body size has remained consistently positive. These patterns suggest that selection for smaller body size is not a general phenomenon, and hence that adaptive evolutionary responses to changed selection pressures imposed by a warming climate, as would have been expected under Bergmann's rule, is unlikely to be a general explanation for recent declines in body size where they have occurred. While it is tantalizing to consider that large-scale biogeographic rules might explain contemporary patterns of body size change (e.g. a temporal Bergmann cline; [7]), our results suggest caution is warranted in deriving contemporary predictions from such rules. Our results are consistent with a recent qualitative review that found little evidence for adaptive body size reductions with climate warming [6], as well as a recent analysis of 952 bird and mammal species that found little support for consistent declines in body size among populations that varied in temperature [7]. Although evidence for adaptive evolutionary responses will ultimately require genetic as well as phenotypic data, we can still infer these that evolutionary responses are unlikely to be a ubiquitous pressure towards shrinking body size, because adaptive evolution requires both selection in the appropriate direction and genetic variation in body size.

Of course, the expression of genetic variation is also not necessarily fixed and may vary with environmental conditions through time. However, few studies have assessed how temperature may affect the expression of genetic variance underlying traits. The majority of these studies are laboratory-based, and have suggested that temperature can generate differences in expressed genetic variation—although these generalities are not specific to body size [55]. Moreover, to date, evidence for genotype–environment interactions affecting heritable traits in wild populations is mixed (see review in [52,53]). Most importantly, changes in the expression of genetic variation in response to environmental variation are unlikely to affect the direction of adaptive evolution through time, at least over shorter-term time scales considered here, underlining the requirement for selection pressures to act in the appropriate direction if adaptive reductions in body size are to be considered a general phenomenon.

Overall, the modest slopes of the regressions of selection coefficients on temperature, relative to the positive intercepts, mean that directional selection on body size was on average positive. This result is consistent with previous comparative analyses of directional selection on body size in animals [19,39]. We also found selection to be invariant in response to temperature or year. Extrapolating (excessively) from the meta-analytical model, the trend present in the fixed regression for selection coefficients predicts an eventual shift towards selection for smaller body sizes (i.e. negative values), particularly for ectotherms. Thus, with continued temperature increases, there may be an eventual reduction in the strength of directional selection that currently, on average, favours larger-bodied individuals. However, as with any statistical model, an abundance of caution is warranted in extrapolating beyond the available data. Nevertheless, the predicted increases in temperature over the next several decades [49], along with sustained efforts to maintain long-term studies of selection in the wild [54], will provide an opportunity to evaluate this hypothesis.

The interaction between temperature, body size and fitness that would underlie Bergmann's rule requires that the slope of the relationship between expected absolute fitness and body size is more negative at high temperatures, but positive at low temperatures. However, it is worth noting that the summary statistics by which the form of directional selection is typically reported—selection gradients and differentials—can change in value between different replicate estimates of selection, because of changes to various aspects of the trait-fitness relationship other than its slope; e.g. changes to the distribution of phenotypes [56,57]. Consider a population at a selective optimum, such that its mean body size is at an optimum in the body size-fitness function. Imagine that, due to phenotypic plasticity, an increase in temperature causes a decrease in mean body size (e.g. according to the temperature-size rule for ectotherms, or as recently found in endotherms [18]). In the absence of any effects of temperature on the fitness function, the population will now experience directional selection for larger body size, because most phenotypes will now be in an area of the fitness function that is positively sloped, on average. Such a mechanism would mask, or reduce in magnitude, any pattern of interaction between temperature, body size and fitness that would generate a temporal Bergmann pattern. Unfortunately, most studies of phenotypic selection on body size do not report mean size, so we are unable to evaluate this possibility with the available database. Future studies addressing biogeographic patterns of body size and selection would benefit greatly if summary statistics about trait distributions and absolute fitness were regularly reported.

Although the emerging general pattern may be for no decline in animal body size [6–8], and our analyses found no evidence that selection on body size has changed over the past approximately 5 decades, there are examples where body size has declined through time as environments have warmed; some of these responses may have been adaptive [1,6]. However, for reasons that frequently hamper attempts to infer adaptive evolutionary responses, it is often unclear if these changes necessarily represent adaptive evolution. To our knowledge, only four longer-term studies have directly investigated the role of adaptive evolution as an explanation for contemporary declines in body size [29,58–

60]. These studies all used breeding values (i.e. estimates of individuals' additive genetic merit for body size): three of the four found no evidence of selection for smaller body sizes, nor of a genetic basis for observed size changes [29,58,59], whereas Bonnet *et al.* [60] found that, despite a positive phenotypic association between body size in snow voles and fitness, there was evidence of a genetic change towards smaller body size. The latter indicates an adaptive evolutionary response to viability selection, perhaps driven by changes in the snow-free season favouring juveniles that become small adults [60]. Importantly, these latter results show that the adaptive evolutionary response towards smaller size and the selection pressures driving it were not apparent from phenotypic data alone, because they were masked by plasticity and a non-genetic positive association between body size and viability, respectively [60]. Understanding both the environmental factors generating selection and the potential for evolutionary responses to changing climate remains an important endeavour.

Such findings suggest that explorations of alternative explanations for temporal trends in body size are warranted [31]. For instance, it may be that the observed declines in body size in some populations, especially among endotherms, might be driven by phenotypic plasticity in response to altered environmental conditions that affect growth rates, such as food availability [1,6,29]. As noted by Teplitsky *et al.* [29], such reductions in body size might therefore be a foreboding signal of populations experiencing increasingly deteriorating conditions, rather than examples of adaptive evolutionary rescue in response to a changing climate. Recent experimental work has also shown that reductions in body size in birds in warmer environments can be explained by phenotypic plasticity in growth (e.g. climate-dependent developmental plasticity) in response to temperature during development, even in the absence of changes in food availability [18]. Clearly, a better understanding of how temperature-size patterns emerge and the genetic basis for them are necessary, especially studies investigating the mechanistic basis of these associations [28]. Finally, changes in body size in relation to temperature might also vary among taxonomic groups, and therefore may not be a universal pattern [1]. For instance, Teplitsky & Millien [6] found that although declines in body size with temperature in birds were common, this pattern was rare among mammals. While it would be interesting to examine if associations between selection and temperature differ among these two groups, there are currently too few data for a robust analysis.

Despite using the most comprehensive datasets of selection and climate available, our study is not without limitations. Two caveats in particular may affect our ability to detect a possible association between selection on body size and temperature. First, annual mean temperatures may not always represent the critical thermal window that could generate an association between selection on body size and temperature. For example, selection on body size might occur via extreme thermal events that occur over a brief time window [61–63], even if they do not substantially shift annual mean temperature. A population might be reasonably well adapted to a given temperature regime, such that even a single episode of extreme temperatures might generate very strong selection [62]. These potential episodic bouts of selection may be major drivers of evolutionary change [63,64], but

505 may be difficult to observe, even among longer-term datasets
 506 [8,65,66]. Importantly, however, our analyses demonstrating
 507 stasis in selection coefficients across years (figure 3) suggest
 508 that there was no hidden temperature–selection relationship
 509 that would be revealed by some alternate choice of a thermal
 510 window. Indeed, identifying more precisely how climate
 511 might influence the dynamics of natural selection in wild
 512 populations remains a challenge [6,40]. This is one issue
 513 with meta-analytical studies such as ours that are conducted
 514 across disparate studies where it is unclear what the critical
 515 thermal window may be [40,47,48]. To the best of our knowl-
 516 edge, none of the studies in our database were designed
 517 specifically to examine any possible association between
 518 selection and temperature. On the one hand, this is a limit-
 519 ation, as above. On the other hand, it also reduces bias in
 520 our dataset, in that there should be no ‘file-drawer effect’
 521 (that is, underrepresentation of studies exhibiting no relation-
 522 ship between temperature and selection).

523 A second caveat arises from the fact that most studies of
 524 selection on body size typically extend over a few years,
 525 whereas many of the studies of body size trends span several
 526 decades [1,6,8]. Because changes in average temperature
 527 through time are subtle, it may be that longer-term datasets
 528 are the most informative for detecting the overall magnitude
 529 of these associations. However, even relatively short-term
 530 datasets remain valuable in detecting temperature–selection
 531 couplings, because the general expectation is simply that
 532 declines in body size through time are linear. Thus, even
 533 short-term data sets from temporally replicated studies of
 534 selection in wild populations should not preclude our ability
 535 to detect selection–climate associations, as we have
 536 previously found [40].

538 5. Conclusion

539 Overall, based on (i) our analyses finding that selection on
 540 body size has not consistently changed with temperature or
 541 time and (ii) recent comprehensive analyses of body size in

relation to temperature and time showing that body sizes
 are not uniformly declining [6–8], we find little support for
 the idea that increasing global temperatures are resulting in
 widespread adaptive evolutionary shifts towards smaller
 body size. Whether and how the long-term impacts of a
 warming climate—and changes in other climate components
 such as precipitation regimes—will generate adaptive
 responses thus remains unclear. Studies of selection and the
 genetic underpinnings of adaptive evolutionary responses
 in wild populations will continue to be of considerable
 value in understanding how adaptive evolution may play a
 role in allowing populations to persist or perish in the face
 of a changing climate.

Data accessibility. All data and code used in analyses are available from the Dryad Digital Repository at: <https://doi.org/10.5061/dryad.7md1755> [67].

Authors' contributions. L.E.B.K. and K.D.W. came up with the original idea followed by refinement by all authors, especially J.G.K.; M.B.M. developed analytical approaches and M.B.M., A.M.S. and L.E.B.K. analysed the data; C.D.F. assembled climate data; K.D.W. directed assembly of the phylogeny; A.M.S. and S.M.C. lead development of the selection database; A.M.S. drafted the ms and all authors contributed to the writing.

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