Decreases in beetle body size linked to climate change and warming temperatures

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Abstract

1. Body size is a fundamental ecological trait and is correlated with population dynamics, community structure and function, and ecosystem fluxes. Laboratory data from broad taxonomic groups suggest that a widespread response to a warming world may be an overall decrease in organism body size. However, given the myriad of biotic and abiotic factors that can also influence organism body size in the wild, it is unclear whether results from these laboratory assays hold in nature.

2. Here we use datasets spanning 30 to 100 years to examine whether the body size of wild-caught beetles has changed over time, whether body size changes are correlated with increased temperatures, and we frame these results using predictions derived from a quantitative review of laboratory responses of 22 beetle species to temperature.

3. We found that 95% of laboratory-reared beetles decreased in size with increased rearing temperature, with larger-bodied species shrinking disproportionately more than smaller-bodied beetles. In addition, the museum datasets revealed that larger-bodied beetle species have decreased in size over time, that mean beetle body size explains much of the interspecific variation in beetle responses to temperature, and that long-term beetle size changes are explained by increases in autumn temperature and decreases in spring temperature in this region.

4. Our data demonstrate that the relationship between body size and temperature of wild-caught beetles matches relatively well with results from laboratory studies, and that variation in this relationship is largely explained by interspecific variation in mean beetle body size.

5. This long-term beetle dataset is one of the most comprehensive arthropod body size datasets compiled to date, it improves predictions regarding the shrinking of organisms with global climate change, and together with the meta-analysis data, call for new hypotheses to explain why larger-bodied organisms may be more sensitive to temperature.

KEYWORDS

body size, carabidae, climate change, coleoptera, museum, temperature–size rule

†These authors contributed equally.
1 | INTRODUCTION

Organism body size is a fundamental trait in ecology (Calder, 1996; Kingsolver & Huey, 2008; Peters, 1983). Body size is correlated with ecological processes across multiple scales, including individual fecundity (Honěk, 1993), population biology (Siemann, Tilman, & Haarstad, 1996; White, Ernest, Kerkhoff, & Enquist, 2007), disease transmission (Russell et al., 2011), food web structuring (DeLong et al., 2015; Griffiths, 1986) and ecosystem services (Baudron, Needle, Rijnsdorp, & Tara Marshall, 2014; Sheridan & Bickford, 2011). Understanding variation in body size thus informs both fundamental and applied ecological research.

Many laboratory studies have shown that temperature mediates organism body size (Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011). The phenotypically plastic decrease in body size at warmer rearing temperatures is known as the temperature–size rule (TSR; Atkinson, 1996). The TSR is based on observations from controlled laboratory studies, and is one of the most taxonomically widespread patterns in biology (Angilletta, Steury, & Sears, 2004; Atkinson, 1994; Atkinson & Sibly, 1997).

Despite a century of data supporting the TSR, whether temperature explains long-term trends in organism body size in nature is unknown. Given the myriad of biotic and abiotic factors that mediate organism body size in nature, one might expect that the effect of temperature in the wild is not as pronounced as it is in the laboratory. In their recent reviews of the effects of temperature on body size, both Gardner et al. (2011), and Sheridan and Bickford (2011), stress the importance of using of natural history or museum collections to inform whether organisms in nature are in fact responding as predicted by laboratory assays. In this study, we use long-term museum collections to investigate the effect of temperature, as well as other climate-related variables, on the body size of beetles, one of the most diverse and widespread orders of the animal kingdom (New, 2007). Additionally, we frame these data using a quantitative synthesis of short-term laboratory assays of the response of 22 beetle species to temperature.

Atkinson (1994) reviewed published studies of the effect of temperature on organism body size (primarily laboratory-reared) and reported that out of 109 studies reviewed, 83.5% of taxa, including animals, plants, protists and bacteria, showed a reduced size at a given stage of development when grown at elevated temperature. Recent syntheses on the response of arthropods to increased temperature have further confirmed the widespread nature of the TSR, and these studies have also begun to document taxa- or environment-specific TSR patterns. For example, aquatic invertebrates appear to show a greater response to temperature compared with terrestrial invertebrates, and within aquatic invertebrates, larger-bodied species tend to shrink disproportionately more than smaller-bodied species when reared at warmer temperatures (Forster, Hirst, & Atkinson, 2012; Horne, Hirst, & Atkinson, 2015; Horne, Hirst, Atkinson, Neves, & Kiarboe, 2016). This pattern could perhaps be due to the ‘oxygen hypothesis’, which posits that there is a greater cost for larger organisms to uptake oxygen in warmer water (Forster et al., 2012; Horne et al., 2015; Woods, 1999). Terrestrial species appear not to exhibit this same pattern (Horne et al., 2015), but this result was based on analysis of a limited number of species and may change as more species are examined.

To contribute to this field, here we (1) compiled perhaps one of the most comprehensive body size–temperature datasets (in terms of duration, sample size and species number) on a wild-caught taxon (Coleoptera: Carabidae), and used this large dataset to ask whether the TSR and/or climate can explain decadal variation in beetle body size. Concurrently, we conducted (2) a quantitative synthesis of published laboratory studies to address whether the beetle body size responses in nature (part a) are similar to the declines observed in laboratory-reared beetles. Lastly, we (3) examine whether decadal variation in beetle body size reflects ongoing gradual increases in global temperature, in a manner predicted by the TSR. Given the high prevalence of TSR in laboratory settings, we expected to see a strong effect of temperature on body size across published laboratory studies. However, because many other potential stressors likely affect beetle body size in nature, we expected temperature to explain a small component of body size variation in wild-caught beetles. Understanding whether body size variation, as predicted by the TSR, can be extended to wild-caught organisms over long time-scales is especially relevant given ongoing rapid changes in regional and global climate (Sheridan & Bickford, 2011). Finally, beetles represent a significant fraction of global animal biodiversity (New, 2007); thus understanding whether temperature and other climate variables can explain variation in beetle body size can also enhance predictions of how the ecological functioning of beetles and other arthropods, may shift with ongoing temperature change.

2 | MATERIALS AND METHODS

2.1 | Study organisms

There are more than 350,000 described species of beetles (Insecta: Coleoptera), making them one of the most diverse groups of animals on the planet (New, 2007). Not surprisingly, beetles are found in almost every ecosystem, and play diverse ecological roles, ranging from ecosystem engineers (e.g. mountain pine beetle; Gurney & Lawton, 1996), to biological control agents (e.g. Larinus sp. on knapweed; Myers, Jackson, Quinn, White, & Cory, 2009), to global invaders (e.g. harlequin ladybird; Roy et al., 2016). The Carabidae, the family for which we have up to 100 years of museum collections, contain c. 40,000 described species, and are distributed across almost all continents and islands (Larochelle & Lariviére, 2003; Lövei & Sunderland, 1996). Carabids are terrestrial, omnivorous, effective predators of invertebrate pests, and are often used as environmental indicators (Brooks et al., 2012; Larochelle & Lariviére, 2003).
2.2 | Part 1. Quantitative analysis of published experiments

We compiled a dataset of studies that used controlled laboratory experiments to investigate the effect of temperature on pupal or adult body size of terrestrial beetles. To find suitable papers, we searched the Web of Science using the keywords: “Coleoptera” and “temperature”. We also included studies from previously published dataset compilations when appropriate. In all studies, larval beetles were reared at minimum three assay temperatures, and life-history traits were recorded (e.g. age at maturity, size at maturity, growth rate; Table S2). Data were extracted from tables, or were digitized from figures using the Figure Calibration plug-in for ImageJ (Hessman, 2009; Rasband, 2016). We converted wet mass to dry mass using the formula: dry mass = (0.4)*wet mass (Hirst, Horne, & Atkinson, 2015; Table S1). We log-transformed dry mass to reduce the large interspecific range in body sizes, and to maintain consistency with previously published studies (Forster et al., 2012; Horne et al., 2015).

We used a linear mixed-effects model to examine whether temperature had a significant effect on beetle body size across published studies. We included ‘log-body mass’ as the dependent variable, ‘temperature’ as the fixed effect independent variable, and ‘species’, and ‘sex’ as random effects. When data were available, we separated males and females of the same species because we expected the intercepts, but not the slopes, of the body size–temperature relationship to vary between the sexes (Hirst et al., 2015). Analysing the sexes separately did not change the overall result (data available upon request).

Next we used major axis regression to examine whether the temperature–size response (the slope of the body size–temperature regression) was correlated with the average body size for each beetle species. Following Forster et al. (2012) and Horne et al. (2015), we first transformed the species-specific slopes of the relationship between log dry mass vs. temperature to % change in mass per °C, using the equation: \(\exp(\text{slope}) - 1\) * 100. We then regressed % change in mass per °C on log dry mass. Males and females of the same species were included as separate entries when data were available, or coded as B (both) if sex was not reported in the original study. The relationship between beetle body size and % change in mass per °C remained negative and statistically significant if females or if males were removed from the analysis, thus we included all data here for completeness. Lastly, if data were originally reported for multiple populations per species, we used the average species-specific slope across all populations. A list of studies included in this analysis can be found in the Data Sources section following the References.

2.3 | Part 2. Long-term beetle collections

2.3.1 | Data collection

Approximately 7,000 individual beetle specimens from eight species of Carabidae in the Spencer Entomological Collection at the Beaty Biodiversity Museum (University of British Columbia) were photographed, and collection data (e.g. collection location, date, collector name) were transcribed manually from specimen labels. The eight species were: Scaphinotus angusticolis (von Waldheim 1823), Carabus nemoralis (Müller 1764), Pterostichus melanarius (Illiger 1798), Pterostichus algidus (LeConte 1852), Euryderus grossus (Say 1830), Harpalus fraternus (LeConte 1852), Cymindis planipennis (LeConte 1863) and Amara quenesis (Schönherr 1806). These beetles were primarily collected by George Spencer, (founder of the Spencer Entomological Collection), and Geoffrey Scudder (former director of the collection), to augment the overall entomological collections. All beetles were collected using pitfall traps. In British Columbia, Canada, these species are generally active from March/April to September/October, with mating and egg laying occurring in the late spring. Development time from egg to egg-laying adult of Carabidae is highly variable, and can range from a few months to a few years. Carabidae overwinter as adults or larvae, and most are iteroparous and predatory, except for species in the Amara and Harpalus genera, which mainly feed on fruits, seeds and other vegetation (Larochelle & Lariviére, 2003; Lövei & Sunderland, 1996).

The eight beetle species originated from two ecoprovinces in British Columbia, Canada: Georgia Depression (GD), and Southern Interior (SI). The GD is a 24,000-hectare region located in the southwest corner of British Columbia while the SI is a 35,000-hectare region in south-central British Columbia (Demarchi, 2011). Climate data for the GD ecoprovince were taken from near the Vancouver International Airport (49.194°N, -123.185°W), because this area is located in the centre of the ecoprovince. For the SI collections, we limited our dataset to beetles collected within 50 km of the Haynes Ecological Reserve, Osoyoos (49.087°N, -119.52°W), because: (1) this is where the bulk of the collections originated, and (2) climate within the SI varies more with latitude than does that in the GD, and we aimed to minimize any confounding effects of latitude. Climate data for the SI were taken from the Haynes Ecological Reserve. The collection dates for specimens from GD spanned from 1915 to 2015, while those from SI ranged from 1980 to 2015. Data are available in the Dryad Digital Repository (Tseng et al., 2017).

We measured the length of the left elytron (medial margin) using ImageJ (Rasband, 2016). When more than 50 individuals were collected in a given year from a given site, 50 individuals were selected at random and measured. Although we were unable to distinguish between males and females, our meta-analysis here, and a recent study (Hirst et al., 2015) both report little to no difference between the sexes in the relationship between body size and temperature. To convert elytron length to full body length, we measured 75 individuals across the eight Carabidae species and calculated the elytron to body length conversion as: body length = (1.56)*elytron length. We converted body length to log dry mass using the formulae: mass = 0.03069*(body length)^{2.6385} (Jaroslík, 1989), and log(dry mass) = log(0.4[wet mass]) (Hirst et al., 2015; Table S1). We conducted all analyses using log dry mass as the dependent variable (see below). Using elytron length as the dependent variable did not change the results of statistical analyses (data available upon request). We remeasured 155 beetles to confirm the precision of the elytron length measurements and found a correlation of 97% between the original and the remeasured value.
We obtained data for 26 climate variables related to temperature and precipitation (Table S1) for each region using ClimateWNA_MAP, a program developed by the Centre for Forest Conservation Genetics at the University of British Columbia (Wang, Hamann, Spittlehouse, & Murdock, 2012). We included precipitation data because patterns of precipitation are predicted to shift with climate change (Portmann, Solomon, & Hegerl, 2009). While previous studies have shown that precipitation levels can mediate beetle community assemblages (Lövei & Sunderland, 1996; Pozsgai, Baird, Littlewood, Pakeman, & Young, 2016), whether precipitation affects beetle body size over long temporal scales is unknown, and we address this question here.

2.3.2 | Data analysis

We performed two sets of analyses to investigate (1) whether beetle body size has changed significantly over time, and (2) whether temperature- and precipitation-related climate variables explained intraspecific variation in beetle body size. For both types of analyses, we also examined whether the mean size of the beetle species explained interspecific variation in body size-by-time or body size-by-climate relationships. We repeated the analyses with both time and climate variables included in the same model and the results were qualitatively similar to those where time is analysed separately from climate (Table S3). Separating ‘time’ from ‘climate’ allows for more straightforward interpretation of the results and thus we present the separated analyses here.

Relationship between beetle body size and time

We examined whether the body size of museum specimen beetles has changed over time using linear regression with ‘Year’ as the independent variable and ‘log dry mass’ as the dependent variable. We then transformed the species-specific slopes of the log dry mass-by-year regressions to % change in mass per year, using the equation: 
\[
\text{exp}^{\text{slope}} - 1 \times 100 \quad \text{(Forster et al., 2012; Horne et al., 2015)}.
\]

We used major axis regression to investigate whether mean body size of the beetle species explained interspecific variation in the ‘% change in body mass per year’. This analysis addresses the question of whether larger-sized beetles have changed disproportionately more over time compared to smaller-sized beetles. For this test, the dependent variable was the ‘% change in body mass per year’, and the independent variable was the mean ‘log dry mass’ of the beetle species. We restricted this analysis to beetles collected after 1970 to maximize the amount of overlap in collection years between GD and SI species. For completeness, we report the GD results for the entire collection period (1915–2015) as well as the truncated period (1970–2015) (Table 1).

### Relationship between beetle body size and climate variables

We used multiple regression to explore whether climate variables explained intraspecific variation in beetle body size. To remove collinearity between climate variables, we followed the approach advocated by Zuur, Ieno, and Elphick (2010). For each beetle species, we first conducted a multiple regression with all climate variables included as main effects in the model. We then dropped the variable with the largest variance inflation factor (VIF) and recalculated all VIFs. We repeated this process until all VIFs were smaller than 3 (Zuur et al., 2010). We then sequentially dropped highly non-significant terms (p > .5). We did not test for significant effects of interactions among climate variables.

After correcting for collinearity, 12 of the 26 initial climate variables were dropped from the analyses overall. We examined the relationship between beetle body size and each of the 14 remaining climate variables in greater detail by regressing beetle body size against each climate variable, for each species. Lastly, we used major axis regression to examine whether interspecific variation in the body size-by-climate response was explained by the mean body size of the species. For these regressions, we first converted the slope of the body size-by-climate response to ‘% change in mass per unit increase in climate variable’ using the equation \((\exp^{\text{slope}} - 1)^{100}\). For all regressions, the dependent variable was the ‘% change in mass per unit increase in climate variable’, and the independent variable was the mean.

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Summary of linear regression analyses of the relationship between beetle body size and time, for two time periods (1915–2015, 1970–2015)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
<td><strong>Dry mass (mg) ± SD</strong></td>
</tr>
<tr>
<td>Georgia depression</td>
<td></td>
</tr>
<tr>
<td>Pterostichus algidus</td>
<td>6.9 ± 1.6</td>
</tr>
<tr>
<td>Pterostichus melanarius</td>
<td>14.9 ± 4.1</td>
</tr>
<tr>
<td>Carabus nemoralis</td>
<td>43.3 ± 10.7</td>
</tr>
<tr>
<td>Scaphinotus angusticollis</td>
<td>31.3 ± 9.6</td>
</tr>
<tr>
<td>Southern Interior</td>
<td></td>
</tr>
<tr>
<td>Amara quenseli</td>
<td>2.2 ± 0.5</td>
</tr>
<tr>
<td>Cymindis planipennis</td>
<td>3.8 ± 0.9</td>
</tr>
<tr>
<td>Harpalus fraternus</td>
<td>9.9 ± 2.9</td>
</tr>
<tr>
<td>Euryderus grossus</td>
<td>10.8 ± 3</td>
</tr>
<tr>
<td>Statistically significant relationships are in boldface.</td>
<td></td>
</tr>
</tbody>
</table>

We used major axis regression to explore whether climate variables explained intraspecific variation in beetle body size. For this test, the dependent variable was the ‘% change in body mass per year’, and the independent variable was the mean ‘log dry mass’ of the beetle species. We restricted this analysis to beetles collected after 1970 to maximize the amount of overlap in collection years between GD and SI species. For completeness, we report the GD results for the entire collection period (1915–2015) as well as the truncated period (1970–2015) (Table 1).
In previous studies (Hirst et al., 2015; Horne et al., 2015). Although they were included in previously published TSR syntheses, we did not include data from Galford (1974) because the study reported maximum, rather than mean beetle weight, and did not include data from Stillwell, Moya-Laraño, and Fox (2008) because the study included only two assay temperatures. Beetle dry mass ranged from 0.2 to 531.20 mg, and assay temperatures ranged from 10°C to 44°C (Figure 1a). In 21 of the 22 species, either one or both of the sexes showed a decrease in body size when reared at increased temperature (Figure 1a, Figure S2). Overall, beetle body size decreased by c. 0.008*\log\text{dry mass} (±0.003 SE) per °C (\chi^2(3) = 35.8, p < .001).

We found that larger beetles tended to shrink disproportionately more when reared at warmer temperatures compared to smaller-sized beetles (RMA regression: p = .02; r^2 = .11; Figure 1b). Across all studies, the average change in body mass per °C was −0.77% (±0.46 95% CI). Carabidae body size (\log\text{dry mass}) specifically decreased on average by 1.05% (± 0.44 95% CI) per °C.

3.2 | Long-term beetle collections

3.2.1 | Relationship between beetle body size and time

Mean beetle body size ranged from 2.2 ± 0.5 (A. quenseli) to 43.3 ± 10.7 (Ca. nemoralis) (Table 1). Variation in beetle body size appears large in some years, and is likely due to sexual size dimorphism, or to variation in microclimate and resource availability among collection locations.

Across all collection years, three species of beetles decreased in size (S. angusticollis, Cy. planipennis, E. grossus), two increased (P. algidus, A. quenseli) and three did not change (P. melanarius, Ca. nemoralis, H. fraternus), (Table 1, Figure 2a,b). If we restrict the GD dataset to only those beetles collected after 1970 (to facilitate comparisons across beetles collected in GD vs. SI), the change in body size over time becomes statistically significant for P. melanarius, and non-significant for P. algidus (Table 1). The results for the other two GD species (Ca. nemoralis, S. angusticollis) are qualitatively similar to those from the full dataset.

The amount of change in beetle body size across species ranged from a 0.36% increase per year (A. quenseli), to a 0.88% decrease/year (S. angusticollis) (Figure 1c). Overall, 50% of the interspecific variation in the body size–time response between 1970 and 2015 was explained by mean body size of the beetle species, with larger beetle species showing larger decreases in size over time compared to smaller-sized beetles (Figure 2c).

3.2.2 | Relationship between beetle body size and climate variables

Intraspecific variation in body size for each beetle species was explained by a different subset of climate variables (Table 2). No single climate variable significantly predicted body size across all eight species. We next examined the relationship between each climate variable and body size for each beetle species (Figure 3, Figures S2–S15, parts a,b in each figure). As expected, there was considerable variation in the predictive power of individual climate variables among

**FIGURE 1** Meta-analysis results. (a) The effect of temperature on beetle body size. Overall, temperature decreased beetle body size by 0.008*\log\text{dry mass} (±0.003 SE) °C−1 (\chi^2(3) = 28.8, p < .001; solid black line). Species names are available in the supplementary data file (Table S1). For clarity only female data are shown here; the full figure is available in the supplementary materials (Figure S2); (b) The effect of beetle body size on the temperature–size response. Larger beetles shrunk disproportionately more with increased temperature compared to smaller beetles (MA regression: p = .02; r^2 = .11) [Colour figure can be viewed at wileyonlinelibrary.com]
FIGURE 2  Beetle body size for species collected in (a) the Georgia Depression (1915–2015), or (b) Southern Interior (1980–2010). The solid line represents the linear relationship between log dry mass and year. Asterisks denote statistically significant relationships between body size and year (*p < .05; **p < .01; ***p < .001). See Table 1 for full statistics.

(c) Interspecific variation in the body size–time relationship is explained by mean body size, with larger beetles shrinking more over time compared with smaller-bodied beetle species [Colour figure can be viewed at wileyonlinelibrary.com]
<table>
<thead>
<tr>
<th>TABLE 2</th>
<th>Multiple regression coefficients from analyses examining the effect of climate variables on beetle body size</th>
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<tbody>
<tr>
<td><strong>Georgia depression ecoprovince, 1915–2015</strong></td>
<td><strong>Southern interior ecoprovince, 1980–2015</strong></td>
</tr>
<tr>
<td></td>
<td><strong>Pt. algidus</strong></td>
</tr>
<tr>
<td>Intercept</td>
<td>0.08</td>
</tr>
<tr>
<td><strong>Temperature variables</strong></td>
<td></td>
</tr>
<tr>
<td>Warmest month</td>
<td>0.0082</td>
</tr>
<tr>
<td>Temperature differential</td>
<td>0.0098</td>
</tr>
<tr>
<td>Spring maximum</td>
<td>0.0332***</td>
</tr>
<tr>
<td>Summer maximum</td>
<td>0.0254*</td>
</tr>
<tr>
<td>Autumn maximum</td>
<td>0.0089</td>
</tr>
<tr>
<td>Spring minimum</td>
<td></td>
</tr>
<tr>
<td>Autumn minimum</td>
<td></td>
</tr>
<tr>
<td>Summer heat moisture ind.</td>
<td>0.0036***</td>
</tr>
<tr>
<td>Annual heat moisture ind.</td>
<td></td>
</tr>
<tr>
<td><strong>Precipitation variables</strong></td>
<td></td>
</tr>
<tr>
<td>Precipitation as snow</td>
<td>−0.00014</td>
</tr>
<tr>
<td>Winter precipitation</td>
<td>−0.00009*</td>
</tr>
<tr>
<td>Spring precipitation</td>
<td>−0.0002**</td>
</tr>
<tr>
<td>Summer precipitation</td>
<td></td>
</tr>
<tr>
<td>Autumn precipitation</td>
<td>0.0002***</td>
</tr>
<tr>
<td>Adjusted R²</td>
<td>.193</td>
</tr>
</tbody>
</table>

The – symbol denotes a negative relationship between body size and the climate variable (*p < .05; **p < .01; ***p < .001). An empty cell denotes that the climate variable was not included in the model for that species. See Methods for more details.
Thus variation in this climate variable was likely not a key driver of mate variable has not changed over time in the SI ecoprovince, and beetle body size did not explain variation in body size—by—size—by—precipitation relationships (Figures S11–S15). Interspecific variation in body size also did not explain variation in body size—by—temperature responses for Temperature Differential, Summer Heat Moisture Index, Summer Maximum Temperature and Minimum Spring Temperature (Figures S7–S10). Lastly, although larger-bodied beetle species were significantly more likely to decrease in size with increases in Mean Warmest Month Temperature (Figure S6), this climate variable has not changed over time in the SI ecoprovince, and thus variation in this climate variable was likely not a key driver of beetle body size decreases over time. Individual species—by—climate variable regressions and statistics are available in Figures S2–S15.

Overall, this long-term beetle dataset demonstrates that some beetle species have increased in size over the last 30 or 100 years, while others have decreased. Importantly, this interspecific variation in how body size has changed over time is explained by mean beetle body size, with larger beetles shrinking disproportionately more than smaller beetles. Lastly, interspecific variation in beetle body size is strongly correlated with significant increases over time in Maximum Autumn Temperature, Minimum Autumn Temperature and Annual Heat Moisture Index, and with significant decreases in Maximum Spring Temperature over time.

4 | DISCUSSION

This long-term beetle dataset demonstrates that larger-bodied, but not smaller-bodied beetles have decreased in size over a 30- or 100-year time span. Additionally, this body size—temperature pattern is tightly correlated to temperature, but not to precipitation changes in this region during this time frame. That larger-bodied beetles decreased in size with long-term increases in Autumn Maximum and Minimum Temperature, and Annual Heat Moisture Index is consistent with our quantitative synthesis of laboratory experiments, which demonstrated that larger beetle species were more likely to decrease in size with increased rearing temperature.

Interestingly, we also found that Maximum Spring Temperature in this region has decreased over the last 45 years, and that larger beetles showed a positive relationship between this climate variable and body size. While this pattern is consistent with the observed overall decrease in beetle body size over time, it suggests that increased temperature does not categorically result in smaller beetle body sizes.
These data provide indirect support for laboratory studies demonstrating that the effect of temperature on insect body size can be dependent on photoperiod (Kutcherov, 2015; Kutcherov, Lopatina, & Kipyatkov, 2011; Xi, Wu, Nylin, & Sun, 2016). Additionally, if increased spring temperature (but not increased autumn temperature) is associated with an elevated availability of resources, these beetle data would support the Supply-Demand (SD) model of the temperature–size rule (DeLong, 2012), which posits that variability in resource availability can mediate the effect of temperature on ectotherm body size. Overall, these climate and body size patterns suggest that responses of beetle body size to climate change in the future will depend on the balance between decreases in spring temperatures, vs. increases in mean and autumn maximum/minimum temperatures.

This study demonstrates that the long-term effect of temperature on beetle body size is observable and measurable despite the multitude of biotic and abiotic factors that are likely to mediate organism body size in nature. Although the total number of beetle species included in this study is a small fraction of the 350,000 described Coleoptera, the general congruence between the laboratory assays and the natural history collections, and the fact that this beetle dataset is one of the largest of its kind in terms of species number, collection duration and total sample size (Table S4), allows us to at least preliminarily conclude that the temperature–size relationships seen here may be widespread across this animal group.

The pattern of larger-sized insects showing greater sensitivity to increased temperature in the laboratory has mainly been observed in aquatic arthropods (Forster et al., 2012; Horne et al., 2015). In this latter group, the pattern has been attributed to the 'oxygen hypothesis' (see Section 1). A terrestrial version of the 'oxygen hypothesis' is possible given that atmospheric levels of O₂ (relative to N₂) have decreased.

**FIGURE 4** Mean beetle species body size explains significant interspecific variation in the body size–temperature relationship for (a) Maximum Autumn Temperature, (c) Minimum Autumn Temperature, (e) Annual Heat Moisture Index and (g) Maximum Spring Temperature. Maximum Autumn Temperature, Minimum Autumn Temperature and Annual Heat Moisture Index have all increased over the last 45 years (Figure 4b,d,f), while Maximum Spring Temperature has decreased over time (Figure 3h). Asterisks denote statistically significant relationships (*p < .05; **p < .01; ***p < .001), and the panels in Figure 3b,d,f, and h represent the climate for each collection region [Colour figure can be viewed at wileyonlinelibrary.com].
steadily since at least 1989 (Keeling, 2016), and that larger beetles are more affected by hypoxia compared to smaller beetles (Harrison, Kaiser, & VandenBrooks, 2009). However, whether these changes in atmospheric $O_2$ are biologically relevant are unknown. Our data suggest that new hypotheses that can explain the body size–temperature relationship in both aquatic and terrestrial arthropods are needed.

In general, the decrease in beetle body size with increased temperature seen in larger-bodied beetle species is consistent with the temperature–size rule in ectotherms (Atkinson, 1994; Kingsolver & Huey, 2008). In some taxa, this pattern has been attributed to increased organism metabolism at warmer temperatures, leading to shortened development time and smaller size at maturity (Atkinson, 1994; Kingsolver & Huey, 2008). The effect of temperature on ectotherm size at maturity can also be mediated by resource availability (DeLong, 2012), however a general mechanism applicable to the taxonomically and geographically widespread organismal groups in which the TSR has been observed is lacking (Angilletta et al., 2004).

On average, laboratory-assyed beetles decreased in body mass by 0.77% per °C, and museum specimen beetles decreased by 1.56% per °C (average of: $T_{max, at}$, $T_{min, at}$ and AHM slopes). To compare these results to previously published data, Forster et al. (2012) found the average decrease in body mass per °C to be 1.45% for laboratory-reared terrestrial arthropods, and Horne et al. (2015) reported a 0.35% decrease for the same group. It is clear that there is considerable variation in the temperature–size response within and among arthropod orders, and some of this variation is thought to be attributed to variation in voltinism (Horne et al., 2015). Unfortunately we have no information on patterns of voltinism for the populations of museum species examined here. One future challenge is to increase the number of species represented in each arthropod order, as we have done here with Coleoptera, to better understand whether current broad-scale estimates of the temperature–size response are accurate.

It is curious that body size of laboratory-reared beetles decreased by approximately half as much per °C compared to wild-caught beetles. This result, while preliminary, is consistent with a synthesis of phenological shifts of plants in response to temperature change (Wolkovich et al., 2012). Using a quantitative literature review, the authors demonstrated that laboratory warming experiments underpredicted the phenological response of plants to temperature in nature. The authors proposed that non-optimal laboratory growing
conditions hindered plant growth, and that organismal responses to 
temperature in nature are likely the result of complex interactions 
among multiple drivers. While it is too early to tell whether similar fac-
tors underlie the observed differences in temperature-size responses 
between laboratory-assayed beetles and those collected in the wild, it 
would be worthwhile to explore how often results from in situ studies 
of organisms to temperature differ from those of laboratory experi-
ments (Horne et al., 2016).

This study adds to a growing body of literature examining patterns 
in organism body size over time (Babin-Fenske, Anand, & Alarie, 2008; 
Baudron et al., 2014; Blanckenhorn, 2015; Caruso, Sears, Adams, & 
Lips, 2014; Fenberg, Self, Stewart, Wilson, & Brooks, 2016; Gardner 
et al., 2014; Sheridan & Bickford, 2011). Some of these studies (and 
references within) also show decreases in organism body size with 
increased temperature, but the pattern is not universal. Given the 
importance of organism body size for predicting population dynamics 
(White et al., 2007) and ecosystem-level processes (DeLong et al., 
2015; Garibaldi et al., 2015; Hébert, Beisner, & Maranger, 2015), 
a pressing challenge moving forward will be to continue to explain 
drivers of body size variation in nature.

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AUTHORS’ CONTRIBUTIONS

M.T. conceptualized the study; all authors collected museum specimen 
data: M.T., D.C., K.K. and K.S. collected data for the meta-analysis; 
M.T. analysed the data with help from D.C., K.K., K.S., S.S.P. and C.Y.; 
M.T. wrote the manuscript; M.T., D.C., K.K., K.S., S.S.P., A.T., H.T. and 
K.F. edited the manuscript.

DATA ACCESSIBILITY

Data from meta-analysis portion of the study are available as on-
line supplementary materials. Museum specimen and associated cli-
mate data are available from Dryad Digital Repository: https://doi. 
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REFERENCES

rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. 
or/10.1093/icb/44.6.498


temperature. In I. A. Johnston & A. F. Bennett (Eds.), *Animals and tem-
perature: Phenotypic and evolutionary adaptation* (p. 419). Cambridge, 
UK: Cambridge University Press.

Atkinson, D., & Sibly, R. (1997). Why are organisms usually bigger in 
S0169-5347(97)01058-6

cal change in stream beetle museum specimens correlates with climate 
or/10.1111/j.1365-2311.2008.01018.x

Warming temperatures and smaller body sizes: Synchronous changes 
https://doi.org/10.1111/gcb.12514

Blanckenhorn, W. U. (2015). Investigating yellow dung fly body size evo-
lution in the field: Response to climate change? *Evolution*, 69, 2227– 
2234. https://doi.org/10.1111/evol.12726

Brooks, D. R., Bater, J. E., Clark, S. J., Monteith, D. T., Andrews, C., 
Kingdom monitoring network increases evidence for a widespread 
https://doi.org/10.1111/j.1365-2664.2012.02194.x

Publications.

rapid reductions in body size of adult salamanders in response to 
or/10.1111/gcb.12550

DeLong, J. P. (2012). Experimental demonstration of a “rate – size” trade-
off governing body size optimization. *Evolutionary Ecology Research*, 14, 
343–352.

DeLong, J. P., Gilbert, B., Shurin, J. B., Savage, V. M., Barton, B. T., 
Clements, C. F., ... O’Connor, M. I. (2015). The body size dependence of 
or/10.1086/679735

Victoria, BC: Ministry of Environment.

Exploring the universal ecological responses to climate change in a uni-
or/10.1111/1365-2656.12492

in body size are greater in aquatic than terrestrial species. *Proceedings 
of the National Academy of Sciences of the United States of America*, 109, 
19310–4. https://doi.org/10.1073/pnas.1210460109

Galford, J. R. (1974). Some physiological effects of temperature on artifi-
cially reared red oak borers. *Journal of Economic Entomology*, 67, 709– 
710. https://doi.org/10.1093/jee/67.6.709

Gardner, J. L., Amano, T., Backwell, P. R. Y., Ikin, K., Sutherland, W. J., 
size responses to broadscale environmental change over the last 
jav.00431

(2011). Declining body size: A third universal response to warming?


