

Mammalian body size is determined by interactions between climate, urbanization and traits

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Abstract

Anthropogenically-driven climate warming is a hypothesized driver of animal body size reductions. Less understood are effects of other human-caused disturbances on body size, such as urbanization. We compiled 140,499 body size records of over 100 North American mammals to test how climate and urbanization, and their interactions with species traits, impact body size. We tested three hypotheses of body size change across urbanization gradients; urban heat island effects, fragmentation, and resource availability. Our results unexpectedly demonstrate urbanization is more tightly linked with body size changes than temperature, most often leading to larger individuals, thus supporting the resource availability hypothesis. In addition, life history traits, such as thermal buffering, activity time, and average body size play critical roles in mediating the effects of both climate and urbanization on intraspecific body size trends. This work highlights the value of using digitized, natural history data to track how human disturbance drives morphological change.

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Abstract: Anthropogenically-driven climate warming is a hypothesized driver of animal body size reductions. Less understood are effects of other human-caused disturbances on body size, such as urbanization. We compiled 140,499 body size records of over 100 North American mammals to test how climate and urbanization, and their interactions with species traits, impact body size. We tested three hypotheses of body size change across urbanization gradients; urban heat island effects, fragmentation, and resource availability. Our results unexpectedly demonstrate urbanization is more tightly linked with body size changes than temperature, most often leading to larger individuals, thus supporting the resource availability hypothesis. In addition, life history traits, such as thermal buffering, activity time, and average body size play critical roles in mediating the effects of both climate and urbanization on intraspecific body size trends. This work highlights the value of using digitized, natural history data to track how human disturbance drives morphological change.

INTRODUCTION

Body size is an easily measured, integrator trait that scales with many other life-history characteristics of organisms (Gould 1966; Brown & Maurer 1986; Brown et al. 1993). Because of this, understanding drivers of body size has been a central goal of ecology over the last half century. Macroscale studies of body size across broad environmental gradients date back centuries, to the seminal work of Carl Bergmann (1847), although with much debate about the generality of patterns and underlying mechanisms (Ashton et al. 2000; Meiri & Dayan 2003; Riemer et al. 2018). Some species - but not all - follow predicted responses to temperature, with smaller average body size in warmer climates. In addition to temperature, food availability strongly determines species' body size changes (Alroy 2001; Pineda-Munoz et al. 2016).

Much less attention has been paid to anthropogenic influences on body size that play out at the local or regional scale, which provides a distinct set of challenges and opportunities for organisms. While urbanization may increase potential for novel human-caused conflict (including traffic) and predation, these novel environments can also lead to decreased predation rate (Fischer et al. 2012) and increased food resources. The complexity of urban environments provides an opportunity to examine species responses to a variety of major ecological gradients in real time, and to test the applicability of longstanding ecogeographic rules within the human-built environment. For example, Ives et al. (2016) found Australian cities harbor a large number of threatened species, which may be due to a high amount of landscape heterogeneity (e.g. plant cultivation) in urban areas.

Understanding the magnitude and direction of body size variation due to human alteration of landscapes is complicated by multiple possible, non-mutually exclusive drivers. First, due to human activity and built infrastructure, cities are generally warmer than surrounding areas, a phenomenon known as the urban heat island effect (Oke 1982). Animals inhabiting urban heat islands are expected to be smaller in body size based on Bergmann's Rule (Bergmann 1847). There has been limited empirical support for urban heat island effects driving decreases in body size (but see Merckx et al. 2018), especially for endotherms; however, in a large-scale study of body size variation in the North American deer mouse (*Peromyscus maniculatus*), Guralnick et al. (2020) found mice were shorter (but not lighter) in more urbanized areas. Those authors postulated a heat island effect could be driving body size change, but also suggested this could represent a selective response to avoid detection (i.e. crypsis). Second, heterogeneity in urban areas can contribute to increased food resources and water availability compared to rural areas (McKinney 2008), which could further mediate body size change in urban areas (i.e., a resource rule, McNab 2010). It is also possible that the compounding effect of urbanization on top of climate change may amplify adaptive or plastic changes in body size. Finally,

Schmidt and Jensen (2003, 2005) suggested that species that experience landscape fragmentation driven by urbanization and an increased human footprint should either go extinct or adapt through changes in life history traits, namely increasing body size for smaller species and decreases for larger species. Each of these hypotheses have clear, alternate predictions about the overall effects of urbanization, and can be emplaced in the broader context of overall climatic gradients.

Mammals represent a good test case for examining the potentially multifaceted effects of climate and urbanization on body size in the same modeling framework, in order to understand the relative importance of different drivers across species with widely varying body sizes and life history traits. Mammals have evolved to fill a large variety of niches including aquatic, terrestrial, and even subterranean habitats, often facilitated by the evolution of key functional, morphological, or behavioral traits. These traits are expected to strongly mediate current and future responses of organisms to climate change. Few studies have directly examined how these factors may influence spatiotemporal trends to recent global change responses of mammals (but see Lindstedt & Boyce 1985; McCain & King 2014; Naya et al. 2017). Habitat buffering, a suite of behaviors such as nocturnality, or spending portions of the life cycle underground, may be critical for coping with unsuitable climatic conditions especially in the short term; body size changes may thus be weaker in species with such buffering capability (Johnson 1931; Terrien et al. 2011). Finally, mammals are well-sampled in many biodiversity datasets, with body size measurements often taken in the field as part of long-standing collection practices. This creates an opportunity to analyze records for a vertebrate clade spanning over 100 years, providing ample data, albeit with associated challenges of dealing with spatiotemporal collecting biases which need to be carefully considered in downstream modeling.

In this study, we compiled multiple datasets containing 140,499 mass and body length records spanning more than 100 mammal species and 80 years to address broad-scale spatial trends of mammalian body size (Fig. 1, S1). Our overarching question is whether and how much climate and human population density, the latter of which represents a proxy for the human built environment, impact mammal body size. We first addressed the relationship between body mass and head-body length, as each is commonly used as a body size metric but the former can vary seasonally due to age, reproductive status, or food availability (McNab 1980), potentially weakening mass-length allometries at range-wide scales (Guralnick et al. 2020). We then use a hierarchical modeling framework to identify the main drivers of body size variation, accounting not only for climate and urbanization but also broad differences in habitat and species-specific trends. Drawing on Bergmann’s Rule, we predicted that temperature would negatively impact both metrics of body size (i.e. increasing temperatures lead to smaller size). We also expected that increasing human population density would drive smaller body size due to heat island effects, thereby amplifying Bergmann’s-like patterns. Alternatively, and given recent results from single species studies (e.g., Guralnick et al. 2020), it may also be that body mass increases while body length decreases in urban areas as increased food availability allows for more weight but need for crypsis or heat island effects drive decreasing length. Further, urbanized areas may mimic islands given often fragmented habitats, driving larger species to decrease in size and smaller species to increase in size.

To develop a more integrative framework for understanding body size variation in mammals, we extended our work beyond focusing on broad-scale climate and urbanization gradients and examined species traits that are likely to modify and interact with both these drivers, especially ability to buffer thermal environments. Therefore, we predicted weaker responses of body size change from species that hibernate or utilize habitat buffering as they are able to avoid extreme climates. We also considered traits such as diurnality and expected that nocturnal mammals should increase in size more than diurnal species in urban areas since they can more easily avoid humans but still benefit from food resources. Lastly, based on the hypothesis of more fragmented, island-like habitats in human built environments, we predicted that larger species may decrease in body size and smaller species increase in size in areas of higher human population density. Small size is also predicted to be favored as a greater number of microhabitats are available to escape unfavorable temperatures and avoid human detection (Cardillo et al. 2005; Huey et al. 2012; Scheffers et al. 2014).

METHODS

Data sources & aggregation

We obtained mammal body size data from three repositories: VertNet (Guralnick & Constable 2010), the National Ecological Observatory Network (NEON 2019; <https://www.neonscience.org/>), and the North American Census of Small Mammals (NACSM; Calhoun 1948, 1949, 1950, 1951, 1956; Calhoun & Arata 1957a, 1957b, 1957c, 1957d). Standard body mass and total body length measures were extracted from the VertNet corpus following the approach of Guralnick et al. (2016). NEON data were obtained using the “neonUtilities” R package (Laney & Lunch 2019), but only body mass was used from NEON survey events because accurate length measures are difficult to obtain on live, unanesthetized, mammals (Guralnick et al. 2020). We found no systematic biases of body mass measures from NEON or other sources. NACSM data were obtained via manual digitization from published reports, and were extracted for a subset of species that had body size measurements and which were also obtained from VertNet and NEON. We aggregated VertNet data with corresponding species from NEON and NACSM and harmonized data field names across the three sources.

Any migratory species were removed as they can experience a wide breadth of environmental conditions. Measures of head-body length were then derived by subtracting tail length from total length for each individual. As a preliminary step, we filtered the data to those species with a minimum of 100 records for body mass or length count.

Data filtering

Additional filtering included removal of records lacking; 1) latitude and longitude; 2) sex, including ambiguous sex assignments (e.g. “female?”); 3) date information – we required month, day, and year for each record. However, for some specimen records with missing locality, we first aimed to manually georeference data when possible using the protocols of Chapman and Wieczorek (2006), which uses a combination of Google Maps (<https://www.google.com/maps>) and the MaNIS georeferencing calculator (Wieczorek et al. 2001; <http://manisnet.org/gci2.html>). Manual curation based on locality was also necessary in some instances. For example, several records of *Canis lupus* came from zoos or sanctuaries; all zoo records were removed by hand. We next created two additional fields from the record dates, “season collected” and “decade”. Month of collection was used to bin the records into spring (March-May), summer (June-August), fall (September-November), and winter (December-February) seasons. In some species, tail length is not reported due to very small or missing tails, and in those cases we relied on total length. We also filtered juveniles from the dataset based on age assignments in the Darwin Core field “lifeStage” (for VertNet) or based on body size measurements below a lower threshold for each individual species based on literature searches and reputable online databases (see Table S1). To remove any additional erroneous data values (e.g., digitization errors), we used a 95% dispersion-based threshold using the “OutlierDetection” R package (Tiwari & Kashikar 2019). Taxonomy was updated for all records to ensure scientific names were synonymous across data sources.

Relationship between body mass and head-body length

We ran simple univariate linear regressions where \log_{10} head-body length predicts \log_{10} body mass for each species. Correlations were generally weak among species as indicated by the vast majority of the fits with $r^2 < .5$ (Table S1). As such, we compiled two body size datasets: body mass and head-body length which were used separately as response variables in downstream models.

Population density and climate

As a proxy for urbanization, we used high-resolution (1 x 1 km) decadal human population density data for the conterminous USA (years 1940-2010) from Fang and Jawitz (2018). We selected human population density over impervious land cover as our measure of urbanization because it more directly accounts for anthropogenic effects (e.g. food waste). Human population density data were appended to each record by first aggregating density data to a resolution of 10 x 10 km and indexing this value by decade collected and record locality using an R (R Core Team 2018) script. Human population density was \log_{10} transformed for statistical analyses. Historical climate data were obtained from the PRISM Climate Group (PRISM

Climate Group, 2020) for both historical and contemporary body size observations. We extracted mean annual temperature (MAT) and mean annual precipitation (MAP) from PRISM based on observation year and geocoordinates.

Spatial regions

To control for habitat differences across our region of interest, we included ecoregional membership as a random effect in each model. We used the United States Environmental Protection Agency (EPA) Level 1 ecoregions (<https://www.epa.gov/eco-research/ecoregions>), but further divided three ecoregions given the large climate and latitudinal range. We split the ‘Great Plains’, ‘Northwestern Forested Mountains’, and ‘North American Deserts’ ecoregions at 42 degrees latitude and renamed the ecoregions: ‘Northern and Southern Great Plains’, ‘Northern and Southern Cordilleras’, and ‘Northern and Southern Desserts’, respectively (Fig. 1).

Phylogeny and mammal traits

We obtained a global mammal phylogeny from Upham et al. (2019; <http://vertlife.org/data/mammals/>) and pruned the tree to match the species present in the two datasets (body mass, $n = 101$; HB length, $n = 99$). We also compiled life history traits for the final species sets that likely influence body size response to environmental change. These traits include hibernation ability (binary, Y/N), habitat buffering (e.g. fossorial vs. terrestrial; binary, Y/N), daily activity pattern (diurnal, nocturnal, or both), reproductive rate (high = 1-4 litters/year or more, medium = 1-3 litters/year, low = 1-2 litters/year or less), and average body size binned into small ($<500\text{g}$; $<200\text{mm}$) and large ($>500\text{g}$; $>200\text{mm}$) categories (Fig. S2, sources provided in Table S1).

Mixed-modeling framework

To examine drivers of mammalian body size variation, we initially used linear mixed-effects models (LMM), using the R package *lme4* (Bates et al. 2014). We \log_{10} transformed measures of body mass and HB length as mammal body size ranges vary by orders of magnitude (Brown 1995). In addition, we \log_{10} transformed human population density and log transformed MAP to normalize data. We mean-centered and standardized all continuous predictors to have standard deviations of 1, except decade, which we treated as a numeric variable that starts at zero. All models were run separately for body mass and head-body length (Table S2).

We used a set of global models that included fixed effects of Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP), sex, season collected (spring, summer, fall, and winter), human population density, and the traits listed above (‘Mammal traits’). Inclusion of traits as fixed effects allowed us to model variation in traits associated with size across the mammalian body size spectrum (e.g., Smith et al. 2004). To model how these same traits mediate body size variation in specific climate contexts and how effects of urbanization change across climate contexts, we also examined the interactions of MAT x human population density, MAT x hibernation, MAT x habitat buffering, MAT x small/large mammals, population density x diurnal/nocturnal, and population density x small/large mammals. We included three random intercepts of ecoregion, decade, and species (Table S2).

After running each global model, we used backward stepwise selection with the step function in the R package *lmerTest* (Kuznetsova et al. 2017) to find the best-fit model. We checked residuals of the final models, minus the random effect of decade (due to matrix complexity), and found no evidence of spatial autocorrelation (Fig. S3). Marginal and conditional R^2 s were obtained for the best-fit models using the R package *MuMIn* (Barton 2012).

To account for potential effects of evolutionary history in these models, we re-ran the best-fit body mass and head-body length models using phylogenetic generalized linear mixed models (PGLMMs) using the R package *phyr* (Li et al. 2020). PGLMM and LMM results were largely concordant (Table S3), thus only LMM results are presented in the main text.

RESULTS

Aggregation of data across multiple sources, generated a significant dataset to examine spatially-structured changes in mammal body mass and head-body length in relation to climate, human population density, and a key life history traits. The top model of body mass variation included the following covariates: Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP), season, sex, human population density, all traits except reproductive rate, and all interactions besides population density x small/large mammals (Marginal $R^2 = 0.36$, Conditional $R^2 = 0.98$). Significant main effects include MAT, MAP, season, sex, human population density, hibernation, and small/large mean binned body mass (Table 1a). This model also included strong interactive effects between MAT, population density, and traits. The negative interaction between MAT and population density implies that while mammal body mass increases with decreasing MAT in general, this trend is much stronger in areas with higher densities of humans ($\beta = -0.003$, $p < 0.001$; Table 1a, Fig. 2).

Traits strongly mediated responses of body mass to climate and urbanization. With increasing MAT, species that hibernate decrease in body mass, whereas non-hibernators increase in body mass ($\beta = -0.021$, $p < 0.001$; Table 1a, Fig. 3A). Buffered and non-buffered species decrease in body mass with increasing MAT, but the strength of the decrease is stronger for buffered species ($\beta = -0.018$, $p < 0.001$; Table 1a, Fig. 3B). Diurnal species are larger in body mass and decrease in mass with increasing population density ($\beta = -0.014$, $p < 0.001$; Table 1a, Fig. 3C), compared to nocturnal species or those scored as “both” (Table 1a, Fig. 3C). Both large and small mammals (binned mean size) decrease in body mass with increasing MAT, but the strength of the decrease is stronger for larger species ($\beta = 0.023$, $p < 0.001$; Table 1a, Fig. 3D).

When examining head-body length as a body size metric, the best-fit model consisted of MAT, MAP, season, population density, all traits besides reproductive rate, and all interactions except MAT x human population density (Marginal $R^2 = 0.50$, Conditional $R^2 = 0.98$). Significant single predictors are MAP, season, human population density, hibernation, and small/large mean binned head-body length (Table 1b). MAT is not significant in the top spatial models on its own, but is important when conditioned by traits. There is a strong main effect of increasing head-body length with increasing human population density ($\beta = 0.009$, $p < 0.001$; Table 1b).

Similar to body mass, we find strong interactive effects between MAT and population density with traits. Head-body length is negatively correlated with MAT for species that hibernate, but positively correlated with MAT for non-hibernators ($\beta = -0.008$, $p < 0.001$; Table 1b, Fig. 3E). Species that utilize habitat buffering decrease in head-body length with increasing MAT at a faster rate than non-buffered species ($\beta = -0.004$, $p < 0.001$; Table 1b, Fig. 3F). Both diurnal ($\beta = -0.007$, $p < 0.001$;) and nocturnal ($\beta = -0.009$, $p < 0.001$; Table 1b, Fig. 3G) species decrease in head-body length with increasing population density, whereas species that display both tendencies increase in head-body length with increasing population density. The effect of the decrease in head-body length with increasing MAT is stronger for larger mammals compared to smaller species ($\beta = 0.005$, $p < 0.001$; Table 1b, Fig. 3H). Small mammals decrease slightly with increasing population density, while large mammals increase in head-body length with increasing population density ($\beta = -0.003$, $p < 0.001$; Table 1b, Fig. 3I).

DISCUSSION

Climate as a driver of animal body size change has been well documented across both space and time (Smith et al. 1995; Gardner et al. 2011; Sheridan & Bickford 2011). However, a myriad of anthropogenic global changes (e.g. habitat degradation and fragmentation, pollution, overpopulation) can also impact organisms at both local and regional scales, promoting complex responses that may be difficult to contextualize with regard to longstanding ecogeographic rules. Further, these responses likely vary among species and clades because life history traits mediate exposure and thus the intensity of changing conditions. Here, we investigate how climate (a more constant global change driver over earth history) and urbanization (a novel disturbance) influence mammalian body size, and how life history traits mediate those effects. We test these ideas by utilizing hundreds of thousands of compiled mammal body size records from natural history collections and field censuses, spanning 80 years and over 100 North American species.

Despite nearly two centuries of work examining the links between climate and body size, we unexpectedly found urbanization has equally strong or stronger effects on mammalian body size compared to temperature. In all cases, the main effect of increased urbanization was larger body size, consistent with mammals benefiting from increased food resources, ecological release (i.e., from predators and competitors), or both. Conversely, we found no evidence for urban heat island effects on body size. We had considered that such interactions between climate and urbanization would mean that heat island effects might only be present in the coldest areas. But here as well, we found the opposite - mammals in urbanized, cold areas have larger, not smaller, body masses than their rural counterparts, a result that likely speaks to more available food in urban areas. The overall result across all mammals examined is that head-body lengths are greater in urban areas regardless of temperature.

Our results suggest that one key outcome of urbanization is provisioning of novel, reliable food resources. Yom-Tov (2003) found a similar result for carnivorous body size; increased body size was related to increased anthropogenic food sources and not temperature. In addition to increased food, cities provide reliable water resources and shelter by use of built structures, which might decrease energetic costs and benefit growth rate and body condition (Bateman & Fleming 2012). The one exception to this pattern is that body mass was lightest in the warmest, most urbanized areas. It is possible that predictable food resources in urban settings results in low starvation risk (Lima 1986; Cuthill et al. 2000), or that a temperature threshold exists above which increased body size becomes less energetically advantageous (regardless of available food). This pattern may also emerge if constant food availability permits survival in milder winters where fat reserves are less critical, potentially also aiding quicker locomotor movements to escape predation or reductions in foraging time (Metcalf & Ure 1995; Kullberg et al. 1996; Downes 2001; Macleod et al. 2005). Future studies quantifying food availability between spatially distinct regions is warranted as some mammals appear to be adapting to novel food resources in urbanized areas (e.g., Harris & Munshi-South 2017).

We acknowledge that some species may be urbanophobic or unable to exploit resources provided in urban areas. Our strict filtering criteria limited our analyses to abundant and well collected mammal species, but these same species are likely to be urbanophilic or urban-neutral given that many collections are near human-populated areas. Thus, our combined results do not necessarily apply to all North American mammal species, and it is known that the percentage of urbanized area plays a role in determining which species occupy those areas (Ordeñana et al. 2010). Ultimately, life history strategies as well as morphological traits facilitate the ability to occupy urban environments, and filter out species lacking suitable characteristics (Croci et al. 2008; Jokimaki et al. 2016; Jung & Threlfall 2018). Thus, species inhabiting the most urbanized areas are likely those with suites of traits that allow utilization of the novel resources in cities. Even so, Parsons et al. (2018) found no difference in species diversity or richness along an urban-wild gradient, and suggested mammals have likely adapted to developed areas over the last few decades. Further studies investigating species occupancy across developed gradients will help elucidate adaptive trait responses to human-dominated landscapes.

Species traits directly related to thermoregulation and energetics appear to play an integral role in mediating the effects of climate and urbanization on body size, but not in the directions we predicted from theory. We predicted species that utilize thermal buffering (i.e., habitat buffering and hibernation) would show weaker responses of body size change with warming temperatures as these traits allow for the avoidance of unfavorable climatic conditions (Fuller et al. 2016). In contrast, we found species that use these behaviors are more sensitive to warming temperatures than non-buffered species, and respond to warming temperatures with stronger decreases in body size. Thus, for hibernators, exposure to temperatures during the active season alone may still represent a sufficiently strong selective pressure. For species with thermal buffering, lack of sufficient microhabitat heterogeneity due to extreme climates, clearcutting of forests, or increases in forest fires can result in decreased variation in ambient temperatures between exposed and buffered areas and ultimately reduce the effectiveness of that behavior (Huey et al. 2012; Suggitt et al. 2018). Another unexpected result relates to our finding of an increase in body size for mammals that do not hibernate. Further work to better understand physiological tolerances for thermal buffering species in relation to patterns of global change are necessary. These relationships may be complex and involve multiway interactions between landscape change, climate change, and species traits.

Daily activity pattern represents another important trait for adaptation to changing environments. Flexibility in activity times appears to be an advantage in more urbanized areas. McCain and King (2014) found that mammals that can switch between diurnality and nocturnality were the least likely to respond negatively or respond at all to climate change, and postulated this was due to the ability of these species to select climatic conditions that are suitable for activities. Relative to mammals that are flexible in their activity times, we found diurnal species decrease in body size with increasing urbanization. Decreases in body size may represent an adaptation to avoid predation, including human detection (i.e. crypsis; Stankowich & Campbell 2016; Guralnick et al. 2020). With increasing urbanization, nocturnal mammals also decreased in head-body length, but increased in mass in relation to species that are active anytime. Decreases in head-body length are also suggestive of an adaptive response to avoid detection, while increasing body mass is indicative of nocturnal mammals benefiting from increased food resources in urban areas. The same idea may hold for species that are able to selectively avoid human detection by being flexible in activity times.

Finally, our results provide new insight into average body size itself as a trait that can modulate responses to changing environments. With warming temperatures, we found larger mammals are decreasing at a faster rate than smaller mammals. This result is in contrast to the meta-analysis of Ashton et al. (2000), who found no difference between small or large mammals. However, a reanalysis of that dataset demonstrated no general tendency for small mammals to increase or decrease in size, while larger mammals tended to display a Bergmann’s-like response (Freckleton et al. 2003), which is consistent with our results. In another meta-analysis of 73 North American mammal species, McCain & King (2014) found that the largest mammals examined were 27 times more likely to respond to climate change compared to the smallest mammals. These previous studies are all limited in that they are meta-analyses (also see Nengovhela et al. 2020), vary in statistical approach, and do not leverage the dense intraspecific sampling we achieved here. Our work draws strength from the use of a single hierarchical modeling framework for separate measures of body mass and head-body length and reveals a robust signal of larger mammals being more sensitive to changes in temperature, and conforming to Bergmann’s Rule. Lastly, small or large size does not mediate changes in body mass with increasing human population density; however, we did find large mammals increase in head-body length, while small mammals decrease slightly. These results do not lend support to the Island Rule, where we would expect body size homogenization with increasing urbanization (Schmidt & Jenson 2003). Instead, increasing length for larger species may aid movement across fragmented landscapes (Merckx et al. 2018).

In this work, we have focused primarily on the utility of digital biodiversity datasets such as natural history collections and ecological monitoring efforts to examine spatial trends in mammal body size. However, we recognize that temporal changes may also be inherent given well-known climate and urbanization changes over the timescale of our dataset. We explicitly fit a decadal random term to control for this variation, but the constituent datasets themselves are also temporally structured, complicating issues with controlling for methodological issues (Guralnick et al. 2020). One future possibility is to add a spatially controlled time series, which would provide a strong basis for examining temporal trends across multiple sites. In addition, finer-scale regional or community-level ecological studies would provide a more detailed understanding of the presence and drivers of temporal changes (Ohlberger 2013).

Our understanding of how human-mediated pressures impact mammalian body size has remained limited for decades, and is often tied to simplistic ecogeographic “rules”, whose validity continues to be called into question (Reimer et al. 2018). Our data-intensive work showcases the importance of incorporating other human disturbances beyond climate change, and also reflects how multiple pressures interact with species traits to influence change in body size. Beyond the finding that urbanization had a strong impact on body size, it was surprising that species with climate buffering traits were more sensitive to temperature. This has major implications for management of native species and suggests that these species may be under increasingly intense selection not just for life history parameters such as phenology, but also morphological traits like body size. Further collection and digitization of trait data remains essential for improved understanding of large-scale spatial and temporal patterns of body size change, especially given accelerating climate warming and urbanization (Grimm et al. 2008; Seto et al. 2012; Christensen et al. 2013).

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TABLES

Table 1. Top (A) body mass and (B) head-body (HB) length model results. Bold effects are significant.

	Term	Estimate	Std. Error	p-value
(A)	<i>Body mass</i>			
	Intercept	3.446	0.156	<0.001
	MAT	-0.014	0.003	<0.001
	MAP	-0.001	0.000	0.001
	Season:spring	0.025	0.001	<0.001
	Season:summer	0.013	0.001	<0.001
	Season:winter	-0.007	0.001	<0.001
	Sex:male	0.002	0.000	<0.001
	Population density	0.008	0.001	<0.001
	Hibernation:yes	-0.359	0.121	0.004
	Buffered:yes	-0.012	0.111	0.917
	Diurnal/nocturnal:diurnal	0.343	0.175	0.053
	Diurnal/nocturnal:nocturnal	-0.013	0.145	0.932
	Small/large body mass:small	-1.838	0.123	<0.001
	MAT x small/large body mass:small	0.023	0.003	<0.001
	MAT x population density	-0.003	0.000	<0.001
	MAT x hibernation:yes	-0.021	0.001	<0.001
	MAT x buffered:yes	-0.018	0.001	<0.001
	Population density x diurnal/nocturnal:diurnal	-0.014	0.001	<0.001
	Population density x diurnal/nocturnal:nocturnal	-0.002	0.001	0.003
(B)	<i>HB length</i>			
	Intercept	2.677	0.052	<0.001
	MAT	-0.001	0.001	0.115
	MAP	-0.001	0.000	0.007
	Season:spring	0.008	0.000	<0.001
	Season:summer	0.002	0.000	<0.001
	Season:winter	0.000	0.000	0.433
	Population density	0.009	0.001	<0.001
	Hibernation:yes	-0.141	0.041	0.001
	Buffered:yes	-0.052	0.037	0.166
	Diurnal/nocturnal:diurnal	0.075	0.059	0.205
	Diurnal/nocturnal:nocturnal	-0.047	0.049	0.340
	Small/large HB length:small	-0.587	0.041	<0.001
	MAT x small/large HB length:small	0.005	0.001	<0.001

Population density x small/large HB length:small	-0.003	0.001	<0.001
MAT x hibernation:yes	-0.008	0.000	<0.001
MAT x buffered:yes	-0.004	0.001	<0.001
Population density x diurnal/nocturnal:diurnal	-0.007	0.001	<0.001
Population density x diurnal/nocturnal:nocturnal	-0.009	0.000	<0.001

FIGURE LEGENDS

Fig. 1. Body mass and HB length record localities. Designated spatial ecoregions are colored and the key shows the total number of body mass and head-body (HB) length records from each ecoregion.

Fig. 2. Mammalian body mass is influenced by the interaction between human population density and mean annual temperature. In colder and more urbanized areas mammal body mass is the heaviest, while in the warmest areas that experience the highest levels of urbanization, body mass is the lightest.

Fig. 3. Mammalian body mass is influenced by the interaction between (A) hibernation and mean annual temperature; (B) habitat buffering and mean annual temperature; (C) activity time (diurnal/nocturnal) and human population density; (D) and large/small size and mean annual temperature. Mammalian head-body (HB) length is influenced by the interaction between (E) hibernation and mean annual temperature; (F) habitat buffering and mean annual temperature; (G) activity time (diurnal/nocturnal) and human population density; (H) large/small size and mean annual temperature, and (I) large/small size and human population density.

FIGURES

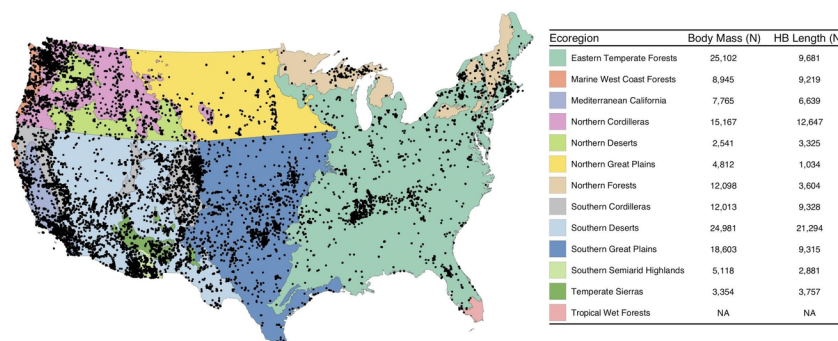


Fig. 1.

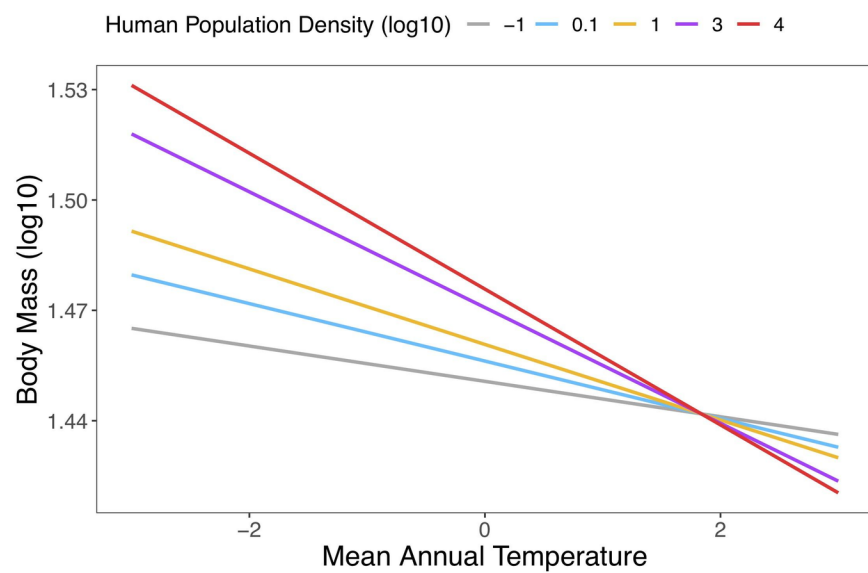


Fig. 2.

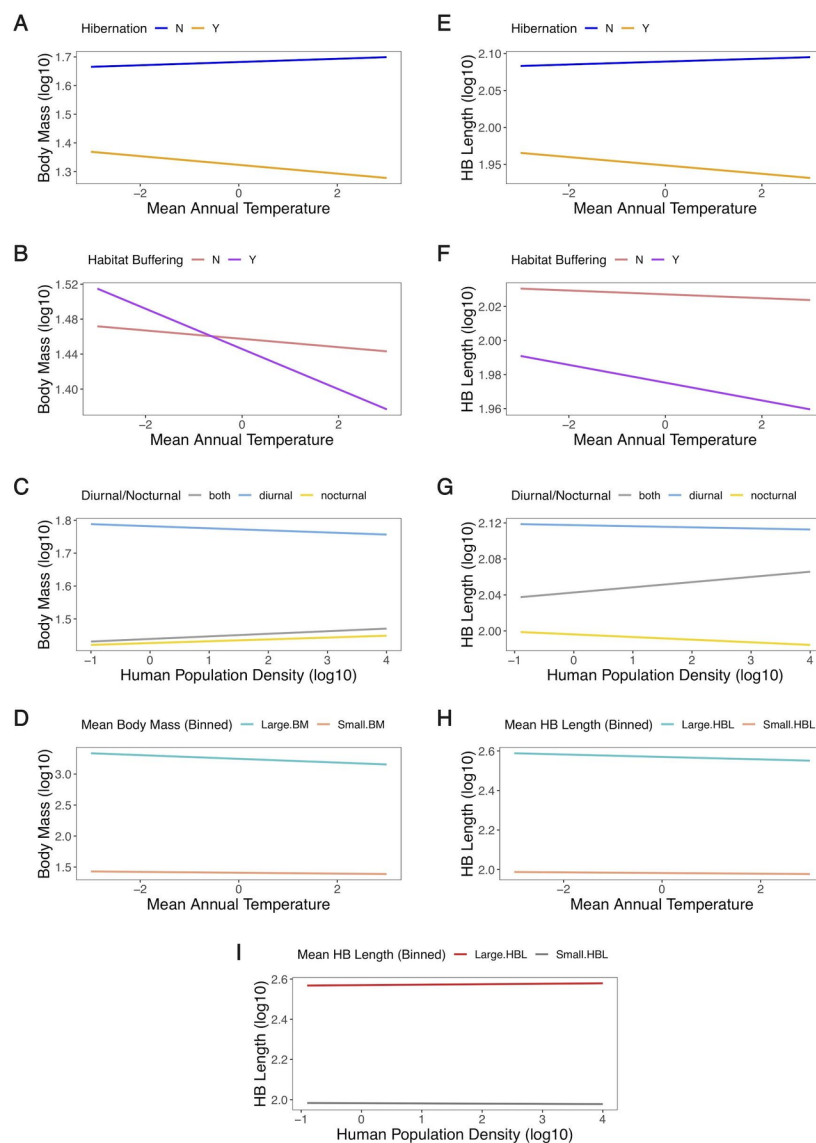


Fig. 3.

SUPPLEMENTAL FIGURES

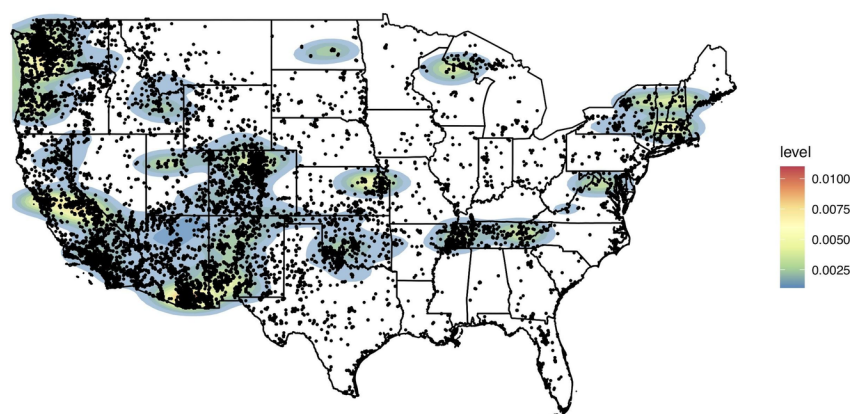


Fig. S1. Heat map of mammal record densities.

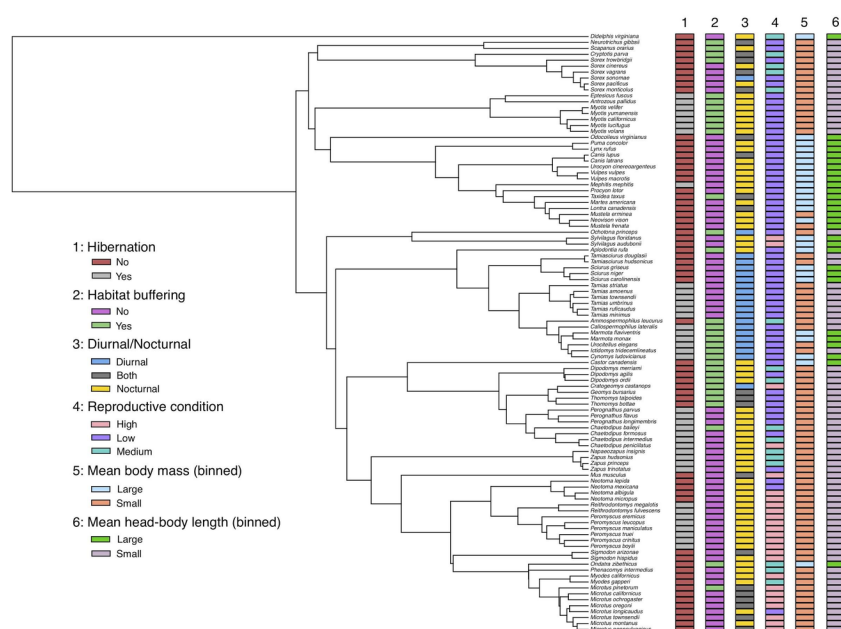


Fig. S2. Phylogeny of study species trimmed from the tree of Upham et al. (2019; <http://vertlife.org/data/mammals/>) including traits used in this study. Hibernating species include those that experience daily torpor or more prolonged hibernation bouts. Mammals that utilize habitat buffering include species that are fossorial, volant, and subterranean, while non-buffered species in our study are terrestrial and arboreal. Species with a high reproductive condition have 1-4 litters/year or more, medium refers to 1-3 litters/year, and low is 1-2 litters/year or less. Species with a large mean body size are >500g; >200mm, while small species are <500g; <200mm. Subset phylogenies of species in separate body mass and head-body length data datasets were used in the PGLMM analyses.

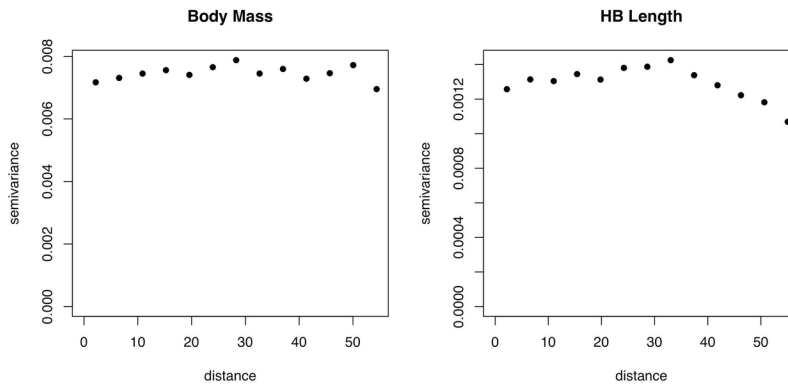


Fig. S3. Spatial autocorrelation residuals of the final body mass and head-body (HB) length models.

SUPPLEMENTAL TABLES

Table S1. Body mass, total length, tail length, and head-body (HB) length ranges extracted from the literature. R2 values are based on regressions of log₁₀ head-body length and log₁₀ body mass for each species.

Species	Mass range (g)	Total length range (mm)	Tail length range (mm)	HB length range (mm)	R2 (mass-length)	References
<i>Ammospermophilus leucurus</i>	94-118	188-240			0.03	1,2
<i>Antrozous pallidus</i>	13-30		30-60		0.07	1
<i>Aplodontia rufa</i>	700-1400	290-500	9-40		0.47	1,3,4,5
<i>Callospermophilus lateralis</i>	120-395	225-305	65-120		0.39	1
<i>Canis latrans</i>	7000-33940	1000-1600	200-450		0.36	1,6
<i>Canis lupus</i>	23000-80000	1000-1800	150-600	700-1400	0.13	1,7
<i>Castor canadensis</i>	13000-32000	900-1200			0.46	1
<i>Chaetodipus baileyi</i>	21-45	170-245		60-115	0.25	1,8
<i>Chaetodipus formosus</i>	10.5-26	75-215	80-120		0.21	1,9
<i>Chaetodipus intermedius</i>	8-20	156-190	80-112		0.21	1
<i>Chaetodipus penicillatus</i>	10-27	145-205	65-120	60-100	0.32	1,10
<i>Cratogeomys castanops</i>	180-415	220-315			0.51	1,11,12
<i>Cryptotis parva</i>	2.8-6.5	63-92		40-80	0.13	1
<i>Cynomys ludovicianus</i>	615-1675	330-450			0.04	1,13

<i>Didelphis virginiana</i>	1750-6000	330-915			0.19	1,14
<i>Dipodomys agilis</i>	50-87	232-320	130-200	100-135	0.46	15,16,17
<i>Dipodomys merriami</i>	35-55	150-250	78-155	65-122	0.09	1
<i>Dipodomys ordii</i>	50-95	200-365	90-175		0.25	1,18
<i>Eptesicus fuscus</i>	10-30	100-130	30-55		0.14	1,19
<i>Geomys bursarius</i>	250-470	180-360	45-110		0.29	1,20
<i>Ictidomys tridecemlineatus</i>	90-170	200-310	30-105		0.03	1,21
<i>Lontra canadensis</i>	5000-14000	800-1400	300-600	500-900	0.11	1,22
<i>Lynx rufus</i>	4000-15000	650-1050		500-1000	0.33	1,23
<i>Marmota flaviventris</i>	1450-5220	430-700			0.54	1,24
<i>Marmota monax</i>	1820-6000	400-685			0.21	1,25
<i>Martes americana</i>	200-1600	300-700		250-700	0.38	1,26
<i>Mephitis mephitis</i>	700-6300	400-800			0.50	1
<i>Microtus californicus</i>	25-85	125-220	30-75		0.58	1,27
<i>Microtus longicaudus</i>	20-85	140-250	30-105	75-155	0.66	1,28
<i>Microtus montanus</i>	33-90	125-220		80-150	0.33	29
<i>Microtus ochrogaster</i>	25-70	120-180		85-140	0.49	1,30
<i>Microtus oregoni</i>	11.5-34	120-160			0.33	31
<i>Microtus pennsylvanicus</i>	28-70	120-200		80-150	0.38	1,32
<i>Microtus pinetorum</i>	15-40	78-125	10-40		0.45	1,33
<i>Microtus townsendii</i>	42-95	150-235	40-82		0.61	1,34
<i>Mus musculus</i>	10-35	60-105	50-105		0.73	1
<i>Mustela erminea</i>	25-230	150-400		120-280	0.76	1,35
<i>Mustela frenata</i>	70-500	200-500		155-310	0.73	1
<i>Myodes californicus</i>	13-40			80-120	0.61	1

<i>Myodes gapperi</i>	6-45	95-190		55-140	0.62	1
<i>Myotis californicus</i>	2.5-6	65-100	22-45		0.00	1
<i>Myotis lucifugus</i>	4-14.5	65-102	22-65	35-70	0.11	1
<i>Myotis velifer</i>	4.7-17			42-67	0.11	1
<i>Myotis volans</i>	5-10.5	80-110	30-55		0.00	1
<i>Myotis yumanensis</i>	4-8	65-100	25-45		0.07	1
<i>Napaeozapus insignis</i>	15-35	200-260			0.39	1,36
<i>Neotoma albigula</i>	120-300	215-400		75-300	0.34	1,37
<i>Neotoma lepida</i>	95-350	200-415			0.38	1,38
<i>Neotoma mexicana</i>	125-250	250-430	90-185	130-210	0.24	1,39
<i>Neotoma micropus</i>	150-360	280-400	90-175	150-240	0.55	1,40
<i>Neovison vison</i>	400-1700	415-700		290-505	0.53	1
<i>Neurotrichus gibbsii</i>	7-15.5	95-135			0.08	1
<i>Ochotona princeps</i>	118-220	140-220			0.01	1,41
<i>Odocoileus virginianus</i>	30000-150000	1400-2100			0.29	1,42
<i>Ondatra zibethicus</i>	500-1800	400-620		180-400	0.35	1,43
<i>Perognathus flavus</i>	5-12	85-150		45-75	0.16	1,44
<i>Perognathus longimembris</i>	5.5-11	95-160	30-100	45-85	0.20	45,46,47
<i>Perognathus parvus</i>	13-30			60-95	0.21	1,48
<i>Peromyscus boylii</i>	17-45	150-230	50-125		0.25	1
<i>Peromyscus crinitus</i>	11-27	145-202			0.41	1,49
<i>Peromyscus eremicus</i>	15-35		60-140	70-110	0.25	1
<i>Peromyscus leucopus</i>	13-40	120-205			0.44	1,50
<i>Peromyscus maniculatus</i>	9-35	90-228		43-130	0.45	1
<i>Peromyscus truei</i>	15-35	140-240		50-117	0.36	1,51

<i>Phenacomys intermedius</i>	18-55	120-160			0.40	1,52
<i>Procyon lotor</i>	1500-10900	560-1000	150-500	300-700	0.63	1,53
<i>Puma concolor</i>	28000-120000			860-1540	0.29	1
<i>Reithrodontomys fulvescens</i>	9.7-20	117-190		50-100	0.18	1,54
<i>Reithrodontomys megalotis</i>	6.5-23	112-175		50-100	0.34	1,55
<i>Scapanus orarius</i>	50-90	130-180			0.08	1,56
<i>Sciurus carolinensis</i>	300-770	380-530		190-305	0.44	1
<i>Sciurus griseus</i>	350-1000	450-630			0.24	1,57
<i>Sciurus niger</i>	530-1000	420-700			0.10	1,58
<i>Sigmodon arizonae</i>	110-230	180-360		125-190	0.36	1,59
<i>Sigmodon hispidus</i>	65-235	210-370		100-210	0.49	1,60
<i>Sorex cinereus</i>	2.2-6	80-135	20-55	30-125	0.27	1,61
<i>Sorex monticolus</i>	4-11.5	90-160	17-70	40-100	0.37	1
<i>Sorex pacificus</i>	4.8-18	105-160			0.65	62
<i>Sorex sonomae</i>	7.5-17			62-92	0.43	1,63
<i>Sorex trowbridgii</i>	3.7-8	85-140		40-90	0.19	64,65
<i>Sorex vagrans</i>	3-8.5	78-130		40-82	0.36	66,67
<i>Sylvilagus audubonii</i>	705-1200	270-450		250-402	0.05	1,68
<i>Sylvilagus floridanus</i>	800-1550	325-480			0.16	1
<i>Tamias amoenus</i>	25-80	175-250			0.48	1,69
<i>Tamias minimus</i>	37-63	175-235	65-120		0.25	1
<i>Tamias ruficaudus</i>	50-75			117-150	0.30	1,70
<i>Tamias striatus</i>	65-127	210-270		123-170	0.31	1
<i>Tamias townsendii</i>	55-125	190-300	50-150		0.17	1,71
<i>Tamias umbrinus</i>	42-80	190-250		100-145	0.28	1

<i>Tamiasciurus douglasii</i>	135-315	250-355	80-160		0.50	1
<i>Tamiasciurus hudsonicus</i>	165-310	265-390	75-175		0.53	1
<i>Taxidea taxus</i>	3600-12000	500-900			0.40	1,72
<i>Thomomys bottae</i>	70-210	150-300	36-92		0.60	1
<i>Thomomys talpoides</i>	60-160	158-260		105-180	0.55	1,73
<i>Urocyon cinereoargenteus</i>	235-435		45-95	170-280	0.10	1
<i>Urocyon</i>	2000-9000	800-1125	200-600		0.24	1,74
<i>Vulpes macrotis</i>	1600-3075		250-400	400-600	0.10	1,75
<i>Vulpes vulpes</i>	3000-14000		300-600	455-800	0.21	1,76
<i>Zapus hudsonius</i>	13-30	150-245	90-165	55-110	0.29	1,77
<i>Zapus princeps</i>	18-42	200-260	100-165		0.38	1,78
<i>Zapus trinotatus</i>	14-37	210-265	100-167		0.43	1

Table S2. Full linear mixed-effects models (LMM) that were used to test for variation in (A) body mass and (B) head-body length across spatial scales.

Models	Models
A:	Body Mass
	mod1 <- lmer(body_mass ~ MAT + MAP + season + sex + pop_density + hibernation + buffered + diurnal_no
B:	Head-body Length
	mod2 <- lmer(HB_length ~ MAT + MAP + season + sex + pop_density + hibernation + buffered + diurnal_no

Table S3. Top (A) body mass and (B) head-body (HB) length PGLMM model results. Bold effects are significant.

	Term	Value	lower CI	upper CI
(A)	<i>Body mass</i>			
	Intercept	6.897	6.273	7.515
	MAT	-0.033	-0.045	-0.021
	MAP	-0.003	-0.005	-0.001
	Season:spring	0.058	0.055	0.062
	Season:summer	0.029	0.027	0.032
	Season:winter	-0.015	-0.019	-0.011
	Sex:male	0.006	0.003	0.008
	Population density	0.018	0.015	0.021
	Hibernation:yes	-0.922	-1.715	-0.129
	Buffered:yes	0.225	-0.378	0.826

	Diurnal/nocturnal:diurnal	0.395	-0.251	1.040
	Diurnal/nocturnal:nocturnal	-0.275	-0.604	0.052
	Small/large body mass:small	-2.583	-3.112	-2.049
	MAT x small/large body mass:small	0.054	0.041	0.066
	MAT x population density	-0.006	-0.008	-0.005
	MAT x hibernation:yes	-0.048	-0.052	-0.044
	MAT x buffered:yes	-0.042	-0.048	-0.036
	Population density x diurnal/nocturnal:diurnal	-0.033	-0.039	-0.027
	Population density x diurnal/nocturnal:nocturnal	-0.005	-0.009	-0.002
(B)	<i>HB length</i>			
	Intercept	5.732	5.490	5.973
	MAT	-0.006	-0.011	-0.002
	MAP	-0.001	-0.002	0.000
	Season:spring	0.018	0.017	0.020
	Season:summer	0.005	0.004	0.007
	Season:winter	-0.001	-0.003	0.001
	Population density	0.019	0.016	0.022
	Hibernation:yes	-0.366	-0.659	-0.074
	Buffered:yes	0.029	-0.191	0.249
	Diurnal/nocturnal:diurnal	0.108	-0.114	0.330
	Diurnal/nocturnal:nocturnal	-0.099	-0.207	0.010
	Small/large HB length:small	-0.786	-1.015	-0.558
	MAT x small/large HB length:small	0.014	0.009	0.018
	Population density x small/large HB length:small	-0.006	-0.009	-0.003
	MAT x hibernation:yes	-0.018	-0.020	-0.016
	MAT x buffered:yes	-0.009	-0.012	-0.007
	Population density x diurnal/nocturnal:diurnal	-0.016	-0.019	-0.013
	Population density x diurnal/nocturnal:nocturnal	-0.020	-0.021	-0.018

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