Intra- and interspecific phenotypic variation in mammals and its effect on biodiversity under climate warming

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ABSTRACT

Global average temperature is rapidly increasing and is currently the warmest it has been in the Northern Hemisphere over the past centuries, driving species to local extirpation or extinction, to shift their distributional range or to adapt locally to the warming climate. A given species' sensitivity to changes in its environment may be related with patterns and amount of variation in its phenotype. Across their geographic ranges, mammals are thought to vary in body size following Bergmann's rule, which predicts that populations within a species found at higher latitudes, or colder climates, are larger in size compared to populations occurring farther south in warmer temperatures. While Bergmann's rule is well supported by empirical data among mammals, there is more and more evidence for exceptions to the rule, with species either decreasing in size with latitude or displaying no apparent relation between latitude and size. The lack of generality of the rule may lie in the level of study of variation (within or between species), as well as in the phenotypic trait studied.

One application of studies on Bergmann's rule is our ability to better understand the connection between climate and phenotype, and consequently, gain greater insight into the underlying mechanisms driving species' responses to climate warming. As such, a decrease in body size has been proposed as the third universal ecological response to global warming, following distributional shifts and changes in phenology.

In this thesis, Bergmann's rule was tested at an interspecific and intraspecific level using a data-intensive approach across multiple species and traits. The patterns of variation in various morphological traits (skull length, skull width, tooth row length, and body mass) of 17 small and midsize mammalian hosts of Lyme disease were analyzed to determine if body size variation occurred in a predictable manner through space and time. Results suggest little evidence of a generalizable pattern supporting Bergmann's rule within and among species at both a broad spatial and temporal scale. The effect of latitude or time on each of the morphological traits studied were highly variable leading to three types of responses: increases in size, decreases in size, or no changes in size across space and time. Overall, size trends were detected more often in space than through time, as size variation in space was studied over a significantly larger temperature gradient than the recent change in temperature that occurred over the past 120 years. Additionally, large-bodied species were not more likely to conform to Bergmann's rule than small-bodied species, in contrast to what was previously reported in the literature; in fact, this

study showed that small mammals were found to vary more in size with latitude or time than midsize mammals. Contrary to predictions, size trends related to cranial measurements were detected as more likely to conform to Bergmann's rule than body mass, indicating the importance of simultaneously comparing metrics in studies on body size variation across species' ranges. However, body mass was found to have increased amounts of trait variability compared to cranial measurements; along a latitudinal gradient, the direction and magnitude of the variability depended on the size category of the species.

Changes in morphological traits along with northward distributional shifts due to climate change may have many consequences including changes in community composition, increased competitive pressures by invasive species, and the increased frequency and incidence of vector-borne diseases, such as Lyme disease. Climate change is expected to cause the mammalian hosts of Lyme disease to expand their geographic ranges northward, facilitating the establishment of the bacteria and tick populations in southern Canada. For the mammalian hosts of Lyme disease, studies on phenotypic variation can help determine which host species have an increased sensitivity to climate, leading them to more readily track climatic variation. A host's body size variation across its range should be integrated into future species distribution models to increase the model's predictive power. More accurate projections of a host species' future distributional shifts into southern Canada will help determine the human populations most at-risk for Lyme disease in the future.

RÉSUMÉ

Les températures globales augmentent continuellement, et ce particulièrement dans l'Hémisphère Nord lors des derniers siècles, entraînant une variété de réponses incluant l'extirpation ou l'extinction des espèces, des changements de distributions ou des adaptations locales au réchauffement de l'environnement. Puisque la variation morphologique peut différer selon les espèces de mammifères, elle peut être utilisée pour déterminer la sensibilité d'une espèce au changement climatique. Cependant, la plupart des mammifères ont des caractéristiques morphologiques qui peuvent être plus ou moins variable en fonction de l'environnement. La loi de Bergmann prédit que les individus de populations d'une espèce trouvées à des latitudes plus élevées, et donc dans des régions plus froides, sont de plus grande taille que ceux des populations trouvées plus au sud, aux latitudes plus chaudes. Tandis que la loi de Bergmann est bien documentée chez les mammifères, il y a de plus en plus d'exemples d'exceptions à la loi, où des espèces sont plus petites sous des latitudes plus élevées ou n'ont pas de relation entre la latitude et la taille. Ces exceptions à la loi de Bergmann peuvent être dues au niveau taxonomique d'étude (au sein ou entre espèces) ou aux caractéristiques morphologiques considérées.

Une application de la règle de Bergmann est de mieux comprendre la relation entre le climat et le phénotype, et par conséquent, avoir une meilleure compréhension des mécanismes qui affectent la réponse des espèces aux changements climatiques. Ainsi, une réduction de la taille corporelle a été proposée comme la troisième réponse au réchauffement climatique, avec les changements de distributions et de phénologie des espèces.

Dans ce mémoire, la loi de Bergmann a été testée aux niveaux interspécifique et intraspécifique en utilisant une base de données assemblée pour une grande variété d'espèces. Les patrons de variation de traits morphologiques (longueur du crâne, largeur du crâne, longueur de la rangée molaire et masse corporelle) ont été analysés pour 17 espèces de mammifère de petite et moyenne taille pour déterminer si la variation de ces traits dans l'espace et le temps se produit de façon prévisible. Les résultats supportent peu une généralité de la relation entre les traits morphologiques et la latitude ou le temps selon la loi de Bergmann, autant au sein des espèces qu'entre espèces. L'effet de la latitude ou du temps sur la taille des traits morphologiques est très variable, avec trois types de réponses: une augmentation de la taille, une diminution de la taille ou pas de changement de taille dans l'espace et le temps. De plus, il était moins probable que les espèces de taille moyenne se conforment à la loi de Bergmann en

comparaison aux espèces de petite taille, contrairement à ce qui est dans la littérature; en fait, cette étude montre que les petits mammifères varient plus en taille avec la latitude ou le temps que les mammifères de taille moyenne. Contrairement aux prédictions, les tendances des tailles reliées aux mesures du crâne avaient une plus haute probabilité de se conformer à la loi de Bergmann que la masse corporelle, ce qui indique l'importance de comparer différents traits simultanément dans les études sur la variation de taille d'une espèce.

Les changements de caractéristiques morphologiques ainsi que les changements de répartition vers le nord en réponse aux changements climatiques peuvent avoir des conséquences sur la composition d'une communauté, le niveau de pression de compétition avec les espèces invasives, ou la prévalence des zoonoses infectieuses, comme la maladie de Lyme. Avec les changements climatiques, il est prédit que les hôtes de la maladie de Lyme ont une expansion vers le nord dans leur limite de distribution ce qui favorise l'établissement de la bactérie et des populations de tiques au sud du Canada. Pour les hôtes de la maladie de Lyme, les études sur la variation phénotypique peuvent aider à déterminer quels hôtes ont une plus grande sensibilité au climat et sont les plus susceptibles de s'adapter aux variations climatiques. La variation de la taille des mammifères hôtes de la maladie de Lyme à travers leur distribution peut être intégrée dans les modèles futurs de distribution. Des projections plus précises de la répartition future des hôtes de la maladie de Lyme dans le sud du Canada peuvent aider à déterminer quelles populations humaines seront les plus à risque dans les prochaines décennies.

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CONTRIBUTION OF AUTHORS

This thesis consists of two chapters, which includes the second chapter to be submitted in a journal. With the active collaboration of Dr. Virginie Millien, the supervisor of the project, the candidate designed the study, collected specimens, and analyzed the data. Contents of all chapters were written by Kirsten Crandall and were edited and received intellectual input from Dr. Virginie Millien.

INTRODUCTION

GENERAL INTRODUCTION

Morphological trait variation can help determine a given species' plasticity and sensitivity to changes in its environment (Pergams and Lawler 2009). Macroecological rules of variation, such as Bergmann's rule, have been used to assess the extent of body size variation across and within species in a predictable pattern. Bergmann's rule states that populations within a species found farther north at colder latitudes will have a larger body size than populations within a species found further south at warmer latitudes (Rensch 1938, Mayr 1956). However, the relationship between a given species' environment and body size can be highly variable, leading to continuous debate of the validity of Bergmann's rule. Researchers have even questioned whether a decrease in body size should be regarded as the third universal response to climate warming following changes in distribution and phenology (Sheridan and Bickford 2011). Increased temperatures have repeatedly been cited as one of the key drivers in species' responses to climate change, including body size variation and northward distributional shifts (Coristine and Kerr 2015).

At the same time, the warming climate in the past century is partly responsible for the increased frequency and incidence of zoonotic diseases as a result of the shift in the host species' distributions (Wilcox and Gubler 2005). A species' reservoir competence for various zoonotic diseases may be related to its body size variation in response to climate warming. For example, Lyme disease, the most common vector-borne disease in the temperate world, is caused by the bacteria*, Borrelia burgdorferi*, and vectored by blacklegged ticks, *Ixodes scapularis* (Ogden et al. 2014). *I. scapularis* are known to be generalist feeders using a variety of vertebrate hosts including small and midsize mammals (Table 1; Keirans et al. 1996). Small mammals, such as rodents or shrews, are thought to have increased reservoir competence for *B. burgdorferi* compared to other midsize or large mammalian hosts (Ostfeld et al. 2014, Barbour et al. 2015). More importantly, the pathogen may also be transmitted to humans if no other suitable host is found, which is why species distributional models of the different players involved in the Lyme disease transmission cycle are imperative to predict the pattern of spread of Lyme disease (Ogden et al. 2014).

RATIONALE

From 2009 to 2016, the number of reported cases of Lyme disease in Canada has increased dramatically from 144 cases to 987 cases (Figure 1). In 2015, over 91% of these cases were reported in Ontario, Nova Scotia, and Quebec (Public Health Agency of Canada 2017). Southern Quebec is now classified as a region of emerging infectious disease with Lyme disease spreading further northward into the province each year with the number of reported cases increasing exponentially from 32 cases in 2011 to 329 cases in 2017 (Ministre de la Santé et des Services sociaux 2018; Figure 1). The confirmed presence of *Ixodes scapularis* infected by *Borrelia burgdorferi* are found in parts of the Chaudière-Appalaches, Estrie, Laval, Lanaudière, Laurentides, Montérégie, Montréal, Mauricie, Centre-du-Québec, Saguenay-Lac-Saint-Jean, and Outaouais administrative regions of Quebec (Institut national de santé publique du Québec 2018).

The geographic range of Lyme disease is expected to spread with the expansion of the distribution ranges of *B. burgdorferi*, *I. scapularis*, and the various vertebrate hosts (Ogden et al. 2008). A key factor for the spread of the bacteria and tick vector into southern Canada is the northward distributional shift of the mammalian hosts of Lyme disease (Viana et al. 2016). However, researchers are not considering species' ecologies and morphologies when analyzing macroecological rules of variation, such as Bergmann's rule, or modelling species distributions, leading to inaccurate and oversimplistic results. For the mammalian hosts of Lyme disease, studies on body size variation and variability across species' ranges can help determine which species have an increased level of phenotypic plasticity reflected in larger trait variability, allowing them to more readily track climatic variation by locally adapting. Conversely, species with low species-level plasticity who cannot rapidly adjust locally to environmental changes are more likely to shift their distribution northward. A host's level of plasticity can be incorporated into its species distribution model allowing for more accurate predictions of its future distributional shifts into southern Canada. By increasing the predictive power of the models, human populations that will be most at-risk for Lyme disease in the future can be identified.

THESIS OUTLINE

My thesis is divided into two chapters. In the first chapter, I review the literature on species' responses to climate change where distributional shifts can be predicted using species distribution models and where macroecological rules of variation, such as Bergmann's rule, can be used to quantify morphological trait variation. I review the validity of Bergmann's rule by concentrating on studies done at both an interspecific and intraspecific level. Finally, I explore the epidemiology, distribution and host biodiversity related to Lyme disease, all of which will be affected by climate change and increasing temperatures. In the second chapter, I used museum and database specimens for 17 different mammalian hosts of Lyme disease dating from the late 1800s to 2010s to analyze the effect of climate warming on a species' latitudinal body size variation across its ranges at an interspecific and intraspecific level.

Altogether, these chapters represent an integrated approach to investigating Bergmann's rule both theoretically and empirically by determining the role of intraspecific and interspecific variation in morphological traits across a large geographic scale. This information could guide researchers in determining how trait variation may play a role on a species' different ecological processes and its future distributions. A better understanding of species-level plasticity and/or adaptability could allow this variation to be input into species distribution models, providing a more realistic prediction for where the mammalian hosts of Lyme disease may be present in the future, thus identifying human populations potentially at-risk.

RESEARCH OBJECTIVES

This thesis has two research objectives:

1. **Chapter 1: To explore the patterns of Bergmann's rule using morphological trait variation and the effects of climate change on body size variation, which could subsequently affect the spread of Lyme disease.** This objective is carried out in the literature review, where previous research and theory pertaining to Lyme disease, species' response to climate change and its effect on morphological traits at both an interspecific and intraspecific level are discussed.
2. **Chapter 2: To analyze the body size variation in mammalian hosts of Lyme disease at both an interspecific and intraspecific level at broad spatial and temporal scales in the context of Bergmann's rule.** This chapter investigates whether species' morphological traits vary across a latitudinal and temporal range in accordance or opposing Bergmann's rule. Across species, the strength of the slope coefficients of the size-latitude and size-time relationships are used to determine if traits vary in a similar

direction and magnitude across space and time. Trait variability for each species is then quantified to estimate which body size metric is most plastic or locally adapted.

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CHAPTER 1: LITERATURE REVIEW

CLIMATE WARMING

Species responses

Within the last 1400 years, the most recent 30 year-period has been the warmest in the Northern Hemisphere with temperatures predicted to continue rapidly increasing in the future at these latitudes north of the equator (Diffenbaugh and Field 2013, IPCC 2013). The greatest annual warming will take place in the middle to high latitudes of the Northern Hemisphere where species may encounter more extreme weather and climatic events than what they have dealt with in the past, which includes increased global mean surface temperatures, heavy precipitation, heat waves, warm days and nights along with decreased spring snow cover extent and near-surface permafrost extent (Newman 2011, Diffenbaugh and Field 2013, IPCC 2013). In the next five decades, the temperatures in the boreal and temperate zones are predicted to increase by greater than 3°C (Newman 2011, Diffenbaugh and Field 2013). Each species can tolerate environmental shifts to a certain degree, but climate change will challenge the limits of a species' adaptive capacity and its ability to persist in some areas of its original distributional range (McMahon et al. 2011, Roy-Dufresne et al. 2013). Species encountering these novel climate conditions are predicted to respond in three ways: extinctions, distributional shifts, and local adaptations (Pergams and Lawler 2009, Diffenbaugh and Field 2013, Berteaux 2014, McCain and King 2014).

Population decline, extirpation, and extinction

Climate change may drive increases in death rates within populations, declines in population size or extinction. In general, species that are most at-risk for extinction are those that have a combination of a large body size, obligate activity times, narrow thermal tolerances, long generation times and low population sizes; smaller range areas and higher latitudinal or elevational ranges are also characteristics of the species' niche that may put them at-risk for extinction (Sheridan and Bickford 2011, Berteaux 2014, McCain and King 2014, Pearson et al. 2014). Declines in population size and mortality driven by climate change may in turn affect ecological interactions between coexisting species disrupting ecosystem services. The increasing temperatures and water limitations due to climate change could make producers respond more rapidly than higher trophic levels, which may lead to a lack of resources. It is predicted that forest die-off and decreased primary productivity is going to occur due to severe heat and drought in the tropics, temperate and boreal regions (Diffenbaugh and Field 2013). This decrease in primary productivity may directly impact higher trophic levels, leading to reduced population sizes and potential extinction (Sheridan and Bickford 2011, Cahill et al. 2013).

The populations of various North American species have been greatly affected by the environmental changes due to climate warming. Due to their low fecundity and poor dispersal ability, the American pika (*Ochotona princeps*) are extremely sensitive to climate change. Over the last century, the populations throughout the Great Basin ecoregion in the United States have been greatly impacted with a five-fold increase in local extinction rate (Beever et al. 2011). Losses in the northern populations of the pika in the Great Basin were detected during the 1990s with more recent losses occurring across their entire distributional range due to increased climatic stress related to highly variable temperature and precipitation (Beever et al. 2011). A direct consequence of climate change has been the camouflage mismatch in seasonal colour molting species, such as the snowshoe hare (*Lepus americanus*). The seasonal colour of snowshoe hares are strongly linked with their environment, as matching their coat colour to their background via camouflage decreases predation (Zimova et al. 2016). This phenological mismatch is a result of the decreased duration of snow cover throughout the temperate zones, leading to increased predation (Zimova et al. 2016). Weekly survival decreases of up to 7% were found for snowshoe hares due to the mismatches of their coat colour with that of their background. Without an adaptive response to their novel environment, increased mortality costs could lead to strong declines in the snowshoe hare population by the end of the century (Zimova et al. 2016). In southern Canada, the population sizes of the grey jay (*Perisoreus canadensis*) have been rapidly declining along the southern edge of its range because of the warmer autumns associated with climate change (Waite and Strickland 2006). This species uses the cold winter temperatures to store large amounts of food that they collect during the autumn and use as a resource until they breed in the early spring. Warmer autumns have led to increased food perishability affecting the timing of breeding and decreasing the viability in subsequent breeding events, which impacts individual survival and the species' population size (Waite and Strickland 2006).

Changes in distribution range

Range shifts are driven by the effects of climate change on a species, which are limited by its ability to disperse to more suitable locations and overcome novel biotic interactions (MacLean and Beissinger 2017). Because of climate warming, species from a wide range of taxonomic groups are predicted to shift their distributional limits northward within the next few decades (McMahon et al. 2011, Hickling et al. 2006, Berteaux 2014). Hundreds of species, including the vertebrate hosts of Lyme disease, have already had significant shifts towards the poles at approximately 6 to 17 kilometers per decade (Parmesan and Yohe 2003, Chen et al. 2011). Most species distribution models that do not consider a species' dispersal ability or biotic interactions may overestimate its ability to track climate change; instead, these models assume that all organisms will disperse northward in a comparable fashion, although, this assumption is flawed (Urban et al. 2016). The species with the best chances of survival are those with the greatest mobility or dispersal ability, as they can rapidly adjust to environmental shifts and more readily track annual climatic variation (Newman 2011, Roy-Dufresne et al. 2013). Many species may thus have the potential to shift their distributions in tandem with the changing climate, but their dispersal ability may limit their success (Diffenbaugh and Field 2013). Even after successfully dispersing northward, a species' establishment in a novel environment is dictated by its ability to overcome the various biotic limitations they may face. Species will have three options when faced with biotic limitations: completely displace a native species, occupy an unfilled niche, or partition a niche with a pre-existing species (Hutchinson 1959, Estrada-Peña et al. 2014). In general, species will have the ability to adjust their distributions if they are able to overcome both their dispersal and biotic limitations to become established in the community (MacLean and Beissinger 2017).

Changes in species' distributions due to climate warming can change the community composition as southern species replace their northern counterparts rather than being added in the community. In the northern Great Lakes region of the United States, changes in community composition were found among nine mammals species (Myers et al. 2009). Communities were found to have an increased abundance of species with primarily southern distributions along with a decreased abundance of species with primarily northern distributions. Due to climate warming, two species with primarily southern distributions, the white-footed mouse (*Peromyscus leucopus*) and the southern flying squirrel (*Glaucomys volans*), have both extended their range northward by over 225 kilometers in a 30-year period (Bowman et al. 2005, Myers et al. 2009). The distribution of the naïve native species, the northern flying squirrel (*Glaucomys sabrinus*) has been directly impacted by the northward expansion of approximately 22 kilometers per year by *G. volans* (Bowman et al. 2005). In the past decade, *G. volans* has shifted its range into parts of Ontario leading to increased levels of competition with its northern counterpart *G. sabrinus* (Bowman et al. 2005). *Glaucomys volans* can disperse into previously occupied habitats of *G. sabrinus* for two reasons: it is the competitively dominant species of the two with regards to nest territory and it indirectly decreases the population levels of *G. sabrinus* as it is a vector for the nematode pathogen, *Strongyloides robustus* (Wood et al. 2016). Both these factors may lead to future range contractions in *G. sabrinus* along with range expansions in *G. volans* into parts of southern Canada. A similar situation is detected in the southern Appalachian Mountains of the United States for two closely related ant species, the low elevation and warm-tolerant *Aphaenogaster rudis* and the high elevation and cold-tolerant *Aphaenogaster picea*. From 1970 to 2010, the ecotone for the two species has shifted upward by approximately 200 meters where *A. picea* has begun to be replaced by *A. rudis*. This replacement suggests that the warm-tolerant species, *A. rudis*, may be more competitively dominant than the cold-tolerant species*, A. picea*, with respect to climate warming (Warren et al. 2016).

Local adaptation and evolution

Certain species may not be required to assume the risks of shifting their distributions to adapt to a warming climate, but rather rapidly adapt to local conditions by modifying their phenotypes to tolerate significant changes in their current habitat (Newman 2011, MacLean and Beissinger 2017). Phenotypic plasticity is the main mechanism that species use to tolerate rapid environmental changes in their environment and is the result of behavioural and developmental changes of a given species (Pergams and Lawler 2009, Berteaux 2014, McCain and King 2014, MacLean and Beissinger 2017). The level of plasticity and associated changes in the phenotype can change rapidly between generations and can differ across populations with dissimilar habitats (Des Roches et al. 2018). Noting which species are more plastic could determine which organisms may have a future advantage under climate warming. For example, habitat generalists with wide thermal tolerances are expected to have the most plastic ecological traits as a result of their broad ecological niches (Sheridan and Bickford 2011). In general, many species will be driven to modify their body size to adjust to increasing temperatures and variable precipitation (Sheridan and Bickford 2011).

Although a decrease in body size has been hypothesized as a response to climate warming, heterogeneous responses in direction and magnitude of temporal size trends have been detected for various species (Pergams and Lawler 2009, Gardner et al. 2011, Teplisky and Millien 2013). In the meta-analysis by Gardner et al. (2011), selected studies were completed at a large spatial scale across multiple taxonomic groups including birds, mammals, reptiles, and fishes. Highly variable responses were found for both endotherms and ectotherms with the probable drivers of size variation being continuously debated, but most likely due to food availability, competition, phenotypic plasticity, and climate change. Gardner et al. (2011) predicted that the direction of selection on body size will depend on the type of temperature change occurring, as an increase in mean annual temperature may lead to a smaller body size and an occasional exposure to high daily temperatures may lead to a larger body size. These results were corroborated by Teplitsky and Millien (2013) with reported increases, decreases, and non-significant changes in body size across time for various species of birds and mammals. These differences may be due to the various mammalian families (Artiodactyla, Rodentia, Soricomorpha, and Carnivora) and avian families (Galliformes, Charadriiformes, and Passeriformes) responding differently to environmental variables with decreases in size occurring much more frequently in birds than mammals (80% versus 20%). Overall, there is limited support (60% for birds, 8% for mammals) for a decrease in body size over the last few decades (Teplitsky and Millien 2013). Rapid morphological change has been infrequently documented among mammals with a much greater focus on studies on fishes and birds. However, Pergams and Lawler (2009) have found that rapidly changing morphological traits have occurred frequently in rodents over the past 100 years. Both these increases and decreases in size were associated with human population density, current temperature gradients and/or temporal trends in temperature and precipitation, indicating that these changes in size are driven in part by climate change.

SPECIES RANGE ESTIMATES

Species distribution models

Species have exhibited varying responses in their range shifts in recent decades. This variation in response may be the result of interacting drivers of change such as individual physiological constraints, as well as factors not directly linked with the climate such as species interactions. The consensus remains the same; many species are being pushed towards the poles because of rapidly shifting favourable conditions for species due to climate change (Chen et al. 2011). One method to predict changes in a species' distribution is the use of climate envelope models or species distribution models (SDMs). SDMs examine the correlative relationship between a species' observed distribution and environmental variables to predict current and future species ranges (Keith et al. 2008, McMahon et al. 2011, Wisz et al. 2013, Berteaux 2014, Araújo and New 2007). To predict future species distributions, SDMs must consider the projected shifts of a species as a result of the abiotic drivers at both a regional and continental scale (Chen et al. 2011, McMahon et al. 2011, Diffenbaugh and Field 2013).

The assumptions and benefits of SDMs

SDMs can be calibrated and applied to any species of choice, which allows for a vast number of possibilities for researchers (McMahon et al. 2011, Berteaux 2014). These models require little information such as presence and absence data in comparison to mechanistic models that require a priori knowledge or detailed information on the life history of a species (Berteaux 2014). The impacts of climate change on species distributions can be easily represented visually using maps, which are used for conservation planning and aid in determining the extent of public health problems such as the locations of human populations that are most at-risk for contracting Lyme disease (McMahon et al. 2011, Berteaux 2014, Simon et al. 2014). Most SDMs assume that abiotic factors act as the primary determinant of species distributions, resulting in a straightforward approach to determine which parts of a species' environment may be driving its range shift given a set of input climate variables (McMahon et al. 2011). The visual maps of SDMs allow for an easy comparison of the distributions of various species at a regional and continental scale (McMahon et al. 2011). SDMs can be used to track if a species is migrating fast enough with respect to climate change by comparing the observed distributional trends to those predicted by the model (Newman 2011).

The assumptions and caveats of SDMs

SDMs have multiple limitations. Current projections are overly simplistic and tend to over-predict species distributions based on the correlative nature of the model (Araújo and New 2007, Guisan and Thuiller 2005, McMahon et al. 2011). SDMs assume that species are in equilibrium with their environment, thereby disregarding fine scale habitat variability (McMahon et al. 2011, Berteaux 2014, Urban et al. 2016). Two major assumptions in current SDMs are that species are non-interacting entities and important ecological processes such as phenotypic plasticity, and more specifically, intraspecific variation, are omitted (Chen et al. 2011, McMahon et al. 2011, Wisz et al. 2013, Kalmykov and Kalmykov 2016, Urban et al. 2016). Non-climatic factors that may affect species ranges such as species interactions and phenotypic plasticity should be included in SDMs to better understand how biodiversity is changing under climate change (Keith et al. 2008, McMahon et al. 2011, Urban et al. 2016). The inclusion of species interactions and intraspecific trait variation may thus substantially increase model predictive power.

Hutchinson (1959) believed that species interactions may cause species to be excluded from part of their fundamental niche remaining only in their realized niche as a result of biotic interactions, namely competition or predation. It is unknown how much of a species' fundamental niche is represented in SDMs as species are occupying a realized niche that will vary depending on competition, dispersal ability, and trophic level limitations (Guisan and Thuiller 2005, Newman 2011, Kissling et al. 2012, Wisz et al. 2013). Therefore, species with increased dispersal abilities, decreased trophic limitations and that are competitively dominant are expected to have fewer biotic constraints and are assumed to be constrained mainly by environmental requirements, whereas subordinate species have greater biotic constraints, such as competitive and trophic limitations, instead of environmental ones (Guisan and Thuiller 2005, Freilich and Connolly 2015).

Biological mechanisms such as demography, dispersal ability, evolution, and phenotypic plasticity are currently excluded from SDMs as data may be difficult to obtain. Instead, the use of proxies may allow us to infer how much these biological mechanisms may be affecting a species' distribution. The analysis of species' distribution shifts with SDMs would have a more realistic representation with the inclusion of trait-based proxies, such as range size, diet, number of habitats, or morphological trait variation (Keith et al. 2008, Urban et al. 2016, Hatfield et al.

2017). However, ecological models using large scale data tend to disregard intraspecific variation, focusing instead on the average values of traits, which assumes a given species' morphology or ecology will remain consistent across its entire range (Bolnick et al. 2011). This assumption is not realistic. In fact, species' traits will change as environmental conditions fluctuate over time allowing traits to vary dramatically across a species' range (Bolnick et al. 2011). It has been noted that the effects on ecological processes from intraspecific variation may be comparable or greater than species effects (Des Roches et al. 2018). Even with these limitations, SDMs remain a powerful tool to project the future spread of infectious disease vectors by analyzing the distribution of their hosts (e.g. Simon et al. 2014), although, a greater predictive power would be achieved with the inclusion of interspecific interactions and intraspecific variation in SDMs.

PHENOTYPE AND ENVIRONMENT: A FOCUS ON BERGMANN'S RULE

Body size variation can aid in determining a species' adaptive plasticity and sensitivity to climate change, which may in turn affect its distribution (Pergams and Lawler 2009, McMahon et al. 2011). Researchers have questioned whether a decrease in body size should be considered the third universal response to climate warming (Gardner et al. 2011, Sheridan and Bickford 2011, Teplitsky and Millien 2013, Berteaux 2014). Villar and Naya (2018) found that more than one third of rodent species in their study had decreased in body mass during the 20th century. A major caveat to studies on body size variation is that they ignore intraspecific trait variation. To study body size variation, natural history collections can be used as sources of historical data where shifts in size within species can be detected if broad-scale patterns of change are correlated with environmental variables (Lister and Climate Change Research Group 2011, Villar and Naya 2018).

The definition of Bergmann's rule

The major cause of controversy related to Bergmann's rule lies in its original definition. In his original publication, Bergmann (1847) stated that if species were only distinguished by size, the smaller species within a genus of homeotherms would occur in a warmer climate (James 1970). However, Bergmann originally wrote his article in German, which has never been translated to English or provided to the public science sphere (Watt et al. 2010). James (1970) provided translated excerpts from the original work, but these excerpts lack the context of the entire paper, making it hard to establish at which taxonomic level Bergmann's rule should be applied. The most widely-used derived definitions of Bergmann's rule for endotherms are by Rensch (1938) and Mayr (1956), which rely on intraspecific variation to analyze the correlation between size variation and temperature, latitude, or elevation. Each author states that the body size of populations within a species found farther north at colder latitudes should be larger in size in contrast to the smaller body sizes of populations within a species found farther south at warmer latitudes (Rensch 1938, Mayr 1956, Blackburn and Hawkins 2004, Gardner et al. 2011, Clauss et al. 2013, Classen et al. 2017). Bergmann's rule has also been described as a pattern amongst closely related species where a species of a genus in colder climates will have a larger mean body size than species of a genus in warmer climates (Lindsey 1966, Ashton et al. 2000, de Queiroz and Ashton 2004).

The validity of Bergmann's rule

A lot of debate has centered around the validity of Bergmann's rule as a generalized pattern, as it remains unclear if body mass correlates with a geographic gradient. Three types of size-latitude relationships have been documented in homeotherms: following Bergmann's rule, opposing it, or showing no relation (Figure 2). Responses to climatic variation may differ across mammalian species, but most mammals are thought to vary in their morphological traits in accordance with Bergmann's rule (Millien et al. 2006). Bergmann's rule is thought to hold for 62 to 83% of vertebrate species, but many have argued that species tend to vary greatly in their body size with equal numbers of significant and non-significant results, indicating no general body size trend (Meiri et al. 2004, Merritt 2010, Clauss et al. 2013, Gohli and Voje 2016, Classen et al. 2017). Some concluded that the ecogeographical rule is strongly supported by large- and small-bodied species with the main underlying mechanisms being heat conservation, seasonal scarcity of resources, resistance to starvation, and broad ecological niches (Ashton et al. 2000, Blackburn and Hawkins 2004, Millien et al. 2006, Rodríguez et al. 2008, Sheridan and Bickford 2011, Morales-Castilla et al. 2012, Teplitsky and Millien 2013). Other mechanisms thought to influence whether a species conforms to Bergmann's rule includes the amount of pelage in larger species, water requirements, primary plant productivity, the level of phenotypic plasticity and historical processes such as biotic exchanges or Pleistocene glaciations (Ashton et al. 2000, Rodríguez et al. 2008, Pergams and Lawler 2009, Merritt 2010, Morales-Castilla et al. 2012). Although, Olalla-Tárraga (2011) suggests that the broad generalizations of the patterns of body variation across species' ranges have no inherent mechanism and is subject to the scrutiny of empirical investigation.

Intraspecific or interspecific variation?

Discussions as to whether this macroecological rule can be applied at an intraspecific or interspecific level remains a key issue in current studies of this correlative law (Blackburn et al. 1999, Watt et al. 2010, Merritt 2010, Meiri 2011, Olalla-Tárraga 2011). The original definition by Bergmann (1847) indicates that the relationship between body size and geographic gradient should be analyzed at the interspecific level between species within genera, but studies today are conducted both at an interspecific and intraspecific level. Bergmann himself tested the rule among races of domestic animals. He suspected that the rule would be more apparent within species, but was surprised when this was not the case, leading him to only analyze what's known as Bergmann's rule at the interspecific level (James 1970, Watt et al. 2010). With the definition reformulations by Rensch (1938) and Mayr (1956), many studies now only study the rule within species, by comparing populations of species. However, Bergmann himself recognized that testing at other taxonomic levels can be done. This testing could include genera within families, species within genera, or populations within species. The decision for the rule to be associated with species within genera may not have been based on a biological mechanism, but more with the fact that Bergmann found empirical support at an interspecific level rather than an intraspecific level (Meiri and Thomas 2007, Watt et al. 2010, Meiri 2011).

Many mammalian orders, families, species and populations within species are thought to comply with this ecogeographical rule (Mayr 1956, Meiri and Dayan 2003, Millien et al. 2006, Meiri and Thomas 2007). Bergmann's rule and body size variation may be influenced by how the relations within and among species and communities change an individual's capacity to track environmental variation. Contrasting trends in the size and shape of organisms are found at different levels of biological organization, which means that different mechanisms are likely simultaneously shaping traits along climatic gradients (Classen et al. 2017, Villar and Naya 2018). An example of these contrasting drivers was documented by Classen et al. (2017) in their study on bees at Mount Kilimanjaro. On average, the bees became larger in cooler environments at the individual and population level. At the interspecific level, the number of bee species with a larger body size declined and were less variable with elevation, but individuals within a species became on average larger and were also less variable at the intraspecific level. This study is an exception as most studies on body size variation across species' ranges have been analyzed at the intraspecific and interspecific level, albeit, in isolation to the other. Further investigation is required to analyze the generality of Bergmann's rule. Olalla-Tárraga (2011) suggests investigations should be applied to homeotherms and be equally applied to different levels of biotic organization (intraspecific, interspecific, and assemblages), which may help identify the different ecological and evolutionary processes and mechanisms that shape morphological traits and geographic body size gradients.

Intraspecific variation

Intraspecific-level analyses tend to be largely ignored by empirical and theoretical ecologists due to a lack of knowledge of how trait variation may influence the mechanisms underlying ecological dynamics (Bolnick et al. 2011). Intraspecific trait variation is thought to be as influential as interspecific trait variation on community structure and ecosystem function (Des Roches et al. 2018). There are many studies in support or opposing Bergmann's rule at the intraspecific level.

Ashton et al. (2000) found broad support for Bergmann's rule in mammals, where 71% of cases showed a positive intraspecific correlation between size and latitude and 75% of cases showed a negative intraspecific correlation between size and temperature. This trend was found for species across various families and orders, different sizes, different ecologies, and various parts of the world. Meiri et al. (2004) found that 50% of the analyzed carnivore species showed a relation between skull length and latitude that varied in accordance with Bergmann's rule while 11% showed a negative relation, which opposed the rule. However, the presence of a geographical trend for Bergmann's rule may be masked by sexual dimorphism, which was detected in most of the carnivore species, but was not considered in this study (Meiri et al. 2004, Teplitsky and Millien 2013). Families, like carnivores, have wider geographic ranges leading to greater levels of size variation, which could also account for the lower support for Bergmann's rule in this family. Using body masses extracted from VertNet, Riemer et al. (2018) used a broad-scale data intensive approach to analyze Bergmann's rule for hundreds of birds and mammals, and showed that 79% of species did not vary in size with mean annual temperature while only 21% of cases (14% positive, 7% negative) displayed a significant relation between individual body mass and mean annual temperature. Riemer et al. (2018) interpreted their finding as a result of using a data intensive approach instead of a literature review or meta-analysis of Bergmann's rule that concentrates on the trends of various single species studies. Both Rodríguez et al. (2008) and Morales-Castilla et al. (2012) found that temperature strongly influenced broad-scale gradients in mammalian body size in the northern Nearctic with trends supporting Bergmann's rule, but that these gradients were not found in warmer regions such as the southern Nearctic and the Neotropics. Researchers found that the relationship between temperature and body size were non-linear, indicating the presence of a temperature threshold, which may be driven by two mechanisms, heat conservation and habitat availability.

There may be a bias in Bergmann's rule at an intraspecific level. The significance of a relationship with body size and temperature or latitude may be linked to the species' overall size. Larger (greater than 500 grams) and smaller-bodied (4 to 500 grams) organisms may exhibit distinct patterns of variation in size with temperature (Freckleton et al. 2003, Meiri and Dayan 2003, Diniz-Filho et al. 2007). Meiri and Dayan (2003) found that small mammals between 4 and 500 grams may be an exception to the rule with significantly lower or no tendency to conform to Bergmann's rule, especially within the order Rodentia. Freckleton et al. (2003) found that large-bodied species tend to follow the intraspecific version of the rule more closely than small-bodied species. Although, some small species did show consistency in their variation between temperature and body size, others did not. Diniz-Filho et al. (2007) found a similar relation where large-bodied species tended to follow the intraspecific version of the rule more closely when using latitude as the environmental predictor.

Phylogenetic considerations and interspecific variation

A major caveat to interspecific studies of Bergmann's rule is that most researchers study trait variation across a large geographic scale by averaging body size metrics to a single value leading to inaccurate analyses. The reasoning for this averaging is because body size metrics are both difficult and time-consuming to obtain for a wide variety of taxa. In some cases, species of a higher taxon may be pooled together blurring which ecological processes may be driving the correlation between body size and environmental predictors. At the interspecific level, a key driver in the modification of morphological traits between co-occurring species is competition. It may be strongest between phenotypically similar individuals and weak or absent among individuals with different evolutionary histories (Bolnick et al. 2011). When phylogenetic relationships are considered, the relationship between body size and a given climatic variable may change dramatically. By performing a phylogenetic correction and using species as the unit of analysis in studies on body size variation across species ranges, it may be easier to determine which ecological processes are at play (Meiri and Thomas 2007).

At an interspecific level, few studies have found support for Bergmann's rule using phylogenetic comparative approaches to study the relations between body size and environmental predictors. Gohli and Voje (2016) used this approach to analyze Bergmann's rule within 22 mammalian families and test the generality of the rule across mammals. Their results indicated weak support for Bergmann's rule in only one family, Canidae, and an opposite trend for latitude and temperature in pocket gophers, Geomyidae. Diniz-Filho et al. (2007) found significant correlations between body size and the environment, but most of the variation in body size was explained by phylogenetic effects. Ashton et al. (2000) corrected for a phylogenetic effect in their data, yet made all branch lengths equal due to difficulty in parsing out the phylogenetic tree. In their study, they found that all orders and most families bar a few exceptions had more species with positive relations between size and latitude than negative relations. Clauss et al (2013) showed that, in mammals, the majority of closely related species exhibit a highly significant relation between body mass and latitude, but only when the data was phylogenetically corrected. When using conventional methods with no phylogenetic correction, the relation between latitude and body mass was not significant. Alhajeri and Steppan (2016) studied Bergmann's rule in thousands of rodent species and found a weak, positive relation between mean temperature and body mass, which became non-significant when the phylogenetic effect was accounted for. A major caveat in the methods of these various studies is the averaging of a species' body mass to one value across its range, which does not realistically consider the degree of how much body size variation may be present at a broad geographic scale.

Certain studies completed at the interspecific level support Bergmann's rule yet do not take phylogenetic relationships into account. Using an interspecific analysis, Blackburn and Hawkins (2004) found a strong positive relation between the species' average body mass and latitude especially for species in the Nearctic regions, leading them to posit that Bergmann's rule can be considered a pattern at both an inter- or intraspecific level. However, they found that the interspecific version of Bergmann's rule is more closely followed by small-bodied species. This finding may be a result of different factors driving spatial variation in body mass within species and across entire communities. In general, Meiri and Dayan (2003) found that Bergmann's rule was supported at the ordinal and family levels for mammals with a few exceptions including some rodents, bats and carnivores.

Other interspecific level studies found opposing trends to Bergmann's rule. Gardner et al. (2011) provided a summary of studies undertaken since 2000, which investigated body size changes under climate warming. It was found that Carnivora, Rodentia, Lagomorpha, and Soricomorpha had variable body size responses to climate change. Some studies indicated an increase in body size due to food availability, some showed no change at all and others showed a decrease in body size due to increasing temperatures or climate change. The authors explained that the heterogeneous nature in the magnitude and direction of body size temporal responses indicated a need for large-scale phylogenetically controlled analyses. Across general taxonomic groups and within mammal taxa, the heterogeneity in responses between size and climatic variables was corroborated by various studies (e.g. Ashton et al. 2000, Sheridan and Bickford 2011, Teplitsky and Millien 2013). Teplitsky and Millien (2013) found only weak evidence for body size changes through time under recent climate change, as predicted by Bergmann's rule.

Latitude as an environmental variable

Various environmental predictors have been used to estimate the relation between a species' size and climate variation, including latitude, mean and minimum temperature, annual precipitation, evapotranspiration, global vegetation index, and seasonality (Freckleton et al. 2003, Diniz-Filho et al. 2007, Pergams and Lawler 2009, Berteaux 2014). Latitude has frequently been used as a proxy for ambient temperature and other climatic factors acting as a surrogate to these spatially-patterned environmental drivers, which may be hard to find information for across a species' range (Ashton et al. 2000, Freckleton et al. 2003, Blackburn and Hawkins 2004, Millien et al. 2006). However, the variation in latitude and the variation in temperature do not measure the same range of factors, as the two factors are not always highly correlated (Ashton et al. 2000). Temperature alone can make sense in a functional manner in relation to climate change induced size responses, whereas latitude alone has no biological meaning (Ashton et al. 2000, Freckleton et al. 2003, Blackburn and Hawkins 2004, Millien et al. 2006, Sheridan and Bickford 2011). In fact, a combination of environmental predictors such as precipitation, temperature, evaporation, and wind vary with latitude (Yom-Tov and Geffen 2006). With respect to Bergmann's rule, mean temperature and latitude have been identified as equally strong correlates of body size, with no strong evidence that either one is a better predictor (Ashton et al. 2000, Meiri and Dayan 2003).

Morphological trait comparison

Body size can be estimated from a variety of metrics such as cranial measurements, body length measurements and body mass. In most cases, studies reviewing body size variation across species' ranges with multiple morphological traits tend to document distinct patterns of variation, depending on which trait is being measured (Yom-Tov and Geffen 2011, Teplitsky and Millien 2013). This heterogeneity suggests that the choice of metric can have a large impact on conclusions related to the conformity to Bergmann's rule (Teplitsky and Millien 2013). A species' tooth size, a common body size surrogate, may be affected by competitive forces leading some researchers to think that characters other than body mass might not accurately reflect body size (Meiri and Dayan 2003). Studies relying on body mass have the greatest tendency to conform to Bergmann's rule whereas linear and dental measurements have the weakest tendency (Meiri and Dayan 2003, Teplitsky and Millien 2013). However, body mass can be extremely variable depending on seasonal fluctuations and reproductive condition, which is not the case for cranial and dental measurements (Meiri and Dayan 2003, Meiri et al. 2007, Yom-Tov and Geffen 2011). If a species' ecology is to be considered, then there is a need for considering multiple measures of body size simultaneously (Meiri and Thomas 2007). Additionally, certain morphological traits related to a species' body size can be skewed by sexual dimorphism. It remains to be seen if future studies on body size variation across species' ranges that use different body size metrics will influence conclusions on conformity to Bergmann's rule and its generality.

CASE STUDY: LYME DISEASE

Emerging infectious diseases

Zoonotic pathogens depend on a vector to transmit and proliferate in various vertebrate hosts. These pathogens are defined by the fact that they are found in at least one non-human host and can infect humans (Brisson et al. 2008). Certain zoonotic pathogens are also considered emerging infectious diseases (EIDs), as they appear suddenly or increase rapidly either in the number of cases or their geographic distribution (Ostfeld 2010). EIDs are thought to culminate from socio-economic, environmental and ecological drivers. These diseases affect thousands of people worldwide, which consequently puts a strain on the public health and economic sectors (Jones et al. 2008). An example of an EID is Lyme disease, the most common vector-borne disease in the temperate world.

Climate change and emerging infectious disease

Since World War II, the frequency and incidence of zoonotic diseases has increased rapidly because of social, demographic and environmental changes. These environmental changes include changes in land-use, human movement, wildlife movement, and climate change (Wilcox and Gubler 2005). Vector-borne diseases are especially affected by year-to-year environmental variation as well as long-term climate change (Luber and Lemery 2015). The prevalence and severity of EIDs are affected by an increased variability in climate from changes in mean temperature, precipitation and humidity (Wilcox and Gubler 2005, McMichael and Lindgren 2011, Altizer et al. 2013). Jones et al. (2008) reported that vector-borne diseases were responsible for 22.8% of EID events from 1940 to 2004, with a significant rise in the number of EID events over time. Their reasoning for this increase is that climate warming could be increasing the emergence of vector-borne diseases, especially when the vectors are sensitive to environmental changes. Changing climatic conditions may alter the reproduction, growth and viability of the vector. Arthropod vectors are ectothermic, which means they rely on the environmental temperature and humidity to regulate their body temperature. If the conditions are too hot or dry, the vectors will not be able to survive (Luber and Lemery 2015). Recent increases in infectious diseases such as malaria, tick-borne encephalitis, and Lyme disease have been associated with regional warming and altered season length (McMichael and Lindgren 2011). In the case of malaria, a projected increase in temperature may speed up mosquito development, increasing transmission and pathogen growth as the pathogen requires a temperature of at least 20°C to proliferate. Mosquito vectors for the dengue virus may be able to establish and persist in previously failed sites due to an increase in average winter temperature allowing the vector to overcome their inability to survive freezing temperatures. In the case of Lyme disease, the increasing temperature in temperate zones is likely to increase the reproductive number of vectors by shortening their life cycles, increasing their activity time and decreasing their death rate (Ogden and Lindsay 2016).

Epidemiology of Lyme disease

Borrelia burgdorferi, the bacterial agent causing Lyme disease in North America, is vectored in black-legged ticks, *Ixodes scapularis*. These ticks feed on an indiscriminate variety of vertebrate hosts including humans (Ogden et al. 2014, Kilpatrick et al. 2017). *I. scapularis* feed on one blood meal per active life stage during their larva, nymph and adult stages. After the ticks drop off the host, they molt into the next stage or, in adult females, produce eggs and die (Ogden et al. 2008b, Ogden et al. 2014, Kilpatrick et al. 2017). The tick's activity is linked to the seasons, where nymphs and adults are active in the spring, all three life stages are active in the summer, and the larvae and adults are active in autumn (Bouchard et al. 2011). *Borrelia burgdorferi* is acquired by small mammals and ground-foraging birds during the tick's larval or nymphal stages. They latch onto and feed on the hosts passing close to the ground, which are found while they are questing (Viana et al. 2016, Kilpatrick et al. 2017). During the nymph and adult stages, *I. scapularis* can also infect large vertebrate hosts after latching onto them while questing higher up on vegetation (Turney et al. 2014, Kilpatrick et al. 2017).

I. scapularis are known to feed on over 125 North American vertebrates including mammals, birds and reptile species (Keirans et al. 1996). In North America, the most competent reservoir hosts for the tick's larval and nymphal stages are small mammals including the white-footed mouse, American red squirrel, eastern chipmunk, northern short-tailed shrew, and masked shrew (Table 1; Keirans et al. 1996, Brisson et al. 2008, Bouchard et al. 2011, Wood and Lafferty 2013). The white-footed mouse, *Peromyscus leucopus*, has the highest reservoir competence. *Peromyscus leucopus* have a higher probability that a feeding tick will become infected, as greater than 85% of ticks acquired *B. burgdorferi* when feeding on an infected mouse (LoGiudice et al. 2003). However, reservoir competence is highly variable among the different mammalian hosts of Lyme disease, with the competence of other small mammals ranging from 15 to 55%. Dilution hosts of Lyme disease include a variety of species that are incompetent or have very low reservoir competence of 1 to 10% (LoGiudice et al. 2003, Brisson et al. 2008, Bouchard et al. 2013, Wood and Lafferty 2013). The main dilution hosts of Lyme disease are the white-tailed deer, striped skunks, raccoons, and opossums (Table 1; Bouchard et al. 2013, Wood and Lafferty 2013). The white-tailed deer, *Odocoileus virginianus*, are incompetent hosts of *B. burgdorferi* as they are immune to the bacteria. However, they are regarded as one of the key hosts for adult ticks acting as a fundamental part of the Lyme disease transmission cycle. Although they decrease the prevalence of *B. burgdorferi* because of their incompetence, the white-tailed deer maintain the tick populations by the high magnitude of blood meals they provide (Brisson et al. 2008, Kilpatrick et al. 2017).

Distribution of Lyme disease

Borrelia burgdorferi has been around for thousands of years with the earliest known case of Lyme disease occurring in the 5300-year-old Tyrolean Iceman, Ötzi (Keller et al. 2012). In North America, *B. burgdorferi* was identified as the cause of Lyme disease in Lyme, Connecticut during the 1970s when the number of cases suddenly skyrocketed in the region (Brisson et al. 2008, Ogden et al. 2014, Kilpatrick et al. 2017). However, reports from early American settlers indicated the presence of abundant ticks, which is corroborated by the identification of distinctive Lyme disease-causing bacterial genes in ticks and reservoir hosts from museum collections from the 1940s and the beginning of the 20th century (Persing et al. 1990, Sonenshine 1991).

In North America, Lyme disease is predominantly found in the central and eastern United States (Ostfeld 2010, Ogden et al. 2014, Turney et al. 2014). Lyme disease is also prevalent in parts of Europe and occurs to a lesser degree in the western United States and Asia. In each region, different *Ixodes* species, genotypes of *Borrelia* and host communities are present, but the transmission cycle remains the same (Ostfeld 2010, Kilpatrick et al. 2017). The perfect storm must occur between the three players (bacteria, vector, and vertebrate host) occurring in the same location at a given time; the bacteria must be circulating, the vector must be present in moderate numbers and the abundance of susceptible hosts must be high enough for Lyme disease to be transmitted (Estrada-Peña et al. 2014). If these conditions are not met, Lyme disease will not be propagated.

Role of climate change in the spread of Lyme disease

Climate change is thought to influence the distributional shifts and population densities of the vectors and hosts of various vector-borne diseases increasing the number of at-risk human populations (Mills et al. 2010, Estrada-Peña et al. 2014). Vector-borne diseases will expand in geographic range as the distributions of the pathogen will match those of the shifting vertebrate hosts (Mills et al. 2010, Altizer et al. 2013, Simon et al. 2014). The geographic range of Lyme disease is expected to change with the expansion of the ranges for *B. burgdorferi*, *I. scapularis* and the various vertebrate hosts (Ogden et al. 2008a). The key factors to the spread of *B. burgdorferi* and *I. scapularis* are the movement of the different vertebrate hosts and their northern distribution limits (Viana et al. 2016).

Endemic regions of Lyme disease are found in the northeastern United States, whereas emergent regions of Lyme disease are found in Canada. The distributions of *B. burgdorferi* and *I. scapularis* are rapidly expanding into southern Canada from the United States with emerging regions of Lyme disease being found close to the American border. As a result, the Public Health Agency of Canada has declared an environmental risk for Lyme disease in the southern regions of central and eastern Canada due to the increasing number of reported cases each year (Figure 1; Ogden et al. 2014). Climate change is expected to cause the mammalian hosts of Lyme disease to expand their geographic ranges northward, facilitating the establishment of *B. burgdorferi* and *I. scapularis* populations in Canada (Ogden et al. 2008a, Bouchard et al. 2013, Altizer et al. 2013, Simon et al. 2014). Some species such as the white-footed mouse (*P. leucopus*), the main reservoir host of Lyme disease, are shifting their range northward at approximately 8 kilometers per year as a result of the shorter and milder winters. By 2050, it is expected that *P. leucopus* will shift its distribution northward by three degrees latitude, which translates to a total of 300 kilometers (Roy-Dufresne et al. 2013, Simon et al. 2014). In fact, distribution models have shown that *I. scapularis* will be extending its range farther into Canada reaching even higher latitudes (Ogden et al. 2008a).

Lyme disease and biodiversity

Throughout North America, the degree of disease risk and the number of reported human cases are highly variable because of the distribution of the pathogen and the blacklegged ticks, which has led to the identification of different emergent and endemic regions of Lyme disease (Kilpatrick et al. 2017). The direction and strength of the relationship between biodiversity and Lyme disease risk has continued to cause controversy as it is dependent on the degree of establishment, emergent versus endemic, and the resolution of the spatial and temporal scales used in the analysis (Wood and Lafferty 2013, Turney et al. 2014). At a regional scale, where the disease is emergent, the link between host diversity and Lyme disease risk is thought to be positive, resulting in an amplication effect. In contrast, at a continental scale, a dilution effect is thought to occur in regions of endemic disease. The dilution effect is characterized by an increase in the number of dilution hosts, which is believed to decrease the relative abundance of highly competent reservoir hosts as well as disease prevalence (Keesing et al. 2006, Estrada-Peña et al. 2014, Turney et al. 2014, Kilpatrick et al. 2017).

Many failed control strategies result from focusing on a single host species assumed to be the primary reservoir for Lyme disease. To control the spread of Lyme disease, interventions must be targeted for multiple host species, which are all a part of the transmission cycle (Brisson et al. 2008). One of the key research gaps are the factors affecting the abundance and diversity of important hosts of Lyme disease across space and time (Kilpatrick et al. 2017). Among these hosts, there is a need to distinguish between host diversity and host abundance; various types of diversity such as functional diversity and species richness may have different roles in the biodiversity-disease relationship. Further work is required to determine the role of each host and the effect of changes in host communities on the biodiversity-disease relationship.

CONCLUSION

Anthropogenic impacts and climate warming may be driving species to go extinct, shift their distributions northward or change their morphological traits through phenotypic plasticity and/or local adaptation. The mammalian hosts of Lyme disease, the pathogen *B. burgdorferi*, and its vector *I. scapularis* have all moved their ranges northward into the northeastern United States and southern Canada. SDMs can project the future distributions of each of these players in the Lyme disease transmission cycle under climate change. However, these SDMs are oversimplistic and do not accurately predict which human populations will be most at-risk in the future because of one major assumption: that biotic factors, such as species interactions and intraspecific variation, can be omitted. The future extent and risk of the disease depends on how climate change is affecting the mammalian hosts of Lyme disease in their species interactions and their adaptability to a changing environment, which will influence their distributions in the coming decades. To improve the current and future modelled projections, morphological trait data can be analyzed to determine both interspecific interactions and intraspecific trait variation for each species.

Morphological trait variation and more specifically, body size variation, has been analyzed at both an intraspecific and interspecific level in multiple studies of Bergmann's rule. Currently, there is no consensus on whether Bergmann's rule can be generalized or not. However, the conclusions from these studies can be used to inform researchers how a given species may respond to climate warming. Using body size variation data, we may be able to determine which species, in response to climate change, are more likely to shift their distribution northward or adapt their traits to remain within their current distribution due to increased levels of phenotypic plasticity and/or local adaptation. An issue with the current studies of Bergmann's rule is that they are not easily comparable, as different definitions have been used to complete the studies at either an intraspecific or interspecific level depending on which taxonomic level was analyzed. Three components are required for future studies of Bergmann's rule and studies on body size variation across species' range in general: a data-intensive approach using large datasets, a simultaneous view of both the intraspecific and interspecific levels of variation, and the concurrent study of multiple species and phenotypic traits. A study with these three components may shed some light on the generality of Bergmann's rule and illustrate the importance of including both intraspecific and interspecific variation in future SDMs, such as those of the mammalian hosts of Lyme disease.

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TABLE

Table 1: Small and midsize mammalian hosts of Lyme disease found throughout southern Canada and the northeastern United States with their common names, scientific names, families and if published, their estimated average reservoir competence as a percentage (Mather et al. 1989, LoGiudice et al. 2003, Brisson and Dykhuizen 2004, Brisson et al. 2008, Brunner et al. 2008, Keesing et al. 2009, Ostfeld 2011).

Table 1

Family	Common name	Scientific name	Reservoir competence (%)
Didelphimorphia			
Didelphidae	Virginia opossum	*Didelphis virginiana*	2.8
Carnivora			
Canidae	Red fox	*Vulpes vulpes*	-
Mephitidae	Striped skunk	*Mephitis mephitis*	9.7
Procyonidae	Northern raccoon	*Procyon lotor*	1.3
Lagomorpha			
Leporidae	Eastern cottontail	*Sylvilagus floridanus*	-
Rodentia			
Cricetidae	Meadow vole	*Microtus pennsylvanicus*	4.2
	Southern red-backed vole	*Myodes gapperi*	-
	Cotton mouse	*Peromyscus gossypinus*	-
	White-footed mouse	*Peromyscus leucopus*	86.8
	Deer mouse	*Peromyscus maniculatus*	-
Dipodidae	Woodland jumping mouse	*Napaeozapus insignis*	-
	Meadow jumping mouse	*Zapus hudsonius*	-
Sciuridae	Woodchuck	*Marmota monax*	-
	Eastern chipmunk	*Tamias striatus*	60.6
	American red squirrel Grey squirrel	*Tamiasciurus hudsonicus* *Sciurus carolinensis*	14.7
Soricomorpha			
Soricidae	Northern short-tailed shrew	*Blarina brevicauda*	42.8
	Masked shrew	*Sorex cinereus*	45.9

FIGURES

Figure 1: The total number of reported cases of Lyme disease in Canada each year from 2009 to 2016 (left) and in Quebec each year from 2011 to 2017 (right). Data is from the Public Health Agency of Canada and Ministre de la Santé et des Services Sociaux (https://www.canada.ca/en/public-health/services/diseases/lyme-disease/surveillance-lyme-disease.html; accessed 7 April 2018; http://www.msss.gouv.qc.ca/professionnels/zoonoses/maladie-lyme/evolution-de-la-maladie-au-quebec/; accessed 11 August 2018).

Figure 2: Examples of the three theoretical responses of body size to a latitudinal gradient: following or opposing Bergmann's rule, or showing no significant pattern of variation in size.

Figure 1

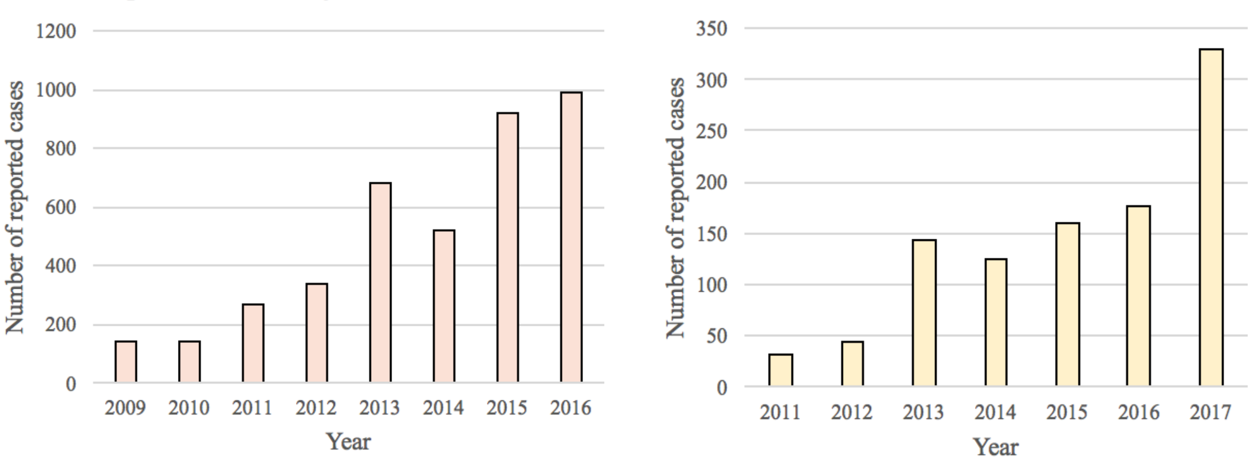
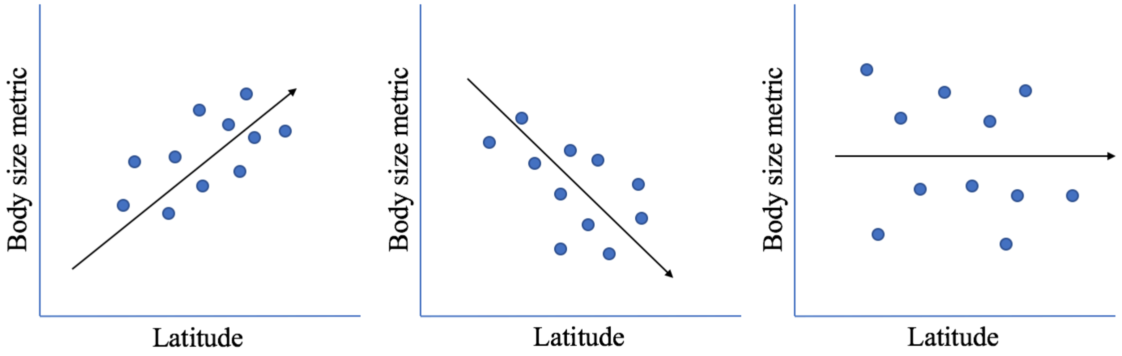


Figure 2



Following Bergmann's rule

Opposing Bergmann's rule

No relationship to Bergmann's rule

CONNECTING STATEMENT

In the first chapter, I reviewed the relationship between the environment and a species' phenotype with a focus on Bergmann's rule in mammals. I argued that incorporating intraspecific variability in size while simultaneously considering multiple species and phenotypic traits into SDMs is key to better predicting the future distributions of species. Such an approach may be applied to the estimation of Lyme disease risk in Canada, where this zoonotic infectious disease is rapidly emerging.

In the subsequent chapter, I investigated the relationship between the cranial measurements, body mass, and temperature gradients across space and time for 17 different mammalian hosts of Lyme disease to analyze Bergmann's rule and the effect of climate warming at an interspecific and intraspecific level. I explored whether responses across space and time were occurring in a consistent pattern that could be generalized. I found no clear support for Bergmann's rule through space or time due to highly variable directional responses among and between species. Overall, skull width tended to be the character most tied to latitude, whereas body mass displayed the largest amount of variability. The heterogeneity in the direction and magnitude of the size-latitude and size-time relations across morphological traits suggests that studies on Bergmann's rule and body size variation across species' ranges should consider more than a single body size metric to determine the amount of future range shift of a given species. In the context of Lyme disease, these results are important as body size variation associated with each mammalian host across its spatial and temporal ranges can be incorporated into species distribution models to better predict both current and future distributional limits and associated risk for Lyme disease in human populations.

CHAPTER 2: Size variation and variability in mammals across space and time and consequences on their response to climate warming

INTRODUCTION

Within the last 1400 years, the most recent 30 year-period has been the warmest in the Northern Hemisphere and temperatures will continue to increase in the future at these latitudes north of the equator (Chen et al. 2011, IPCC 2013). Global warming in the past six decades has been primarily caused by anthropogenic forces with a direct consequence on species' responses to changes in their environment (Ribes et al. 2017). While all species have a thermal threshold for tolerating environmental shifts, not all species can track rapid changes in climate (McMahon et al. 2011, Roy-Dufresne et al. 2013). In the next decades, species will encounter novel climate conditions due to increases in temperature, variability in annual precipitation, and extreme climatic events, which will lead to a variety of responses such as distributional shifts or local adaptations (Newman 2011, Diffenbaugh and Field 2013). Theory predicts that species may rely on a northward distributional shift of up to 20 kilometers per year to remain within their thermal tolerances, whereas others may be able to tolerate significant changes in their environment through modifications in their morphological traits via phenotypic plasticity and/or local adaptation (Pergams and Lawler 2009, Chen et al. 2011, Newman 2011, Diffenbaugh and Field 2013, Berteaux 2014, McCain and King 2014, Coristine and Kerr 2015, MacLean and Beissinger 2017, Millien et al. 2017).

Studies on morphological size variation can aid in determining species-level plasticity and adaptability, noting which species are more sensitive to changes in their environment (Pergams and Lawler 2009, McMahon et al. 2011). Bergmann's rule, one of the best known empirical macroecological patterns of size variation, describes predictable changes in body size across a broad geographical range that generally hold across taxa (Bergmann 1847). The definition of Bergmann's rule, reformulated by Rensch (1938) and Mayr (1956), states that populations within a species will have a larger body size in cooler environments compared to populations found in warmer environments. Body size is expected to vary similarly in direction and magnitude both across space and through time if the studied environmental factor (namely temperature) varies in a similar fashion across spatial and temporal scales (Teplitsky and Millien 2013). As a result, it has been proposed that a decrease in body size through time should be considered a third universal response to climate warming, following changes in distribution and phenology (Gardner et al. 2011, Sheridan and Bickford 2011, Teplitsky and Millien 2013, Berteaux 2014). Temporal morphological change has been infrequently documented among mammals with most studies involving birds and fishes. Although, climate change was shown to be a key driver of rapid morphological change in rodents via decreases in skull size in *Peromyscus maniculatus* and increases in skull size in *Peromyscus leucopus* on contemporary time scales (Pergams and Ashley 1999, Pergams and Lacy 2008, Pergams and Lawler 2009, Millien et al. 2017).

A lot of debate has centered around the validity of Bergmann's rule due to the inconsistencies in its definition and discussion over the driving mechanism behind the rule, resulting in doubts on its generality at both an interspecific and intraspecific level. The original definition of the rule formulated by Bergmann (1847) indicated its use at an interspecific level between species within genera, although, Bergmann recognized that testing could be done at other taxonomic levels (Watt et al. 2010). Currently, many mammalian orders, families, species, and populations within species have been found to comply with Bergmann's rule, but contrasting trends have been reported at different levels of biotic organization (Mayr 1956, Meiri and Dayan 2003, Millien et al. 2006, Classen et al. 2017, Sargis et al. 2018, Villar and Naya 2018). Likewise, inconsistent results were obtained for mammal species, depending on their body size. Small-bodied species between 4 and 500 grams tend to have significantly lower or no tendency to exhibit predictable patterns in body size variation across their ranges in contrast to large-bodied species (Freckleton et al. 2003, Meiri and Dayan 2003, Diniz-Filho et al. 2007).

Few studies on body size variation across species' ranges are completed simultaneously both within and among species; although, there are many studies in support or opposing Bergmann's rule at either the intraspecific or interspecific level. These contradictory results may be caused by a lack of standardization among studies and different definitions of Bergmann's rule (Blackburn et al. 1999, Watt et al. 2010, Merritt 2010, Meiri 2011). Studies on macroecological patterns of variation, including Bergmann's rule, should include these components to more easily reach a consensus as to its generalization: a data-intensive approach using large datasets and a simultaneous analysis at different levels of biotic organization (e.g. interspecific and intraspecific levels) with the use of multiple homeothermic species and phenotypic traits (Olalla-Tárraga 2011). A study with each of these components may lead to a greater consensus on the generality of Bergmann's rule and provide greater insight into the different processes or mechanisms shaping geographic body size gradients.

Body size can be estimated from a variety of metrics such as cranial measurements, body length measurements and body mass. Conformity to Bergmann's rule may be greatly impacted by the choice of body size metric (Teplitsky and Millien 2013). Body mass was found to have the greatest tendency to conform to Bergmann's rule while linear and dental measurements are the least likely to conform to the rule (Meiri and Dayan 2003, Teplitsky and Millien 2013). However, single metric studies may not accurately capture how various morphological traits of a given species vary and the mechanisms driving such variation. A species' tooth size, a common proxy for body size, may be affected by competition, whereas body mass, a highly variable trait, may vary with seasonal fluctuations, reproductive condition, or health status of an individual (Meiri and Dayan 2003, Meiri et al. 2007, Yom-Tov and Geffen 2011). Studies reviewing Bergmann's rule that concurrently use multiple morphological traits document different size trends depending on the trait being measured (Yom-Tov and Geffen 2011, Teplitsky and Millien 2013). With respect to studies on Bergmann's rule, there is thus a need to simultaneously test multiple measures of body size to assess the direction and magnitude of the spatial and temporal trends of each morphological trait.

Species' responses to a warming climate, including distributional shifts and rapid morphological changes, are partly responsible for the increased frequency and incidence of zoonotic diseases, such as Lyme disease, in the past century (Wilcox and Gubler 2005). In the temperate world, Lyme disease has become the most common vector-borne disease (Ogden et al. 2014). The increasing temperatures due to climate change are thought to drive the northward distributional shifts of the bacteria, *Borrelia burgdorferi*, the tick vector*, Ixodes scapularis*, and the various small and midsize mammalian hosts, all of which are a part of the Lyme disease transmission cycle (Mills et al. 2010, Estrada-Peña et al. 2014). In the case of Lyme disease, body size has been linked to a species' reservoir competence; small mammals, such as rodents or shrews, are thought to have a large reservoir competence for *B. burgdorferi* compared to other midsize or large mammalian hosts (Ostfeld et al. 2014, Barbour et al. 2015). Changes in morphological traits such as body size due to climate change may thus have knock-on effects on community dynamics, which could affect distributional shifts of reservoir hosts of Lyme disease thereby changing the prevalence of disease risk in various regions of the northeastern United States and southern Canada.

In this study, size variation in cranial measurements and body mass of multiple mammalian hosts of Lyme disease were analyzed at broad geographic (across the North American continent) and temporal scales (over the past 120 years) using a data-intensive approach. The expectation is that the cranial measurements and body mass both within and among these species will conform to Bergmann's rule with an increase in size occurring with increasing latitude. Additionally, it is expected that species have decreased in size over the past century with a warming climate. Due to the differences in temperature gradient through time compared to across latitudes, more spatial trends are expected to conform to Bergmann's rule than temporal trends (Teplitsky and Millien 2013). Because conformity to Bergmann's rule may depend on a species' size category (large versus small), large-bodied species are expected to follow the predicted body size trends more closely than small-bodied species. As well, trends associated with body mass, despite being a highly variable trait, are predicted to comply with the expected patterns of Bergmann's rule more so than trends in cranial measurements. More variability in body size is expected towards the northern edge of a species' range than in the core or southern edge of its distribution. Future analyses on trait variability across a species' range could be used to help predict if environmental constraints are driving species' range shifts or if species are more likely to increase trait plasticity or locally adapt. The patterns of body size variation – magnitude and variability – in North American mammalian hosts of Lyme disease could then be used in future multi-host species distribution models to predict the extent of the host species' northward shift. These predictive models could determine the expansion of the geographic range and prevalence of Lyme disease, thereby identifying which human populations are most at-risk in the future (Ogden et al. 2008, Bouchard et al. 2013, Altizer et al 2013, Simon et al. 2014).

MATERIAL AND METHODS

HOST SPECIES POOL

A total of 17 small and midsize mammals were selected based on a compiled list of the reservoir hosts of *I. scapularis*, the vector for Lyme disease in eastern North America (Turney et al. 2014). These species belong to various mammalian orders and families and have a wide range in body size, diet, and ecology. These hosts include two shrews (*Blarina brevicauda*, *Sorex cinereus*), an opossum (*Didelphis virginiana*), three carnivores (*Mephitis mephitis*, *Procyon lotor*, *Vulpes vulpes*), a lagomorph (*Sylvilagus floridanus*), and several rodents of varying sizes (*Marmota monax*, *Tamias striatus*, *Tamiasciurus hudsonicus*, *Napaeozapus insignis*, *Zapus hudsonius*, *Microtus pennsylvanicus*, *Myodes gapperi*, *Peromyscus gossypinus*, *Peromyscus leucopus*, *Peromyscus maniculatus*). Specimens were sampled from localities in emergent regions of Lyme disease in southern Quebec and in endemic regions of Lyme disease in 16 different states of the United States (Florida, Georgia, Illinois, Indiana, Maine, Michigan, Minnesota, New York, North Carolina, Pennsylvania, South Carolina, Tennessee, Vermont, Virginia, West Virginia, and Wisconsin). Six of the species (*D. virginiana*, *M. mephitis*, *P. lotor*, *S. floridanus, P. leucopus*, *P. maniculatus*) had distributions that extended into Mexico for which a small sample size of specimens were also included in the study.

DATA ACQUISITION

Museum specimens

A total of 5906 museum specimens including 2292 skull specimens were sampled from four different museums in Canada and the United States: the Field Museum (FMNH), the Musée de la nature et des sciences de Sherbrooke (MS), the Canadian Museum of Nature (CMN), and the Redpath Museum (RM) (Figure 1, Table 1). The sampled localities ranged from 16.62°N to 59.13°N in latitude with the collection year ranging from 1887 to 2017 (Table 2). Catalogue information for each specimen was extracted from online repositories such as VertNet for FMNH specimens (FMNH Mammal Collection 2015), online museum collections for CMN specimens (Canadian Museum of Nature), and museum catalogues for MS and RM specimens. This compiled information included the specimen's catalogue number, country, state or province, county or administrative region, locality, body mass, geographic occurrence (latitude and longitude), year, sex, age, breeding condition, and reproductive condition (pregnant or lactating). At each of the museums, body mass was also recorded from the associated specimen tags, and if missing, this data was completed using the associated databases.

Cranial measurements

Three different cranial measurements were measured in millimeters (mm) on each museum specimen: (1) the condylobasal length of the skull (SL) measured from the anterior points of the premaxilla anterior to the first incisors to the posterior surface of the occipital condyles along the midline of the ventral surface, (2) the skull width (SW) defined as the largest width of the skull in ventral view and was either the zygomatic breadth, the greatest distance between the lateral surfaces or outer margins of the zygomatic arches, or the largest width measured at the level of the braincase in shrews, and (3) the tooth row length (TRL) defined as the alveolar length of the maxillary tooth row excluding incisors and canines (Martin et al. 2001, Sargis et al. 2018). The tooth row was measured on the left side of the maxilla unless broken or incomplete; in that case, measurements were completed on the right side of the maxilla.

The cranial measurements for *B. brevicauda*, *M. pennsylvanicus*, *M. gapperi*, *N. insignis*, *P. gossypinus*, *P. leucopus*, *P. maniculatus*, *S. cinereus*, *S. floridanus*, *T. striatus*, *T. hudsonicus*, and *Z. hudsonius* were obtained using each specimen's photograph. Images were photographed using a Nikon D3100 with a macro lens (Nikon AS-F Micro Nikkor 85 mm 1:3.5 G). Skull specimens were photographed along with a scale and catalogue number while lying flat on the dorsal surface with the occlusal surface of the molars parallel to the camera lens. Some of the images in the RM collection were photographed using a Lumenera Infinity 1 digital camera mounted on a Leica MS5 stereomicroscope. Morphometric analyses were completed using the R package *geomorph* (Adams et al. 2017). For each specimen, six landmarks were digitized on the ventral surface of the skull using the *digitize2d* function (Figure 2A and 2B). SL, SW and TRL were calculated using landmarks 1 and 2, 3 and 4, and 5 and 6, respectively. Distances between landmarks were calculated using the *interlmkdist* function and converted into length measurements in mm using a scale photographed with each specimen. For *D. virginiana*, *M. mephitis*, *M. monax*, *P. lotor*, and *V. vulpes*, cranial and tooth row lengths were measured directly on the skull (Figure 2C) using digital calipers (Mitutoyo Absolute Digimatic Caliper CD-6" CX). Lengths were measured to the nearest 0.02 mm from where the edges of the calipers fit snugly against the bone (Martin et al. 2001).

Database specimens

As the body mass data from the museum specimens of the midsize mammals were insufficient to capture each species' latitudinal range, a database extraction of individual body mass (BM) values in grams was completed using VertNet and combined with body mass for museum specimens (Figure 1; Appendix 1; Constable et al. 2010). The Darwin Core terms used for the database extraction of the midsize mammal species included a basis of record of a preserved specimen, a specified country, and a specified state or province with the given genus and species names placed in quotation marks. Specimens were required to have a mass in their catalogue information and with the record type being that of a specimen rather than an observation. A total of 267 specimens with an associated individual body mass were retrieved for the midsize mammalian hosts of Lyme disease with sampled localities ranging from 25.14°N to 46.81°N in latitude and collection year ranging from 1901 to 2015 (Table 1 and 2).

DATA CLEANING

In this study, only adult specimens were used and juveniles were removed from the dataset. Specimens were removed if the indicated age group was that of a juvenile or young of the year in the catalogue information or if the associated specimen tag from the museum collections indicated that a specimen was a juvenile. For skull specimens, adult individuals were identified based on the complete suture of skull bones and full eruption of the molars (Martins et al. 2001). For all specimens, the ranges of adult body mass for each species were obtained from various literature sources to identify the smallest mass associated with an adult life stage (Appendix 2). All specimens with a body mass lower than this value were removed from the dataset. To analyze cranial measurements, adults with any reproductive condition remained in the dataset as this condition would not affect the specimen's skull size and shape. However, to analyze body mass, only adults that were non-lactating and not pregnant were included. Additionally, five *P. maniculatus* specimens were removed from the dataset as they had been bred in a lab colony.

Locality and Geographic Coordinates

When no county or administrative region were specified, the locality name or geographic coordinates were used to determine the name of the region. For this study, the geographic coordinate system was latitudes and longitudes in decimal degrees using the World Geodetic Datum 1984 (WGS84). Each of the latitude and longitude decimal degrees were re-verified for accuracy on Google Earth based on their given locality name (Google Inc. 2017). When no latitude or longitude information was present, locality names were used to find the geographic coordinates using both the Latitude and Longitude finder on NASA's website and Google Earth (Google Inc. 2017, Ravindran 2017). Latitude and longitude coordinates were converted to a geodetic datum of WGS84 to standardize the various database extractions. The geographic coordinates were converted from North American Datum 1927 (NAD27) and North American Datum 1983 (NAD83) to WGS84 using the Coordinate Conversion Tool from the West Virginia Department of Environmental Protection (2011). Geographic coordinates of the Universal Tranverse Mercator (UTM) system were converted to latitude and longitude decimal degrees using the same Coordinate Conversion Tool. If geographic coordinates were given in degrees, minutes and seconds, they were converted to decimal degrees using the Geographic Unit Converter from Montana State University (2014).

DATA ANALYSIS

TRAIT EFFECT

For each species, a generalized linear model (GLM) was run with the combined four log-transformed morphological traits (SL, SW, TRL, BM) as a dependent variable and latitude, trait, and their interaction as factors. Due to log-transformed size being strictly positive, a gamma family function with an identity link function was chosen. This model was used to determine if the type of trait had a significant effect on a given trait's size-latitude relationship (interaction term: trait x latitude), which would justify the use of multiple traits in further analyses.

VARIATION ACROSS SPECIES

Species effect

GLMs were run to test for the effects of predictor variables (latitude, time, species, and sex) on each of the four log-transformed morphological traits (SL, SW, TRL, BM). Sex was converted to a fixed factor to detect and account for the presence of sexual dimorphism in the analyses. Due to morphological traits being continuous variables that are strictly positive, a gamma family function was chosen. An inverse link function was chosen based on model selection using AIC scores from the *stats* package (R Core Team 2017). All GLMs first included interaction terms between all predictor variables, which was simplified by a step-wise removal of interaction terms when non-significant. For each morphological trait, the model included the main effects of latitude, year, species, and sex and the following interaction terms: species x latitude, species x year, species x sex, latitude x year and latitude x year x species. These models were used to determine if the size-latitude or size-time relations varied across species (interaction term: species x latitude and species x time, respectively), which would justify the need to analyze the relationship between each of the body size metrics with latitude and year at the species-level.

Size category effect

GLMs were run to test for the effects of latitude, time, and size category for each log-transformed morphological trait (SL, SW, TRL, BM). Size category was a two-level fixed factor (small size versus large size). Species in the small size category included *B. brevicauda*, *M. pennsylvanicus*, *M. gapperi*, *N. insignis*, *P. gossypinus*, *P. leucopus*, *P. maniculatus*, *S. cinereus*, *T. striatus*, *T. hudsonicus*, and *Z. hudsonius*. Species in the large size category included *D. virginiana*, *M. monax*, *M. mephitis*, *P. lotor*, *S. floridanus* and *V. vulpes*. For each morphological trait, the model included the main effects of latitude, year, size category, and sex along with several interaction terms (size category x latitude, size category x year, size category x sex, latitude x year, and latitude x year x size category). These models were used to determine if the size-latitude and size-time relation varied across size categories in direction and magnitude (interaction term: size category x latitude and size category x time, respectively). The sign of the relations between latitude and size for each size category was then estimated from linear models to test the hypothesis that small-bodied mammals are more likely to conform to Bergmann's rule than larger-bodied mammals.

Phylogenetic effect

A phylogenetic tree for the 17 mammalian hosts of Lyme disease was created using the *brranching* package in R (Figure 3; Chamberlain 2016). The 17 taxa were listed and extracted from the supertree of Bininda-Emonds et al. (2007) using the *phylomatic* function from this package. The slope coefficients from the linear regressions of each log-transformed morphological trait (SL, SW, TRL, BM) with latitude and time were calculated for each species.

These coefficients were used to assess if there was a phylogenetic non-independence on the size-latitude and size-time relation among the 17 different mammalian species that should be considered in further analyses. For the linear regressions between body mass with latitude and time, only 15 of the species were used as the sample sizes of *M. mephitis* and *V. vulpes* were too low (less than 25 specimens).

Two different approaches were used to quantify the phylogenetic signal of each trait: the K statistic developed by Blomberg et al. (2003) and Pagel's λ (1999). A K value greater than 1 indicates that the phylogenetic covariances among species is stronger than expected under a Brownian motion model, while for a K value less than 1, species are thought to be more phylogenetically independent. Pagel's λ varies from 0, when no phylogenetic signal is present, to 1, when the phylogenetic signal indicates species and trait data are not phylogenetically independent (Pagel 1999). The amount of phylogenetic signal present in the slope coefficients of the linear regressions of the log-transformed size-latitude and size-time relation were assessed using the *phylosig* function in the *phytools* package in R (Revell 2012). Each phylogenetic autocorrelation using the K statistic was repeated for 1000 permutations.

If no phylogenetic signal was found for the slope coefficients of the log-transformed size-latitude or size-time relation of a given trait, then no phylogenetic effect would be present and subsequent analyses did not take phylogeny into account. If phylogenetic signal was present, then the phylogenetic position of the mammals must be considered in further analyses.

VARIATION WITHIN SPECIES

Spatial and temporal trends

To analyze the spatial and temporal variation in size within species, a GLM was run for each species and each trait to test for the effect of latitude and time on trait size within species. Sex was also entered as a fixed factor in each model. The GLMs using cranial measurements as a dependent variable were run for each of the species as there were sufficient sample sizes. The GLMs with body mass as a dependent variable were run for 15 of the 17 species. Due to low sample sizes, this analysis was not run for *V. vulpes* and *M. mephitis* (less than 25 specimens). P-values were corrected using a Bonferroni correction for multiple tests.

A visual inspection of the data suggested that the latitudinal variation in size within some of the studied species was not linear. A piecewise regression using the *segmented* function in the *segmented* package in R was completed to calculate and fit the linear regressions with broken-line relationships for the species who were suspected to have a latitudinal breakpoint in their size-latitude relationships (Muggeo 2008). All plots with a suspected latitudinal breakpoint were analyzed by performing a Davies' test using the function *davies.test* in the *segmented* package to detect if there was a significant change in slope across the latitudinal range (Muggeo 2008).

Finally, to test whether spatial and temporal variation were comparable in direction and magnitude within each species, the slope coefficients of the relation between the log-transformed size of the cranial measurements and body masses with latitude and year were estimated from linear regressions. The coefficients of correlation between the slope coefficients of the size-latitude and size-time relationships were calculated using the *rcorr* function in the *Hmisc* package in R to determine if there was a correlation between spatial and temporal variation (Harrell Jr 2018).

Amount of variability of morphological traits

For each species, the amount of variability in each morphological trait was also evaluated using the coefficient of variation (CV) and the slope coefficient of the residuals-latitude relation. The coefficient of variation (CV) was calculated as a percentage using the *raster* package in R (Hijmans 2017). The CV was used to compare the overall variability for a given morphological trait within each species.

For each morphological trait, a GLM was run to test for the effects of latitude and species along with their interaction on the absolute residuals of the log-transformed size-latitude relation across species. These models were used to determine if the variability around the size-latitude trend was heterogeneous across species (interaction term: latitude x species) with the amount of variability being greater in some species than others. Linear regressions between latitude and the absolute residuals of the log-transformed size-latitude relation were run for each species and each trait. The slopes of the linear models were used to compare the relative variability of a given trait for each species. For body mass, the slope coefficients of the residuals-latitude relation were calculated for *V. vulpes* and *M. mephitis,* although, it should be noted that both species have low sample sizes (less than 25 specimens).

RESULTS

A total of 6173 specimens from both museum collections (5906 specimens) and database extractions (267 specimens) were used (Table 2).

TRAIT EFFECT

A first analysis run for each species separately and combining all the size trait data into a single trait variable revealed a significant interaction term between latitude and trait for some of the species. A significant interaction between latitude and trait was found for *B. brevicauda* ($p < 0.001$), *M. pennsylvanicus* ($p < 0.01$), *P. gossypinus* ($p < 0.01$), *P. maniculatus* ($p < 0.001$), *P. lotor* ($p < 0.001$), and *T. striatus* ($p < 0.001$; Figure 4; Appendix 3). Further analyses were thus run for each trait (SL, SW, TRL, and BM) separately as the slope of the size-latitude relation varied across traits.

VARIATION ACROSS SPECIES

Species effect

GLM models were run for each trait separately combining all species to determine the effects of latitude, year, species, and sex on each log-transformed morphological trait. There was a significant main effect of latitude (all $p < 0.001$), year (all $p < 0.001$), and species (all $p < 0.001$) for each of the four morphological traits (Table 3; Appendix 4). Significant interactions between species and sex (all $p < 0.001$) and between latitude and species (all $p < 0.001$) were detected for each morphological trait. The interaction between year and species was only significant for tooth row length and body mass (both $p < 0.001$). Because of the effect of species detected in all models, whether alone as a main effect or interacting with latitude or year, all further analyses on size variation were conducted within species. Finally, the interaction between latitude x year x species was significant for all morphological traits (all $p < 0.001$), indicating that for a given species, the latitudinal trend in size did vary over time.

Size category effect

GLM models were run for each trait separately combining all species to determine the effects of latitude, year, and size category on each log-transformed morphological trait. There was a significant main effect of latitude (all $p < 0.001$), year (all $p < 0.001$), and size category (all $p < 0.001$) for each of the morphological traits (Table 4; Appendix 5). The interaction between latitude and size category was only significant for tooth row length (both $p < 0.001$). A significant interaction between year and size category was found for all morphological traits ($p < 0.001$), as well as between latitude and year (SL, SW, BM: $p < 0.001$, TRL: $p = 0.002$). Finally, the interaction between latitude x year x size category was significant for each of the cranial measurements and body mass (SL, TRL, BM: $p < 0.001$, SW: $p = 0.009$), indicating that for a given size category, the latitudinal trend in size changed over time.

Across all species, there was a significant decrease in all four morphological traits with latitude and time (all $p < 0.001$, Table 5). However, when species were split into small and mid-size mammals, there was a clear distinction between size categories for the latitudinal and temporal size trends. Small mammals increased in tooth row length ($p < 0.001$) and decreased in skull width and body mass with latitude ($p < 0.01$ and $p < 0.001$, respectively), but there was no significant latitudinal trend in skull length (Table 5). For small mammals, significant negative trends through time were found for each of the morphological traits (SL, SW, BM: $p < 0.001$, TRL: $p < 0.01$). However, for mid-size mammals, all size-latitude or size-time relations were non-significant. Overall, size decreases with latitude and through time, but there was an effect of the size category of mammals on the strength and direction of both their latitudinal and temporal variation in size, with significant patterns detected only in small mammals.

Phylogenetic effect

Prior to conducting within-species level analyses, we tested whether the differences in slope of the latitudinal and temporal trends detected between species may be the result of the evolutionary relations and history of the study species. Blomberg et al.'s (2003) K statistic and Pagel's λ (1999) were used to calculate the phylogenetic signal of the slope coefficient from the regression line between each morphological trait with latitude and time (Appendix 6). The K statistics for all four morphological traits for the size-latitude relation was less than one and non-significant ($K = 0.513$ for SL, 0.589 for SW, 0.368 for TRL, and 0.252 for BM, all $p > 0.05$). Similarly, Pagel's λ was close to 0 (4.41e-5 for SW and 7.18e-5 for the remaining three morphological traits, all p-values of 1). The K statistics for the size-time relation was less than one and non-significant for skull length and body mass ($K = 0.487$ for SL and 0.405 for BM, both $p > 0.05$), whereas it was significant for tooth row length, although less than one (K =

0.733, $p < 0.05$), and skull width (K = 1.448, $p < 0.01$). Similarly, Pagel's λ was less than 1 for skull length ($\lambda = 0.351$, p = 0.681), skull width ($\lambda = 0.929$, p = 0.020), tooth row length ($\lambda = 0.790$, p = 0.153), and body mass ($\lambda = 7.18e-5$, p = 1.000). Overall, there was thus no phylogenetic effect on the latitudinal and temporal variation in size in our data.

VARIATION WITHIN SPECIES

Sexual dimorphism

Sexual dimorphism was detected in 9 species out of the 17 studied. Males had a longer skull length than females in *B. brevicauda*, *D. virginiana*, *P. lotor*, and *V. vulpes* ($p < 0.01$, $p < 0.001$, $p < 0.01$, and $p < 0.01$, respectively, Appendix 7 and 8). *Blarina brevicauda*, *D. virginiana*, *M. gapperi*, and *V. vulpes* also exhibit sexual dimorphism in skull width with males having larger skull widths than females ($p < 0.01$, $p < 0.001$, $p < 0.01$, and $p < 0.01$, respectively). Females had a longer tooth row length than males in *D. virginiana* ($p < 0.001$) and *T. hudsonicus* ($p < 0.01$). Finally, males were heavier than females for *B. brevicauda*, *D. virginiana*, and *M. pennsylvanicus* ($p < 0.001$, $p < 0.001$, $p < 0.01$, and $p < 0.001$, respectively), whereas females were heavier than males for *M. gapperi, N. insignis*, and *P. leucopus* (all $p < 0.01$).

Spatial trends of individual species

Overall, a significant effect of latitude was detected in 44% of the cases studied. A significant latitudinal trend in size was apparent at least for one of the four traits studied in 13 out of the 17 species (76.5%, Appendix 8). However, there were some differences in the direction of the latitudinal trend depending on the species and/or the morphological trait considered.

Species exhibited all three theoretical responses of size with latitude: an increase in size with latitude, a decrease in size with latitude or no significant change in their size (Table 6). When a significant relation was apparent, it was primarily conforming with Bergmann's rule (48% of cases). In some few cases (7 out of 66 cases), non-linear patterns of size variation with latitude were also detected. These non-linear relations took the form of a decrease in size with latitude at lower latitudes followed by an increase in size at higher latitudes in the two voles (*M. gapperi* and *M. pennsylvanicus*), while it was the opposite in a shrew (*S. cinereus*; Appendix 9).

There was also a lot of variability in latitudinal size variation, depending on the morphological traits examined (Table 6). Overall, no particular trait tended to be linked more strongly with latitude than another, with similar proportions of significant cases detected in body mass, skull length, skull width, and tooth row length (40%, 29.4%, 64.7%, and 41.2%, respectively).

The relation between skull length and latitude was significant in 5 out of 17 species (11.8% positive, 5.9% negative, 11.8% non-linear). Latitude had a positive significant effect on skull length for *B. brevicauda* ($p < 0.001$) and *N. insignis* ($p < 0.01$) and a negative significant effect for *M. monax* ($p < 0.001$; Figure 5 and 6). Both *M. pennsylvanicus* ($p < 0.001$) and *M. gapperi* ($p < 0.01$) exhibited a significant non-linear size trend with latitude where a negative relationship was present to 45°N and 46°N, respectively, followed by a positive relationship.

Skull width was the morphological trait that was most significantly related to latitude (Figure 7). A significant effect of latitude on skull width was apparent in 11 species out of 17 (29.4% positive, 17.6% negative, 17.6% non-linear). A significant increase in skull width with latitude was found for *B. brevicauda* ($p < 0.001$), *D. virginiana* ($p < 0.001$), *Z. hudsonius* ($p < 0.01$), *S. floridanus* ($p < 0.01$) and *N. insignis* ($p < 0.001$). Towards more northern latitudes, *M. monax* ($p < 0.001$), *P. maniculatus* ($p < 0.001$) and *V. vulpes* ($p < 0.01$) significantly decreased in skull width. Three species exhibited significant non-linear relationships between skull width and latitude; *Microtus pennsylvanicus* ($p < 0.001$) and *M. gapperi* ($p < 0.001$) moved from a significantly negative to positive relationship with a latitudinal breakpoint around 46°N. *Sorex cinereus* moved from a significantly positive relation to a negative relation with a breakpoint at 46.7°N ($p < 0.001$).

A significant relation between latitude and tooth row length was detected for 7 out of 17 species (17.6% positive, 17.6% negative, 5.9% non-linear). Tooth row length increased with latitude for *D. virginiana* ($p < 0.001$), *N. insignis* ($p < 0.01$), and *T. striatus* ($p < 0.001$), while it decreased for *M. monax* ($p < 0.001$), *M. gapperi* ($p < 0.001$) and *P. lotor* ($p < 0.01$; Figure 8). Here again, *M. pennsylvanicus* had a significant non-linear relationship between tooth row length and latitude ($p < 0.001$) with a decrease in tooth row length until 45°N and then an increase in size at the latitudes further north.

All three types of responses were also found for the relationship between body mass and latitude. Six out of 15 species had a significant relationship between body mass and latitude with species exhibiting a positive relation (26.7%), negative relation (5.9%) or non-linear relation (5.9%; Figure 9). *Blarina brevicauda* ($p < 0.001$), *P. lotor* ($p < 0.001$), *D. virginiana* ($p < 0.001$), and *M. pennsylvanicus* ($p < 0.001$) all increased in body mass with latitude. *Peromyscus maniculatus* decreased in body mass with latitude ($p < 0.001$). *Myodes gapperi* ($p < 0.01$) exhibited a non-linear relationship between body mass and latitude with a decrease in body mass until 46.7°N and then an increase in size towards more northern latitudes.

Temporal trends of individual species

Overall, all three types of responses (increase, decrease, or no change) were detected for temporal variation (Table 6). Once again, most species varied in their response to a temporal gradient depending on the morphological trait considered, but relatively few species exhibited a significant relationship between a given morphological trait and year (Appendix 8). Across all traits and species, a significant effect of time on size was apparent in only 12 (18.2%) cases (5 positive trends, 7 negative trends).

For skull length, 4 out of 17 species had a significant relationship with year (11.8% positive, 11.8% negative). *M. gapperi* and *M. pennsylvanicus* decreased in skull length through time ($p < 0.01$ and $p < 0.001$, respectively), while *B. brevicauda* and *P. maniculatus* increased in skull length (both $p < 0.01$, Figure 6).

For skull width, 4 species out of 17 had significant relationships with year (11.8% positive, 11.8% negative). For skull width, *P. maniculatus* ($p < 0.001$) and *V. vulpes* ($p < 0.01$) both significantly increased their size through time (Figure 7). Negative relationships between skull width and year were found for *M. pennsylvanicus* ($p < 0.001$) and *M. gapperi* ($p < 0.001$).

M. pennsylvanicus was the only species with a significant relationship between tooth row length and year, with a decrease through time ($p < 0.001$; Figure 8).

For 3 out of 15 species, body mass was detected to change through time (20%, Figure 9). *Procyon lotor* increased in body mass through time ($p < 0.001$), while the other 2 species (*M. pennsylvanicus* and *M. gapperi*) decreased in body mass over time (both $p < 0.001$).

Correlation between latitudinal and temporal trends

The correlation coefficients between the slopes of the linear regressions for the size-latitude and size-time relations were calculated for each morphological trait (Figure 6-9). None of these correlations appeared to be significant for each of the cranial measurements or body mass (p = 0.554, p = 0.667, p = 0.763, and p = 0.267, respectively).

Amount of variability of morphological traits

The coefficient of variations (CV) were calculated as a percentage for each trait of a given species (Table 7). The CV for skull length ranged from 2.89% in *S. cinereus* to 9.54% in *M. monax* with an average of 5.24% across all species. The CV for skull width ranged from 3.51% in *S. cinereus* to 13.69% in *D. virginiana* with an average of 5.88%. The CV for tooth row length ranged from 3.67% in *S. cinereus* and *N. insignis* to 7.34% in *M. pennsylvanicus* with an average of 5.12%. The CV for body mass was on average 24.57% and ranged from 10.43% in *T. hudsonicus* to 41.55% in *M. mephitis*.

For each trait, a GLM was run to determine the effects of latitude and species on the residuals of each log-transformed size-latitude relation. The main effect of both latitude and species along with the interaction between latitude and species were significant for skull length, skull width, and body mass (all $p < 0.001$; Table 8). For tooth row length, only the main effect for species and the interaction between latitude and species were significant (both $p < 0.001$).

The slope of the residuals-latitude relation was calculated for each trait of a given species (Table 7). Across all species and traits, slope values were both positive and negative, indicating an increase and decrease in trait variability with latitude, respectively. For skull length, the slope of the residuals ranged from -0.023 in *B. brevicauda* and *N. insignis* to 0.023 in *M. mephitis* with an average of -0.002. The slope of the residuals for skull width ranged from -0.031 in *N. insignis* to 0.029 in *D. virginiana* with an average of -0.001. For tooth row length, the average of the slopes for the residuals-latitude relation was -0.002 and ranged from -0.022 in *S. cinereus* and *N. insignis* to 0.021 in *S. floridanus* and *D. virginiana*. The slope of the residuals-latitude relation for body mass ranged from -0.198 in *P. gossypinus* to 0.190 in *P. lotor* with an average of 0.026.

DISCUSSION

WHICH MORPHOLOGICAL TRAIT IS BEST SUITED TO STUDY BODY SIZE VARIATION IN MAMMALS?

Conformity to Bergmann’s rule may depend on which body size metrics are used, as studies based on body mass are thought to have the greatest tendency to reveal patterns following

Bergmann's rule, compared to linear skeletal and dental measurements (Meiri and Dayan 2003, Teplitsky and Millien 2013). Our study is one of the few studies based on empirical data in which four distinct traits were considered, including body mass, but also skull and dental lengths. Such an approach allowed us to rigorously test the hypothesis and we found that body mass was not more likely to conform with Bergmann's rule than skeletal measurements. Overall, for the 17 mammal species included here, the relation between size and latitude varied across traits (in terms of the direction and magnitude of the trend), and the effect of latitude tended to be stronger for skull width followed by tooth row length than the rest of the morphological traits. Therefore, this variability between the different morphological traits should be considered when comparing body size metrics in studies on Bergmann's rule, as conclusions on the conformity to the rule may change depending on the traits being analyzed.

SEXUAL DIMORPHISM AND BODY SIZE VARIATION

Sexual dimorphism was detected in more than half of the study species. This result indicates that sex should be included as a factor for the species-level analyses in mammals, as size metrics may be skewed by sexual dimorphism. Here, sexual dimorphism was present in a wide variety of species; when significant, longer skull lengths and larger skull widths were found in males compared to females whereas a longer tooth row length was found in females compared to males. Body mass was found to be a sexually dimorphic trait for certain species, but inconsistencies were found among species for which sex had the larger body mass. Given these results, we argue that studies on Bergmann's rule should account for sexual dimorphism, as significant differences between the morphological traits of each of the sexes could be skewing the size relationships across space and time.

EVOLUTIONARY HISTORY AND BODY SIZE VARIATION

A major caveat to some of the studies on Bergmann's rule at an interspecific level is the assumption of phylogenetic independence of the analyzed data. The patterns associated with Bergmann's rule may change in significance once the phylogenetic structure of the data has been accounted for (Clauss et al. 2013, Alhajeri and Steppan 2016). In this study, the phylogenetic signals associated with the slope coefficients of the linear regressions between the morphological traits with latitude or time helped to determine if a phylogenetic effect was driving the size trends across all the mammalian hosts of Lyme disease we analyzed. In general, the K statistic values for each trait were below 1 and the λ values were close to 0, indicating that no phylogenetic signal was present in our data. These low values are evidence of the minimal phylogenetic effect in these slope coefficients across species. The size of the morphological traits are very likely dependent on the phylogenetic position of the different mammal species. However, the direction and magnitude of the size-latitude and size-time relations may not be strongly driven by the phylogenetic history of the study species, as demonstrated here. A similar result was found in a study on tropical montane passerines where there was no relationship between the body masses of the entire passerine avifauna in relation to their elevational distributions at deeper phylogenetic scales (Freeman 2017). Therefore, the size trends found across species are not due to a phylogenetic effect, but because of species behaving differently in their relationships between a given morphological trait and latitude or time.

GENERALITY OF BERGMANN'S RULE

Bergmann's rule, the trend of increasing body size with latitude, is thought to hold for a wide variety of vertebrate species including mammals. However, it has been widely debated whether Bergmann's rule is a generalized pattern (Meiri et al. 2004, Merritt 2010, Clauss et al. 2013, Gohli and Voje 2016, Classen et al. 2017). It is especially relevant to complete these studies on body size variation across species' ranges in the current context of global warming. If Bergmann's rule holds true across space, and assuming the mechanism for it is linked with environmental temperature, it is predicted that it should apply equally in time. With a warming climate, mammal species are thus expected to decrease in size (Gardner et al. 2011, Sheridan and Bickford 2011, Teplistky and Millien 2013, Berteaux 2014).

Overall pattern of size variation across species

Here, at the interspecific level, latitudinal and temporal effects were found for all four morphological traits, with a decrease in size with latitude and time, which conforms to Bergmann's rule through time, but opposes it across space. However, there was some variability in these spatial and temporal size trends across species, both in terms of direction and magnitude of trends. The slope coefficients of the size-latitude and size-time relation differed significantly across species for all the morphological traits. These results justify the need to analyze the relationship between each of the morphological traits with latitude and year at the species-level.

Interestingly, we found that the difference in species response to latitude or time may be linked to the body size of the species: small mammals (up to 240 grams) tended to vary more in size with latitude or in time than midsize mammals (greater than 700 grams). The slope of the size-latitude and the size-time relation varied across size categories for all three cranial measurements as well as body mass. These differences between size categories are thought to be because small-bodied species more closely follow the rule compared to large-bodied species, however, we found that it is not the case (Meiri and Dayan 2003, Blackburn and Hawkins 2004). In fact, small mammals included in our study showed all three types of response (positive, negative, and no response) in the size-latitude relations for each of the morphological traits across space, indicating that they do not conform more strongly to Bergmann's rule than larger mammals, a conclusion also supported by Ashton et al. (2000). Surprisingly, many of the size-latitude relations among small mammals were found to be non-linear across space with the presence of a latitudinal breakpoint. However, while small mammals generally decreased in size through time following Bergmann's rule, mid-size mammals did not.

There are limitations to the conclusions that may be drawn from the data, although, changes in morphological traits such as body size are likely a response to changes in climate, however, biotic interactions such as interspecific competition may also significantly drive variation in size in mammals (Pergams and Lawler 2009). Phenotypically similar individuals, such as species from within the Rodentia order, are expected to experience the strongest amount of interspecific competition compared to the weak or absent amounts of competition among divergent individuals (Brown and Wilson 1956, MacArthur and Levins 1964, Dayan and Simberloff 2005, Bolnick et al. 2011, Stuart and Losos 2013, Millien et al. 2017). The morphological and ecological similarities between these species could lead to increased competitive pressures, which may indirectly affect food web structure and community dynamics (Brown and Wilson 1956, MacArthur and Levins 1964, Dayan and Simberloff 2005, Bolnick et al. 2011, Stuart and Losos 2013, Millien et al. 2017). Competition for resources or habitat may cause species to diverge in their morphological traits such as body size or dental traits (Brown and Wilson 1956, MacArthur and Levins 1964, Dayan and Simberloff 2005, Grant and Grant 2006, Stuart and Losos 2013, Stuart et al. 2014, Millien et al. 2017, Villar and Naya 2018).

Competitive pressures between morphologically similar species either pressures species to use different resources and forage in different microhabitats to co-exist across their geographic distributions or requires species to alter the morphology of their traits related to resource acquisition to reduce competition for resources and habitats (Brown and Wilson 1956, Vickery 1981, Bowers and Brown 1982, Desrosiers et al. 2002, Grant and Grant 2006, Stuart et al. 2014, Villar and Naya 2018). As midsize mammals tend to have dissimilar morphologies and ecologies, these species may not experience as large an amount of competitive pressure as small mammals for resources and habitat and thus will not be as likely to vary their body size through space and time. Clear differences are found between the small and midsize mammals and the effect of latitude and year on a given species' morphological traits must be further investigated using an intraspecific analysis of Bergmann's rule as even within these groupings, species may contrast in the way they vary in size.

Spatial trends within species

At an intraspecific level, three different body size responses to latitude were found with some species increasing in size with latitude thereby conforming with Bergmann's rule, others decreasing in size, or other species not changing in size with latitude. These results indicate that no general trend for Bergmann's rule can be found within species contrasting the studies where over 50% of cases were conforming with Bergmann's rule (Ashton et al. 2000, Meiri et al. 2004). Here, no significant relation between size and latitude was detected in 56% of the cases. When a significant relation was apparent, it was predominantly conforming with Bergmann's rule (44% of the significant cases). Finally, Bergmann's rule was more often detected when using skull width as a size metric rather than body mass or other cranial measurements.

There was no tendency for small-bodied species to more likely conform with Bergmann's rule than larger species, as predicted in some earlier studies (Ashton et al. 2000, Freckleton et al. 2003, Diniz-Filho et al. 2007). However, certain trends with respect to body size metrics and latitude are apparent for different groups of species. The northern short-tailed shrew (*B. brevicauda*) is increasing in size with latitude in skull length, skull width, and body mass. The masked shrew (*S. cinereus*) is also increasing in size in skull width (although only for part of its distribution) with latitude. In shrews, due to their high metabolism, body size changes in their morphological traits are highly linked to food availability and seasonality. An example of seasonal morphological change was detected in another shrew species, *S. araneus*. This species decreases the size of their skulls during the winter, which is believed to help them save energy to survive when food is scarce (Young 2017). Although not present in this study, Yom-Tov and Yom-Tov (2005) found a decrease in the body mass of *S. cinereus* species in colder latitudes, which was attributed to the link between food availability and seasonality, as shrews have limited food resources during the winter months.

Here, *M. monax* is decreasing in size with latitude for all cranial measurements, opposing Bergmann's rule. This result may be due to this species being a habitat generalist with a wide geographical range (Sheridan and Bickford 2011, McCain and King 2014). Other idiosyncrasies were evident in our study. The meadow vole, *M. pennsylvanicus*, and the southern red-backed vole, *M. gapperi*, were consistently variable in their size related to latitude for the various morphological traits except for body mass and tooth row length, respectively. Their size trends showed a decrease in size up to a latitudinal breakpoint of 45°N to 46°N, which then switched to an increase in the size depending on which trait was being analyzed for each species. The results related to *M. gapperi* have also been found by Souto-Lima and Millien (2014) where the skull size of individuals from the Mixedwood Plains ecozone were larger than those from the Boreal Shield ecozone. This variable change in size could therefore be from a shift in ecozone or other potential geographic barriers such as the Great Lakes that are found on the 45th parallel North.

BERGMANN'S RULE THROUGH TIME?

As is the case for spatial variation, at an intraspecific level, we detected three types of body size changes through time with species increasing in size, decreasing in size or not changing in size with year. When significant, the temporal trend was negative more often than it was positive. Individual species had different responses in body size variation to a warming climate on a contemporary time scale, yet certain temporal trends may be apparent for different groups. Surprisingly, *B. brevicauda* only experienced decreases in skull length through time in addition to no significant size trends being found for *S. cinereus*. In contrast to our study, it has been previously found that *S. cinereus* from Alaska significantly increased its body size over the second half of the twentieth century (Yom-Tov and Yom-Tov 2005). In this case, the study was conducted over a regional geographic area and the increase in body size through time was linked to higher food availability due to the milder winters of the past few decades improving the weather conditions for its prey (Yom-Tov and Yom-Tov 2005). Similarly, Rodríguez et al. (2008) and Morales-Castilla et al. (2012) found strong broad-scale trends as predicted by Bergmann's rule where mammalian body size was more influenced by temperature in cold macroclimates compared to warmer macroclimates due to a non-linear relationship between temperature and body size.

Over time, the species' most affected by climate warming were the rodents, which contrasted the results found by Meiri and Dayan (2003). Species from the order Rodentia were found to exhibit the most morphological changes through time with all the significant relationships between a given morphological trait and collection year detected in a rodent species except for one species of shrew (*B. brevicauda*), the red fox, and the raccoon. Within Rodentia, only two species (18% of the cases) exhibit a decrease in size through time in at least one of the size traits we used. Both species of voles experienced decreases in all their morphological traits with collection year except for tooth row length in *M. gapperi*. However, the deer mouse (*P. maniculatus*) increased its skull length and skull width through time. Villar and Naya (2018) found similar variability for various rodent species with greater than a third decreasing in size and the rest showing no significant changes in size through time, yet, only body mass was used to analyze the relationship between body size and time. The difference in our results compared to those of Villar and Naya (2018) may be due to the trait being investigated, as many of the temporal trends we detected in rodents were for cranial measurements (77% of the cases) (Teplitsky and Millien 2013). The variability in the direction of the size responses for rodents has been deemed as a plastic response or local adaptation to either current temperatures or changes in temperature over time, modulated by competitive interactions between co-existing species (Pergams and Lawler 2009, Millien et al. 2017).

Assuming that temperature is the main driver for body size variation across species' ranges, it has been proposed that a decrease in body size through time is expected in response to recent and future climate warming. If a given trait varied through space and time in a parallel fashion, then it increased across the latitudinal range and decreased through time. However, we found no clear evidence for a parallel between spatial and temporal variation in size within our study species for any of the examined morphological traits. In other words, when a significant latitudinal pattern was detected, it did not translate into an equally significant temporal pattern. As in Teplitsky and Millien (2013), spatial latitudinal patterns were also more often detected and stronger than temporal trends. Yet, when species changed in size over the past 120 years, most of them decreased in size, as predicted in Gardner et al. (2011).

VARIABILITY IN SPECIES’ RESPONSES TO CLIMATE GRADIENTS

The strength of the effect of latitude on size may give some insight into how tightly a species is constrained by its environment. A species which shows no latitudinal pattern in body size is likely to tolerate a wider range of environmental conditions across its distribution range, compared with a species displaying a strong increase or decrease in size with latitude. However, another additional indicator of a species’ sensitivity to its environment is the amount of variability in a given morphological trait it displays across its ranges.

Here we used different approaches to estimate the amount of trait variability across each species’ range. The overall variability of a given species was measured using the CV of each morphological trait. CV values tended to be much lower for cranial and dental measurements than body mass, suggesting that body mass is a more variable trait than skeletal ones. We also estimated trait variability in each species by examining the relation between latitude and the absolute residuals of the size-latitude relation. For each species, the slope coefficients related to cranial and dental measurements were much smaller than those associated with body mass, which demonstrates once again the increased variability in body mass. Across all species and traits, the slope of this relation was either positive or negative depending on the size category of the species. In addition, the strength of this latitudinal trend in trait variability differed across species. Generally, the slope coefficients of the midsize mammals as well as the American red squirrel (*T. hudsonicus*) and the eastern chipmunk (*T. striatus*) were positive, indicating an increase in trait variability across latitudes towards the northern edge of their distributions. In contrast, small mammals whose slope coefficients tended to be negative demonstrated a decrease in trait variability across latitudes with species’ varying their traits more towards their southern limit and core distribution.

In mammals, body mass may be easily influenced by various factors such as reproductive condition, season and health status of an individual. These factors greatly increase the degree of variability in body mass in comparison with cranial measurements, that in most cases are minimally affected by pregnancy, lactation, or environmental fluctuations (Meiri and Dayan 2003, Villar and Naya 2018). Therefore, body mass may not be the most reliable trait to use in studies on body size variation across species' ranges, and more specifically Bergmann's rule, if we are to accurately estimate the mechanisms driving such morphological trait variation.

The potential mechanisms driving changes in morphological traits along with their increased variability could be phenotypic plasticity and/or local adaptation (Pergams and Lawler 2009). However, the two mechanisms are difficult to disentangle. Both mechanisms act as a key component to a species' persistence in its environment especially with climate warming (Villemereuil et al. 2018). Adaptive plasticity is the likely mechanism seen at the end of time ecological time scales or near range edges, although, it has the potential to be maladaptive if species cannot cope with their new environmental conditions (Pergams and Lawler 2009, Villemereuil et al. 2018). Morphological changes in body size may also occur via local adaptations as a result of natural selection and genetic change, but this mechanism takes longer to establish (Pergams and Lawler 2009, Villemereuil et al. 2018). Obviously, a combination of both local adaptation and phenotypic plasticity is expected to occur in all the mammalian hosts of Lyme disease, but our study hypotheses that the relative importance of these two mechanisms as a response to climate warming may differ across species. The pattern of body size variation and variability for each of the mammalian hosts of Lyme disease could provide useful proxies to estimate the relative weights of these mechanisms and improve the predictive power of their species distribution models to help determine their potential northward range shifts in response to climate warming.

CONCLUSION

In conclusion, we found little evidence for a generalized pattern of size variation in accordance with Bergmann's rule in the small and mid-size mammalian hosts of Lyme disease. The relationships between body size metrics (cranial measurements and body mass) with latitude and time differed at both an interspecific and intraspecific level. All three patterns of size variation were found empirically between and within species with increases in size, decreases in size or no changes in body size observed across space and time. The mechanisms driving these patterns are diverse. The heterogeneity in patterns of size variation we observed may lie in the variety of mechanisms, which include interspecific competition, food availability, responses to seasonality, and species-level plasticity and adaptability to environmental changes. Body mass was found to be the morphological trait associated with the greatest amount of intraspecific variability, which could potentially affect the patterns associated with geographic body size gradients across species' ranges. To more accurately investigate Bergmann's rule, studies should use a data-intensive approach with large datasets to assess patterns simultaneously at an intraspecific and interspecific level for multiple homeothermic species and traits. Our study demonstrates that the heterogeneity in responses across space and time for intraspecific and interspecific morphological trait variation should be considered when assessing species-level plasticity, adaptability, and sensitivity to climate warming. As a result of climate warming, the heterogeneous changes in morphological traits and patterns in body size variation found in this study may affect the northward distributional shifts of the mammalian hosts of Lyme disease. The inclusion of the body size patterns of variation and variability of the mammalian hosts of Lyme disease in future species distribution models could more accurately predict the future northward distributional shifts of these species, which can help determine the human populations most at-risk in the coming decades.

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FIGURES

Figure 1. Locations of all the museum specimens (top) and database specimens (bottom) in latitudinal and longitudinal decimal degrees from Canada, Mexico and the United States using Google Earth imagery (Google Inc., 2018).

Figure 2. The six landmarks used for morphometric analyses to extract cranial measurements. (A) For small mammal skulls, example of a *Tamiasciurus hudsonicus* specimen. (B) For shrew species (*B. brevicauda* and *S. cinereus*), example of a *Sorex cinereus* specimen. (C) For caliper position on midsize mammals, example of a *Procyon lotor* specimen.

Figure 3. Phylogeny used to test for a phylogenetic signal. The topology and branch lengths in millions of years were obtained from the supertree by Binind-Emonds et al. (2007). Highlighted groups are of the different orders of the studied species (Rodentia, Carnivora, and Eulipotyphla). Each tip represents one of the 17 studied mammalian species.

Figure 4. Relationship between latitude and log-transformed size for the morphological traits of each mammalian host of Lyme disease. P-values for the interaction between latitude and trait are indicated in the top right corner along with the significance level for linear regressions for skull length (red), skull width (blue), tooth row length (purple), and body mass (green). Significant p-values (< 0.05) are indicated in bold.

Figure 5. An empirical example of the three different species' relationships between a given morphological trait and latitude. (A) *B. brevicauda* is increasing in skull length with latitude in accordance with Bergmann's rule. (B) *M. monax* is decreasing in skull length with latitude, opposing to Bergmann's rule. (C) There is no effect of latitude on the skull length in *P. gossypinus*.

Figure 6. Slope coefficients from the linear regression between log-transformed skull length and (A) latitude or (B) year for each species. Significant slope coefficients were indicated using p-values where * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, which were determined by the GLMs between skull length and predictor variables. Values above zero indicate a positive regression coefficient and values below zero indicate a negative regression coefficient.

Figure 7. Slope coefficients from the linear regression between log-transformed skull width and (A) latitude or (B) year for each species. Significant slope coefficients were indicated using p-values where * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, which were determined by the GLMs between skull length and predictor variables. Values above zero indicate a positive regression coefficient and values below zero indicate a negative regression coefficient.

Figure 8. Slope coefficients from the linear regression between log-transformed tooth row length and (A) latitude or (B) year for each species. Significant slope coefficients were indicated using p-values where * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, which were determined by the GLMs between skull length and predictor variables. Values above zero indicate a positive regression coefficient and values below zero indicate a negative regression coefficient.

Figure 9. Slope coefficients from the linear regression between log-transformed body masses and (A) latitude or (B) year for each species. Significant slope coefficients were indicated using p-values where * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$, which were determined by the GLMs between skull length and predictor variables. Values above zero indicate a positive regression coefficient and values below zero indicate a negative regression coefficient.

TABLES

Table 1. Summary statistics (mean, minimum, and maximum) calculated for the four morphological traits. Body mass averages where low sample sizes were used (less than 25 specimens) have been indicated with two asterisks (**).

Table 2. Temporal range in years, latitudinal range in decimal degrees, and sample size of specimens for both the museum dataset and the VertNet dataset.

Table 3. The effect of latitude, year, species and sex on each of the four log-transformed morphological traits (skull length, skull width, tooth row length, and body mass). The model used for each trait was Size ~ Latitude + Year + Species +Sex + Species x Latitude + Species x Year + Species x Sex + Latitude x Year + Latitude x Year x Species.

Table 4. The effect of latitude, year, and size category on each of the four log-transformed morphological traits (skull length, skull width, tooth row length, and body mass). The model used for each trait was Size ~ Latitude + Year + Size Category + Sex + Size Category x Latitude + Size Category x Year + Size Category x Sex + Latitude x Year + Latitude x Year x Size Category.

Table 5. Slope coefficients of the linear regressions between each morphological trait and latitude or year for all species, small mammals, and mid-size mammals. P-values are depicted as * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 6. Summary of the size trends for each of the morphological traits with latitude or year for the 17 mammalian hosts of Lyme disease. For significant size trends, the direction of the relationship for each morphological trait are indicated as positive, negative or non-linear.

Table 7. Trait variability estimated for each species by CV values and the slope of the regression between the absolute residuals of the size-latitude regression and latitude. Slope coefficients where low sample sizes were used (less than 25 specimens) have been indicated with two asterisks (**).

Table 8. The effect of latitude and species on the residuals of the size-latitude relation for the four log-transformed morphological traits (skull length, skull width, tooth row length, and body mass). The model used for each trait was Residuals ~ Latitude + Species + Latitude x Species.

FIGURES

Figure 1.

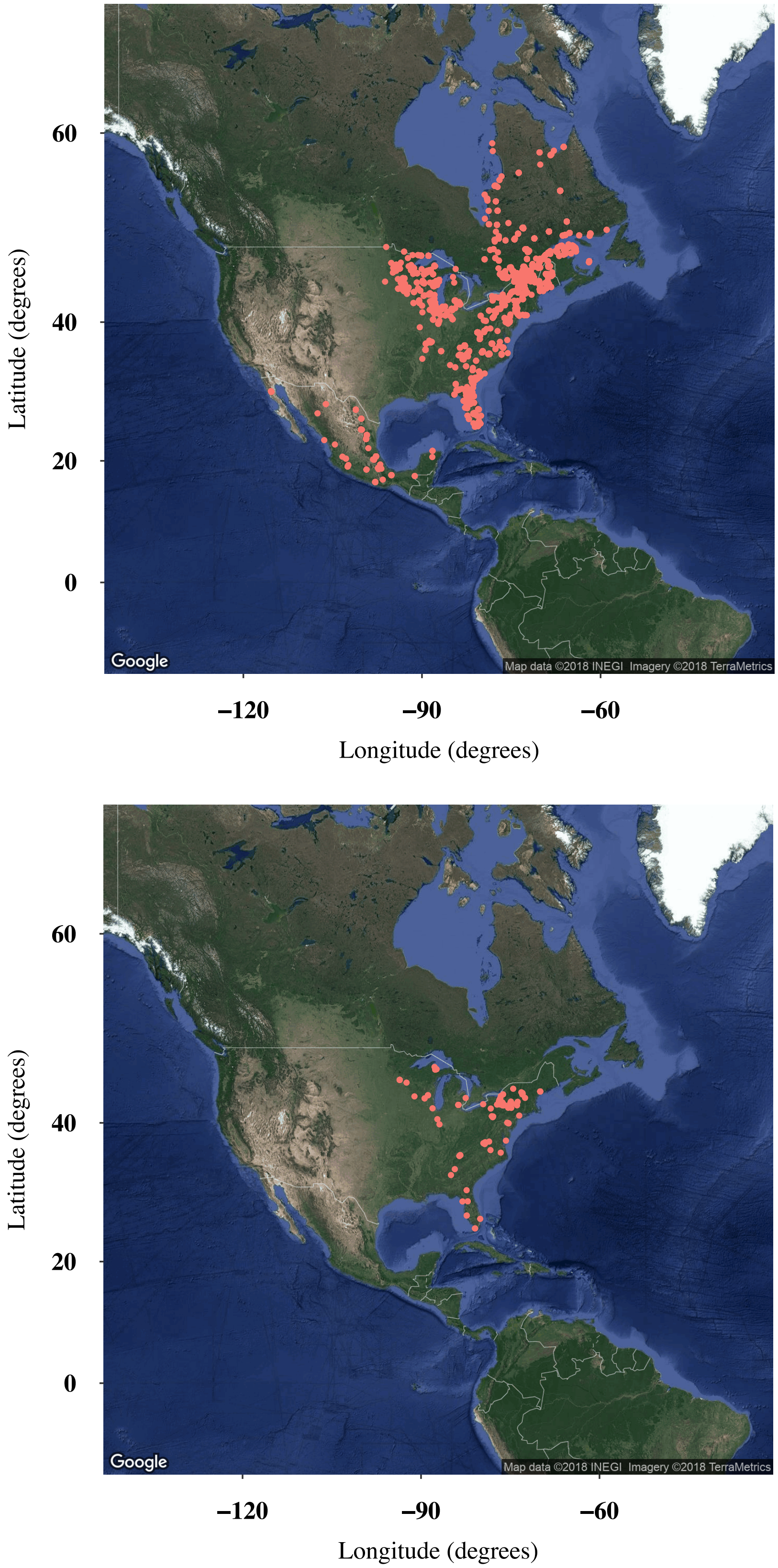


Figure 2.

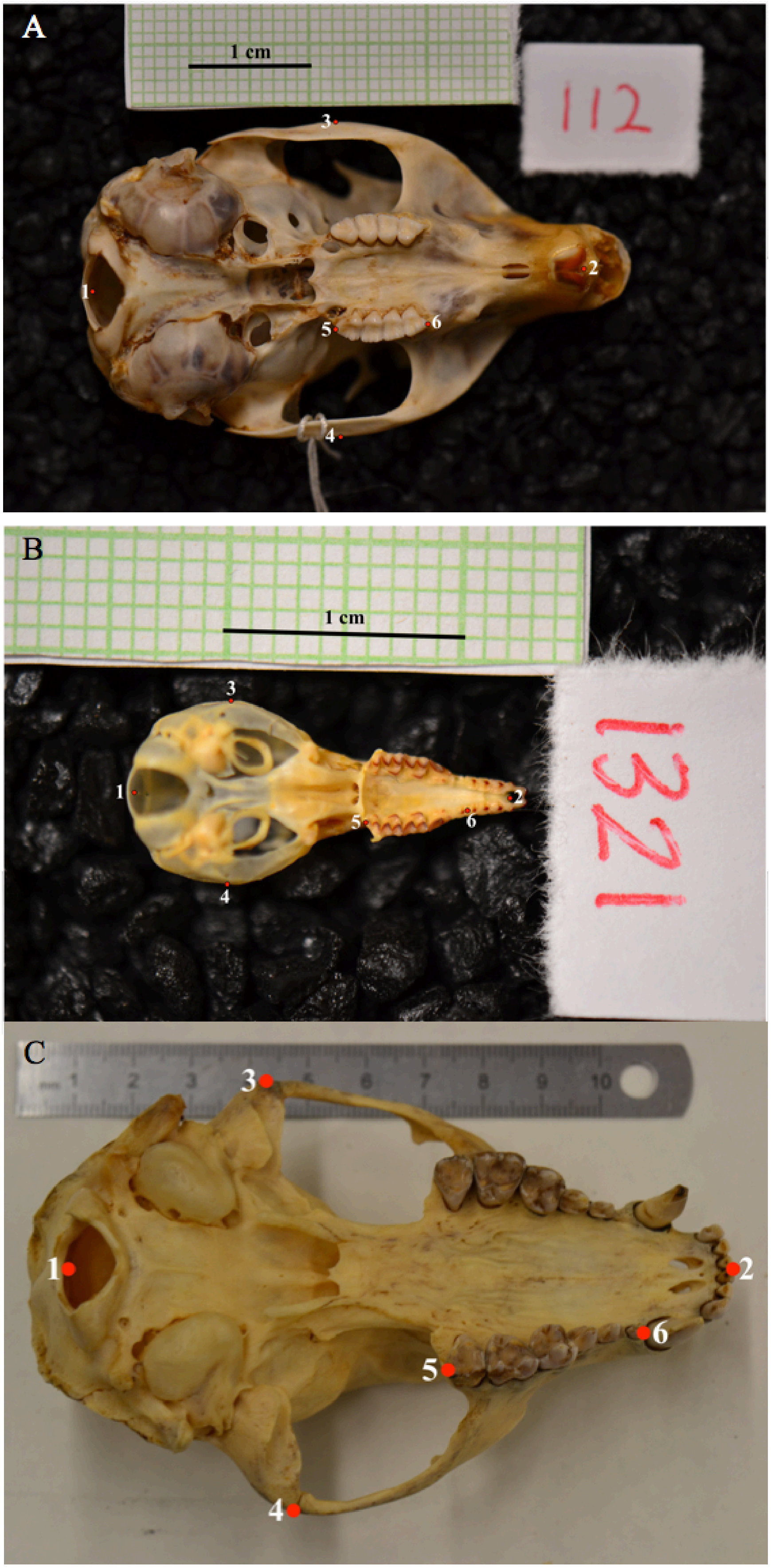


Figure 3.

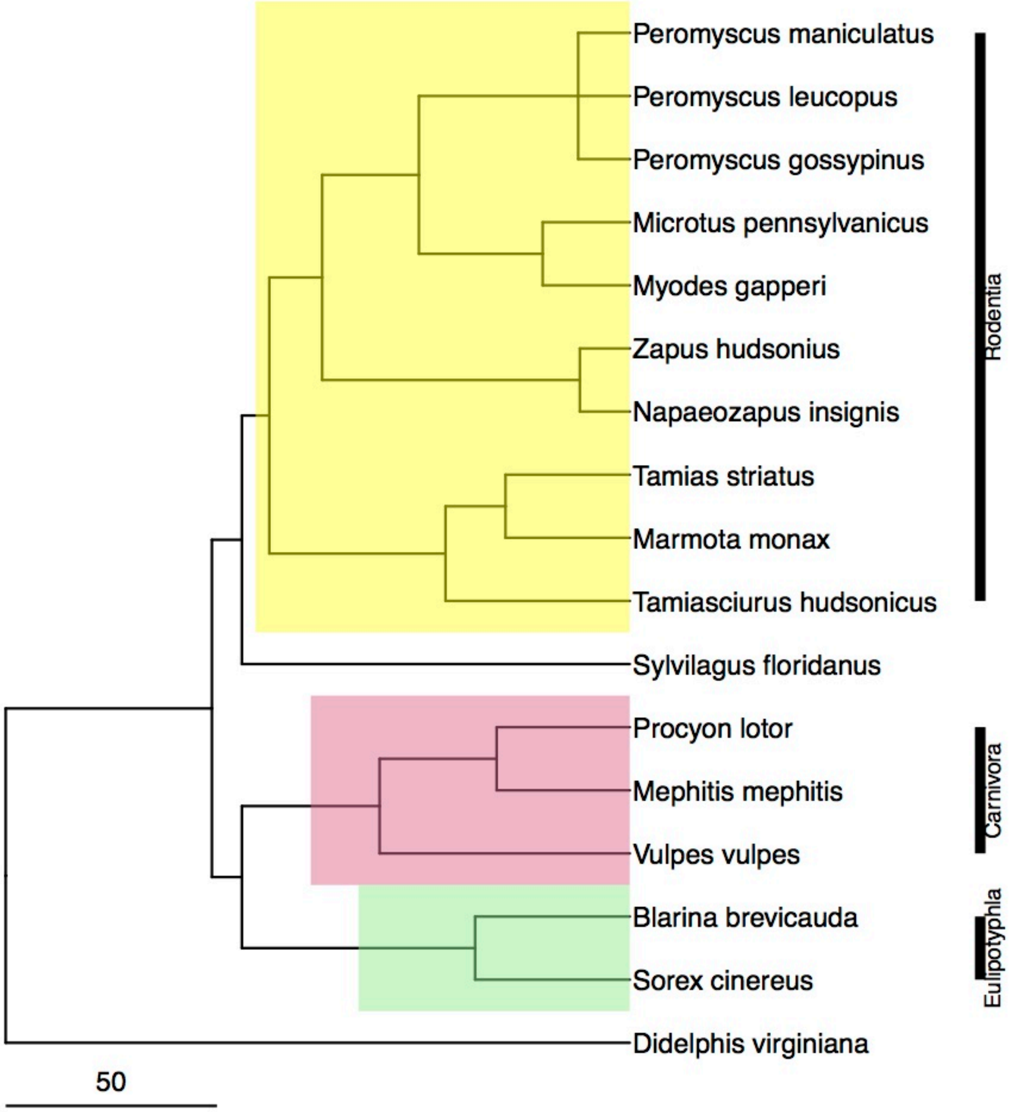
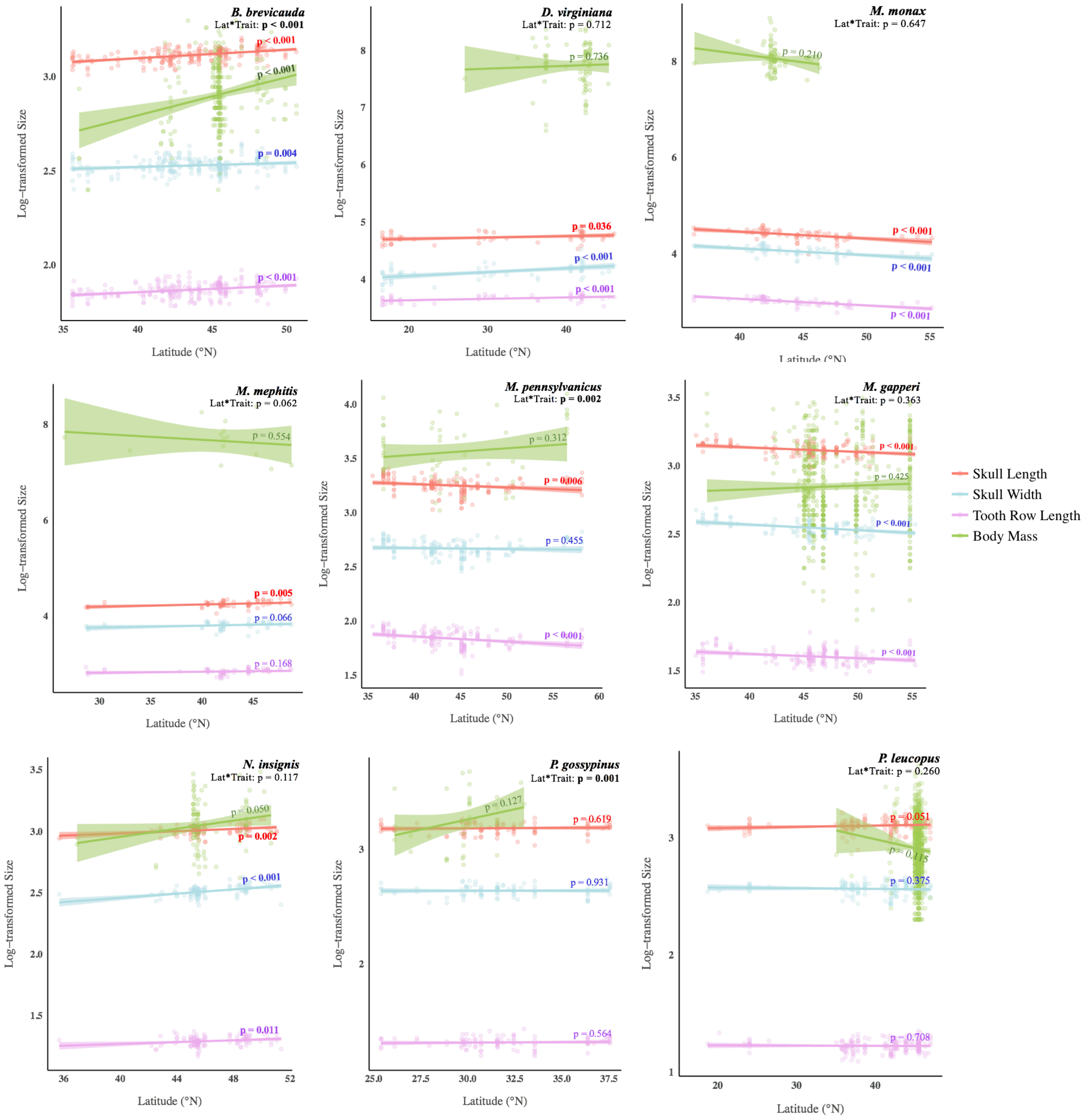

Peromyscus maniculatus
Peromyscus leucopus
Peromyscus gossypinus
Microtus pennsylvanicus
Myodes gapperi
Zapus hudsonius
Napaeozapus insignis
Tamias striatus
Marmota monax
Tamiasciurus hudsonicus
Sylvilagus floridanus
Procyon lotor
Mephitis mephitis
Vulpes vulpes
Blarina brevicauda
Sorex cinereus
Didelphis virginiana
Rodentia
Carnivora
Eulipotyphla
50

Figure 4.


B. brevicauda
Lat*Trait: p < 0.001
p < 0.001
p < 0.001
p = 0.004
p < 0.001
D. virginiana
Lat*Trait: p = 0.712
p = 0.736
p = 0.036
p < 0.001
p < 0.001
M. monax
Lat*Trait: p = 0.647
p = 0.210
p < 0.001
p < 0.001
p < 0.001
M. mephitis
Lat*Trait: p = 0.062
p = 0.554
p = 0.005
p = 0.066
p = 0.168
M. pennsylvanicus
Lat*Trait: p = 0.002
p = 0.312
p = 0.006
p = 0.455
p < 0.001
M. gapperi
Lat*Trait: p = 0.363
p < 0.001
p = 0.425
p < 0.001
p < 0.001
N. insignis
Lat*Trait: p = 0.117
p = 0.050
p = 0.002
p < 0.001
p = 0.011
P. gossypinus
Lat*Trait: p = 0.001
p = 0.127
p = 0.619
p = 0.931
p = 0.564
P. leucopus
Lat*Trait: p = 0.260
p = 0.051
p = 0.115
p = 0.375
p = 0.708
Log−transformed Size
Latitude (°N)
Skull Length
Skull Width
Tooth Row Length
Body Mass

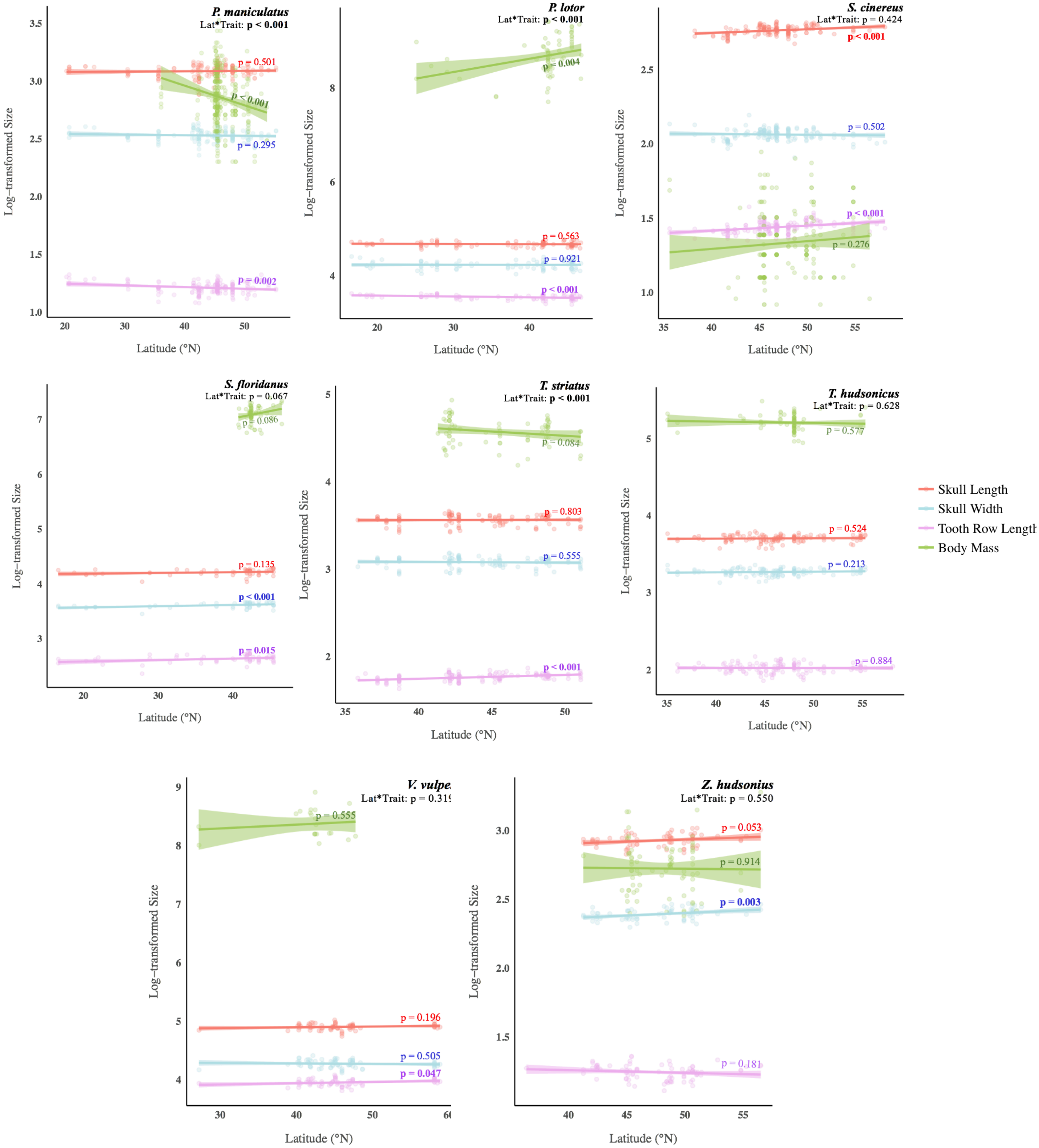

P. maniculatus
Lat*Trait: p < 0.001
p = 0.501
p < 0.001
p = 0.295
p = 0.002
3.5
3.0
2.5
2.0
1.5
1.0
20
30
40
50
Log−transformed Size
Latitude (°N)
P. lotor
Lat*Trait: p < 0.001
p = 0.004
p = 0.563
p = 0.921
p < 0.001
8
6
4
20
30
40
Log−transformed Size
Latitude (°N)
S. cinereus
Lat*Trait: p = 0.424
p < 0.001
p = 0.502
p < 0.001
p = 0.276
2.5
2.0
1.5
1.0
35
40
45
50
55
Log−transformed Size
Latitude (°N)
S. floridanus
Lat*Trait: p = 0.067
p = 0.086
p = 0.135
p < 0.001
p = 0.015
7
6
5
4
3
20
30
40
Log−transformed Size
Latitude (°N)
T. striatus
Lat*Trait: p < 0.001
p = 0.084
p = 0.803
p = 0.555
p < 0.001
5
4
3
2
35
40
45
50
Log−transformed Size
Latitude (°N)
T. hudsonicus
Lat*Trait: p = 0.628
p = 0.577
p = 0.524
p = 0.213
p = 0.884
5
4
3
2
35
40
45
50
55
Log−transformed Size
Latitude (°N)
Skull Length
Skull Width
Tooth Row Lengt
Body Mass
V. vulpe
Lat*Trait: p = 0.31
p = 0.555
p = 0.196
p = 0.505
p = 0.047
9
8
7
6
5
4
30
40
50
6
Log−transformed Size
Latitude (°N)
Z. hudsonius
Lat*Trait: p = 0.550
p = 0.053
p = 0.914
p = 0.003
p = 0.181
3.0
2.5
2.0
1.5
40
45
50
55
Log−transformed Size
Latitude (°N)

Figure 5.

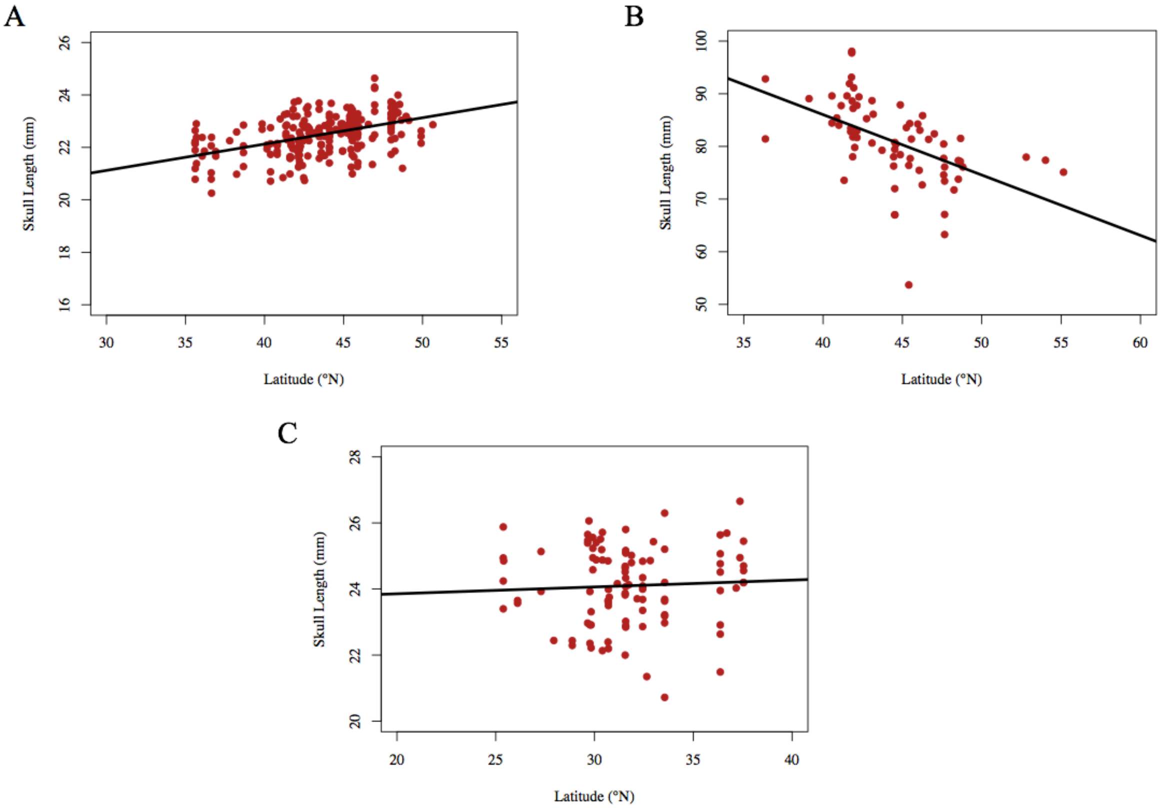
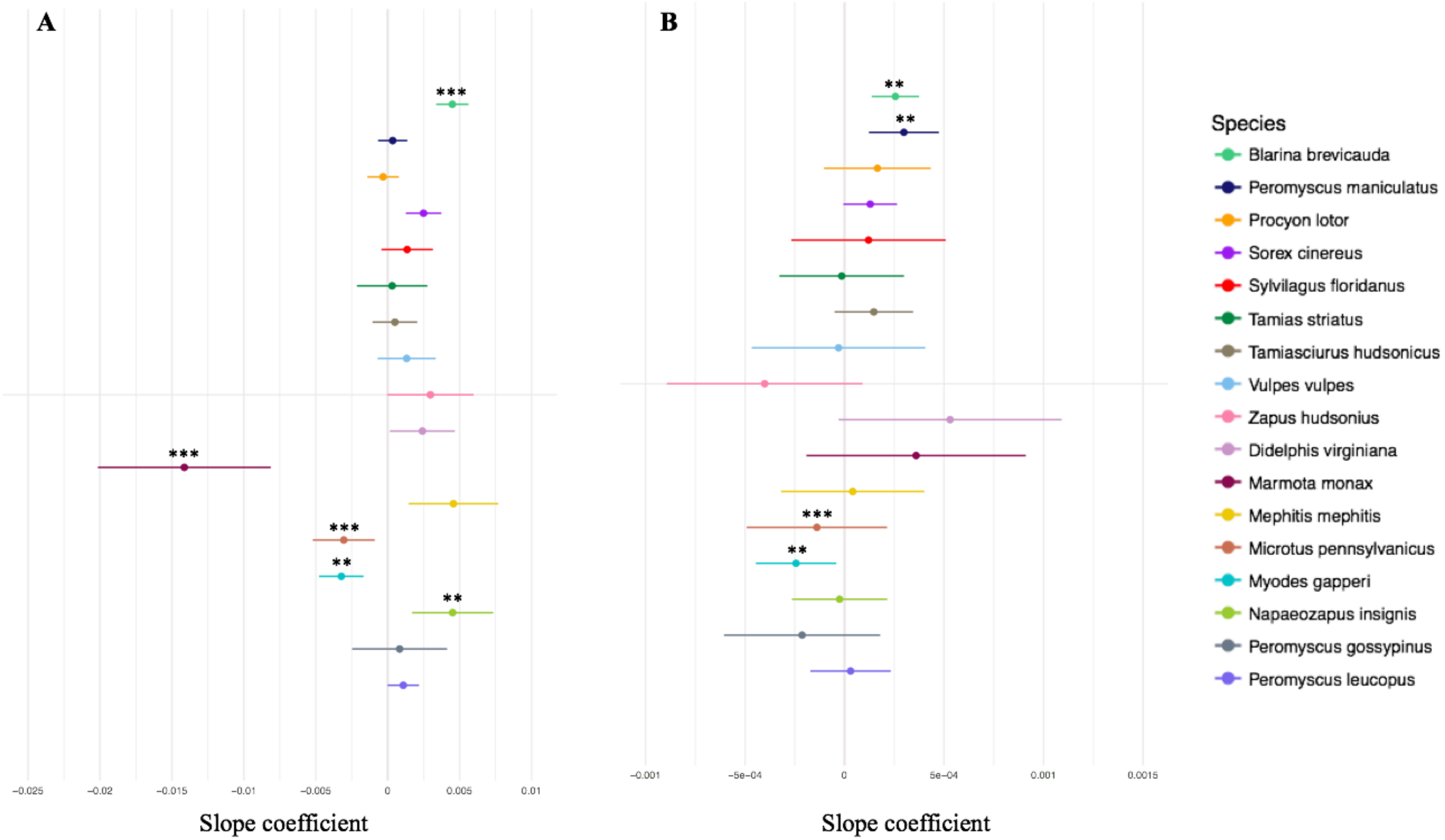
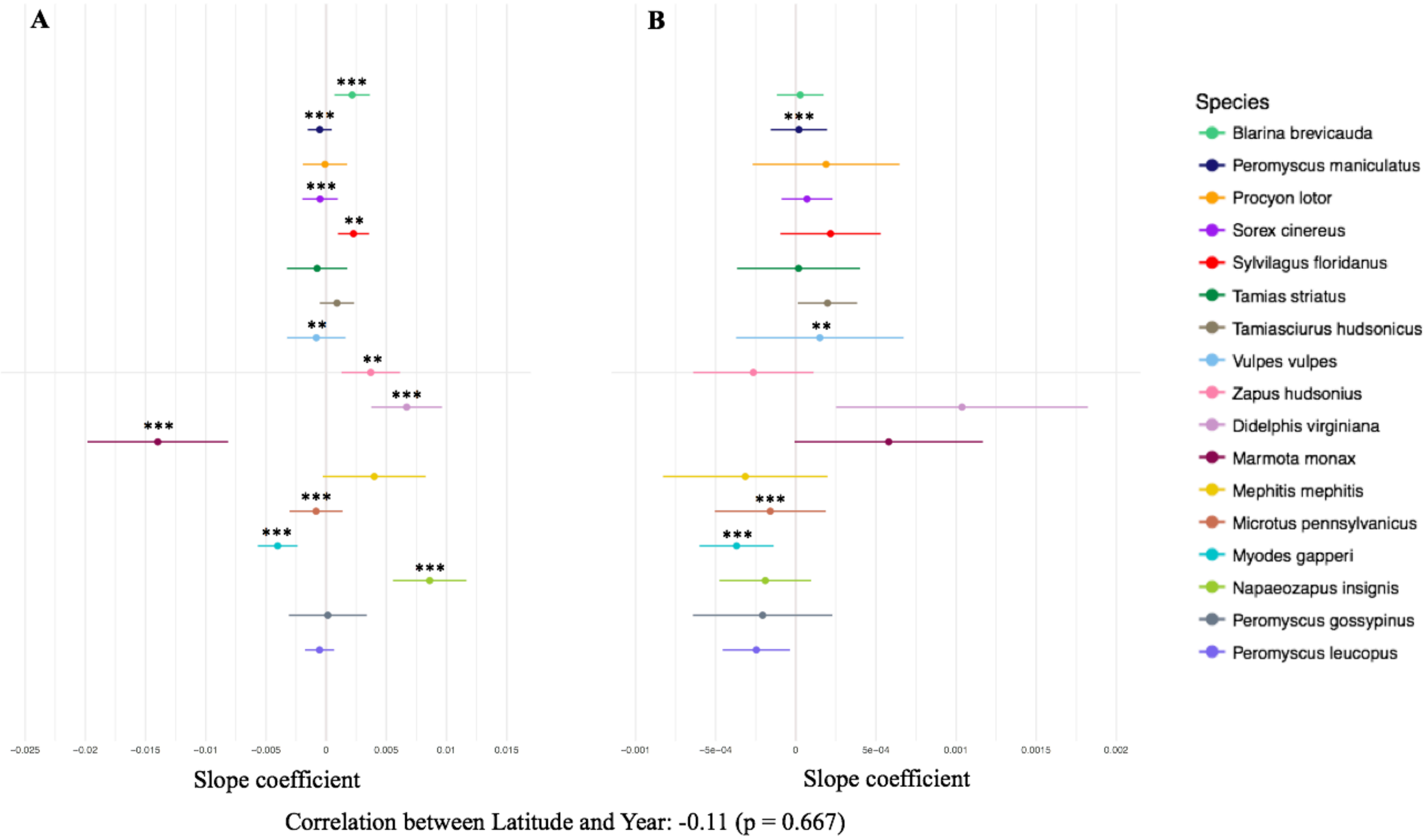

A
Skull Length (mm)
16
18
20
22
24
26
30
35
40
45
50
55
Latitude (°N)
B
Skull Length (mm)
50
60
70
80
90
100
35
40
45
50
55
60
Latitude (°N)
C
Skull Length (mm)
20
22
24
26
28
20
25
30
35
40
Latitude (°N)

Figure 6.



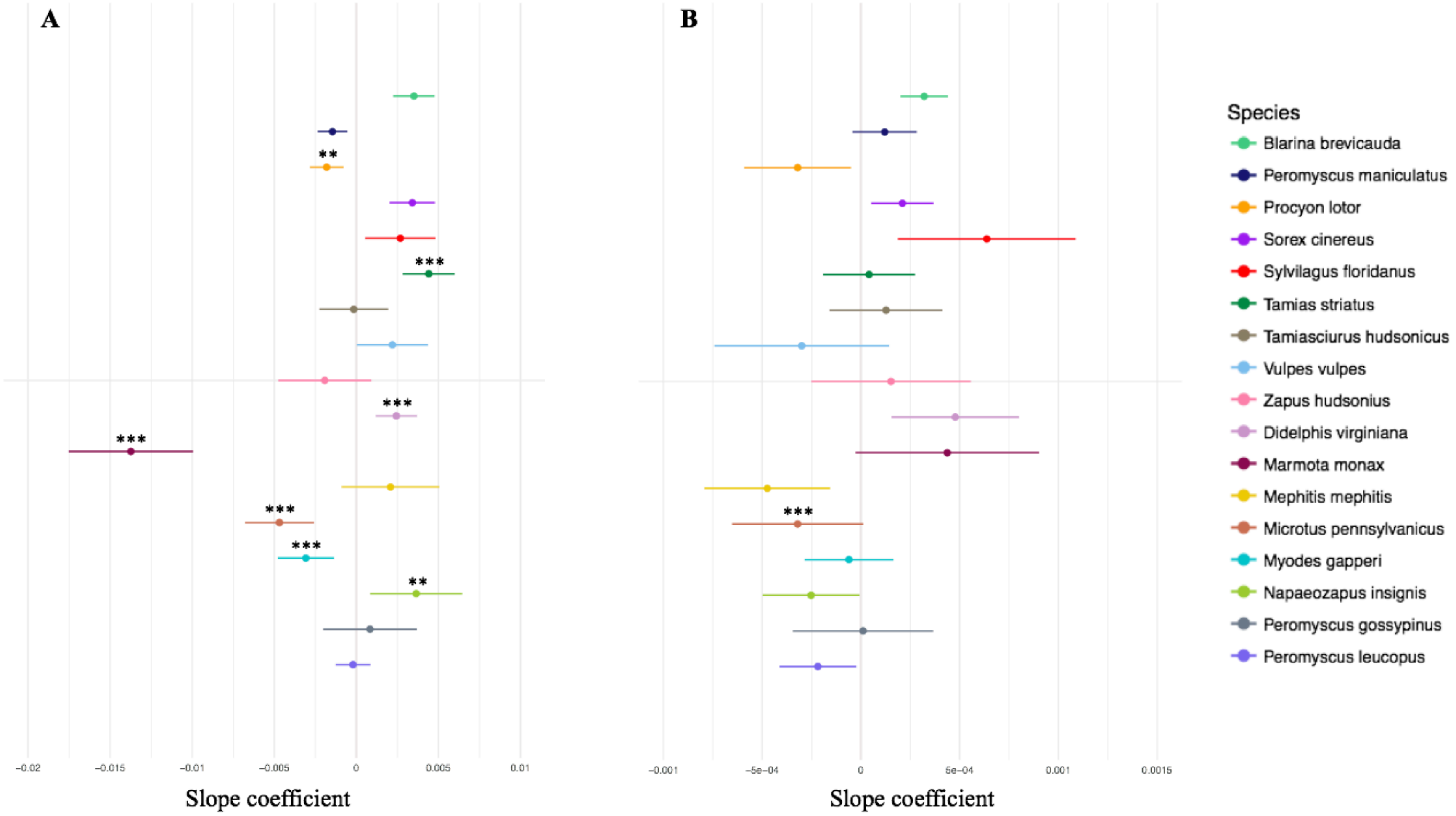
Correlation between Latitude and Year: -0.15 (p = 0.554)

Figure 7.



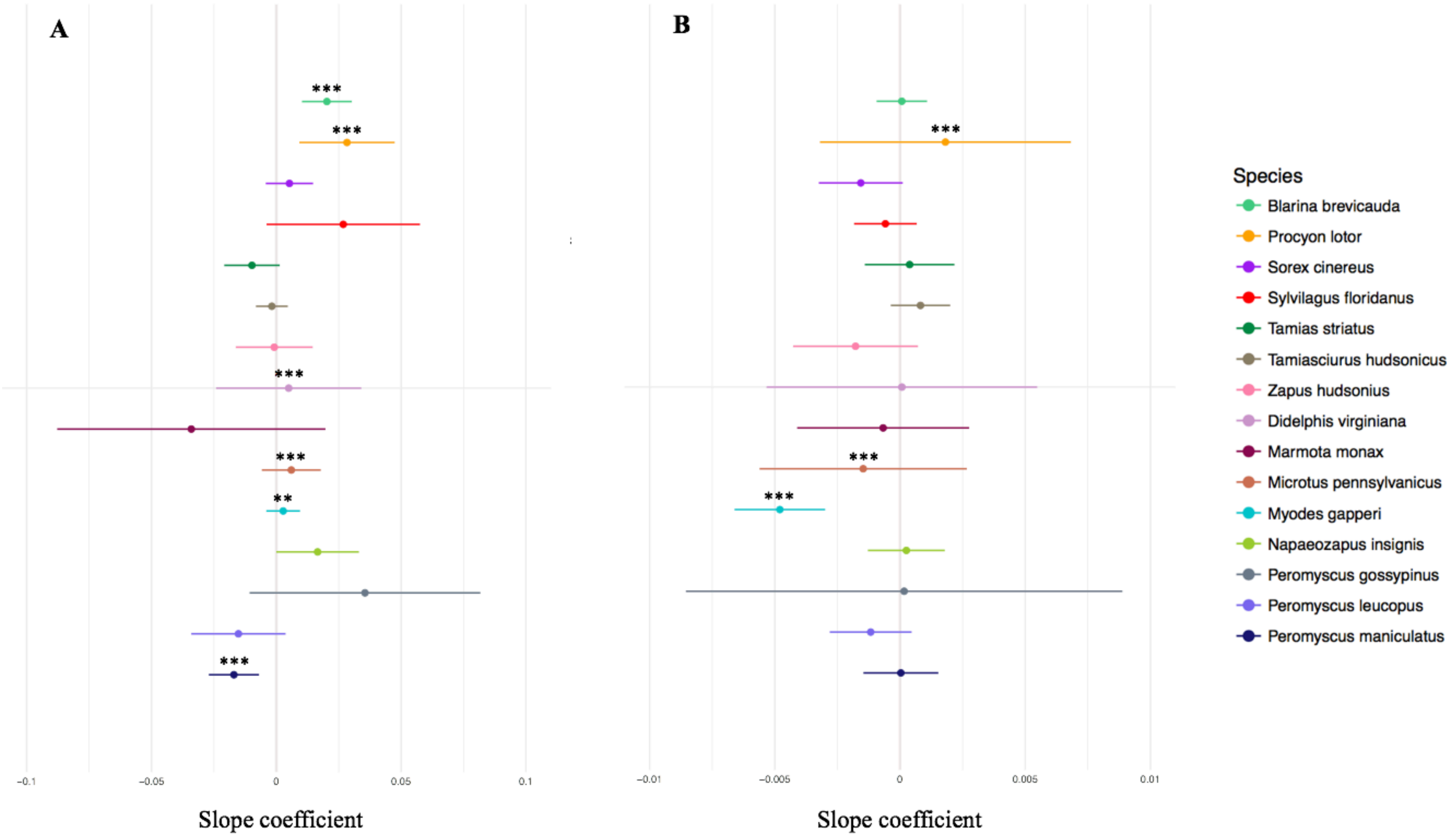
Correlation between Latitude and Year: -0.11 (p = 0.667)

Figure 8.



Correlation between Latitude and Year: -0.08 (p = 0.763)

Figure 9.



Correlation between Latitude and Year: 0.29 (p = 0.267)

TABLES

Table 1.

Order	**Species**	**Skull Length**	**Skull Width**	**Tooth Row Length**	**Body Mass**
		Mean (min-max)	Mean (min-max)	Mean (min-max)	Mean (min-max)
Carnivora	*Vulpe vulpes*	134.84 (114.52-151.37)	71.90 (61.24-82.39)	52.16 (45.22-59.13)	4436.84 (3000.00-7416.00)**
	Mephitis mephitis	69.82 (56.99-78.03)	44.87 (35.59-51.36)	17.02 (14.68-18.87)	2282.95 (1168.40-4309.13)**
	Procyon lotor	107.45 (95.52-118.03)	69.14 (56.49-82.30)	34.74 (29.57-37.96)	6283.10 (2220.00-12247.00)
Didelphimorphia	*Didelphis virginiana*	113.79 (92.69-136.70)	62.84 (44.84-92.26)	38.93 (33.94-42.84)	2434.15 (730.00-5000.00)
Eulipotyphla	*Blarina brevicauda*	22.50 (20.26-24.64)	12.53 (11.04-14.07)	6.48 (5.93-7.19)	18.46 (11.00-27.00)
	Sorex cinereus	15.90 (14.53-16.86)	7.88 (6.74-8.98)	4.21 (3.85-4.83)	3.88 (2.50-7.00)
Lagomorpha	*Sylvilagus floridanus*	67.40 (56.61-73.17)	36.95 (31.51-39.98)	13.89 (10.58-15.45)	1217.98 (850.00-1623.00)
Rodentia	*Microtus pennsylvanicus*	25.88 (20.65-30.09)	14.48 (11.68-16.85)	6.30 (4.53-7.28)	36.57 (20.50-60.10)
	Myodes gapperi	22.56 (19.75-25.19)	12.76 (11.19-14.69)	4.98 (4.37-5.93)	18.08 (6.50-34.00)
	Peromyscus gossypinus	24.10 (20.72-26.66)	13.97 (12.53-15.53)	3.72 (3.30-4.18)	26.35 (17.50-39.40)
	Peromyscus leucopus	22.34 (18.10-24.87)	12.99 (11.38-14.43)	3.40 (2.98-3.85)	18.77 (10.00-37.20)
	Peromyscus maniculatus	21.92 (17.85-24.50)	12.56 (10.57-13.95)	3.37 (2.94-3.77)	17.83 (10.00-34.00)
	Napaeozapus insignis	20.29 (18.36-22.14)	12.32 (10.96-13.78)	3.63 (3.21-3.93)	21.56 (13.70-32.60)
	Zapus hudsonius	18.68 (16.80-20.43)	10.93 (9.94-11.81)	3.48 (3.04-3.90)	15.51 (10.80-26.50)
	Marmota monax	80.93 (53.69-98.06)	57.12 (44.70-68.28)	20.00 (15.90-22.45)	3274.62 (2012.82-7285.80)
	Tamiasciurus hudsonicus	40.64 (35.52-44.41)	26.30 (22.85-28.74)	7.57 (6.39-8.76)	183.75 (140.30-241.00)
	Tamias striatus	35.34 (30.61-39.08)	21.81 (18.96-24.22)	5.85 (5.12-6.49)	97.80 (66.00-139.00)

Table 2.

		MUSEUM SPECIMENS			DATABASE SPECIMENS		
Order	**Species**	Range Year	Range Latitude (°)	Sample size	Range Year	Range Latitude (°)	Sample size
Carnivora	*V. vulpes*	1887-2008	27.17 – 58.82	92	1925-1990	39.94 – 42.65	10
	M. mephitis	1889-2012	28.67 – 48.73	88	1926-1996	26.59 – 45.30	7
	P. lotor	1890-2017	16.62 - 46.76	129	1923-2001	25.14 – 46.81	48
Didelphimorphia	*D. virginiana*	1897-2015	16.62 – 46.07	79	1934-1990	27.08-43.01	81
Eulipotyphla	*B. brevicauda*	1888-2014	35.59 – 50.65	562			
	S. cinereus	1895-2014	35.61 – 58.82	382			
Lagomorpha	*S. floridanus*	1890-2004	16.62 – 45.46	106	1901-2015	40.73 – 46.55	55
Rodentia	*M. pennsylvanicus*	1893-2012	35.49 – 59.13	300			
	M. gapperi	1895-2014	35.05 – 55.28	826			
	P. gossypinus	1889-1989	25.36 – 37.54	233			
	P. leucopus	1889-2014	16.62 – 46.97	1535			
	P. maniculatus	1890-2014	18.86 – 55.82	643			
	N. insignis	1900-2014	35.65 – 51.36	217			
	Z. hudsonius	1897-2014	36.37 – 56.50	156			
	M. monax	1888-2007	36.37 – 55.15	85	1927-2013	36.41 – 45.30	66
	T. hudsonicus	1888-2014	35.04 – 58.10	233			
	T. striatus	1890-2014	35.13 – 51.07	240			
Total sample size				5906			267

Table 3.

	Morphological Traits							
	Skull Length		**Skull Width**		**Tooth Row Length**		**Body Mass**	
Factor	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
Latitude	14791.22	**< 0.001**	16794.24	**< 0.001**	16996.12	**< 0.001**	17392.22	**< 0.001**
Year	6434.46	**< 0.001**	7671.42	**< 0.001**	8794.59	**< 0.001**	36932.38	**< 0.001**
Species	14332.23	**< 0.001**	13787.89	**< 0.001**	27782.30	**< 0.001**	5369.01	**< 0.001**
Sex	1.12	0.291	3.49	0.062	1.46	0.228	0.03	0.866
Latitude*Species	8.56	**< 0.001**	12.05	**< 0.001**	13.28	**< 0.001**	2.86	**< 0.001**
Year*Species	1.30	0.187	1.63	0.055	3.44	**< 0.001**	2.59	**< 0.001**
Species*Sex	5.11	**< 0.001**	8.28	**< 0.001**	2.60	**< 0.001**	3.93	**< 0.001**
Latitude*Year	2.73	0.099	1.29	0.256	0.09	0.762	2.32	0.128
Latitude*Year*Species	3.58	**< 0.001**	4.50	**< 0.001**	3.47	**< 0.001**	3.26	**< 0.001**

Table 4.

	Morphological Traits							
	Skull Length		**Skull Width**		**Tooth Row Length**		**Body Mass**	
Factor	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
Latitude	635.24	**< 0.001**	594.18	**< 0.001**	369.99	**< 0.001**	2576.89	**< 0.001**
Year	276.34	**< 0.001**	271.42	**< 0.001**	191.45	**< 0.001**	5472.03	**< 0.001**
Size Category	8020.45	**< 0.001**	6011.76	**< 0.001**	7656.97	**< 0.001**	9951.62	**< 0.001**
Sex	2.37	0.124	1.38	0.240	17.55	**< 0.001**	1.48	0.224
Latitude* Size Category	2.13	0.144	3.51	0.06107	39.41	**< 0.001**	2.46	0.117
Year* Size Category	36.09	**< 0.001**	27.25	**< 0.001**	38.13	**< 0.001**	59.84	**< 0.001**
Size Category*Sex	0.95	0.330	0.68	0.40848	1.42	0.233	1.33	0.250
Latitude*Year	23.28	**< 0.001**	30.54	**< 0.001**	9.81	**0.002**	16.59	**< 0.001**
Latitude*Year*Size Category	10.92	**< 0.001**	6.92	**0.009**	11.13	**< 0.001**	10.88	**< 0.001**

Table 5.

Size Category	Predictor variable	SLOPE			
		SL	SW	TRL	BM
Overall	Latitude	-0.019***	-0.022***	-0.018***	-0.162***
	Year	-0.004***	-0.005***	-0.005***	-0.043***
Small mammals	Latitude	-0.001^{ns}	-0.004**	0.008***	-0.018***
	Year	-0.001***	-0.002***	-0.001**	-0.011***
Midsize mammals	Latitude	-0.001^{ns}	0.002^{ns}	-0.002^{ns}	0.004^{ns}
	Year	0.001^{ns}	0.001^{ns}	0.001^{ns}	0.003^{ns}

Table 6.

	Predictor variable	Significant size trend			Non-significant size trend
		Positive	Negative	Non-linear	
Skull Length	Latitude	2	1	2	12/17
	Year	2	2	0	13/17
Skull Width	Latitude	5	3	3	6/17
	Year	2	2	0	13/17
Tooth Row Length	Latitude	3	3	1	10/17
	Year	0	1	0	16/17
Body Mass	Latitude	4	1	1	9/15
	Year	1	2	0	12/15
Total cases	Latitude	14	8	7	37/66
	Year	5	7	0	54/66

Table 7.

		Skull Length		Skull Width		Tooth Row Length		Body Mass	
Order	Species	CV (%)	Slope Residual	CV (%)	Slope Residual	CV (%)	Slope Residual	CV (%)	Slope Residual
Carnivora	*V. vulpes*	4.86	0.020	6.06	0.022	5.36	0.020	25.86	0.169**
	M. mephitis	5.73	0.023	7.43	0.026	5.30	0.020	41.55	0.150**
	P. lotor	4.90	0.018	8.14	0.022	4.71	0.016	39.67	0.190
Didelphimorphia	*D. virginiana*	8.72	0.021	13.69	0.029	5.62	0.021	35.62	0.167
Eulipotyphla	*B. brevicauda*	3.35	-0.023	3.96	-0.025	3.67	-0.005	16.93	-0.166
	S. cinereus	2.89	-0.021	3.51	-0.022	3.71	-0.022	22.98	-0.167
Lagomorpha	*S. floridanus*	5.25	0.020	4.52	0.025	6.70	0.021	14.14	0.189
Rodentia	*M. pennsylvanicus*	7.25	-0.008	7.25	-0.010	7.34	0.003	27.76	0.033
	M. gapperi	4.65	-0.015	4.91	-0.018	5.31	-0.015	29.87	0.020
	P. gossypinus	4.94	-0.019	4.74	-0.022	4.47	-0.019	24.08	-0.198
	P. leucopus	4.69	-0.020	4.69	-0.022	4.70	-0.018	22.81	-0.146
	P. maniculatus	4.76	-0.019	4.46	-0.022	4.47	-0.017	22.37	-0.095
	N. insignis	3.40	-0.023	4.14	-0.031	3.67	-0.022	18.87	-0.089
	Z. hudsonius	4.62	-0.022	3.99	-0.026	5.03	-0.016	19.56	-0.057
	M. monax	9.54	0.004	9.18	0.008	7.23	0.004	30.14	0.128
	T. hudsonicus	4.09	0.019	3.89	0.023	5.61	0.018	10.43	0.160
	T. striatus	5.40	0.017	5.42	0.021	4.10	-0.019	15.10	0.152

Table 8.

Skull Length	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	0.04	0.04	16.52	**< 0.001**
Species	16	218.06	13.63	5621.19	**< 0.001**
*Latitude*Species*	16	20.53	1.28	529.20	**< 0.001**

Skull Width	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	0.15	0.15	50.23	**< 0.001**
Species	16	222.97	13.94	4706.19	**< 0.001**
*Latitude*Species*	16	28.76	1.80	607.05	**< 0.001**

Tooth Row Length	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	0.00	0.00	1.91	0.167
Species	16	543.10	33.94	14497.12	**< 0.001**
*Latitude*Species*	16	17.80	1.11	475.62	**< 0.001**

Body Mass	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	3.00	2.62	35.95	**< 0.001**
Species	16	3624.00	226.48	3105.32	**< 0.001**
*Latitude*Species*	16	281.00	17.54	240.48	**< 0.001**

GENERAL CONCLUSION

In this thesis, I assessed the patterns of body size variation for various mammalian hosts of Lyme disease in the context of Bergmann's rule. I analyzed the relationship between cranial measurements and body mass with latitude and time, while taking into consideration the potential for sexual dimorphism to assess the similarities and differences in body size variation both amongst and within species.

Although the generality of Bergmann's rule is continuously debated, recent studies, including this one, have shown that many species are not increasing in body size with increasing latitude nor decreasing in body size through time, as predicted by theory (Riemer et al. 2017, Villar and Naya 2018). However, certain groups of species such as shrews or voles displayed predictable patterns of variation in body size with latitude. Temporal trends in body size also showed heterogeneous responses for some species, especially those within Rodentia. The two most likely mechanisms causing changes in a species' morphological traits, such as body size, are phenotypic plasticity and local adaptation. A combination of adaptive plasticity and local adaptation are thought to act as key features in a species' persistence in its new environmental conditions due to climate warming.

We also detected some differences in the variability of the different morphological traits across species. Body mass had the greatest level of variability across species' ranges when compared to skeletal measurements, which indicated that it was the trait least constrained by changes in abiotic factors and displayed more plasticity and/or local adaptation. The direction and magnitude of a species' trait variability depended on its size category with midsize mammals increasing trait variability towards their northern edge and small mammals, excluding the American red squirrel and the eastern chipmunk, demonstrating a decrease in trait variability with latitude. Future studies on body size variation across species' ranges, including studies on Bergmann's rule, should focus on comparisons between different body size metrics as species may change morphological traits in distinct directions and magnitudes as illustrated here. The choice of body size metric should be done using physical measurements that are more stable and not as easily influenced by reproductive condition, seasonality or an individual's health status. Therefore, cranial and skeletal measurements may more accurately assess responses to climate change than external physical measurements such as body mass.

Overall, it is not possible to argue for the generality of Bergmann's rule based on our results as we found little evidence of a generalized geographic body size pattern for various small and midsize mammalian hosts of Lyme disease, with only a small majority of the species we studied conforming with the rule. Such a result is not surprising and likely stems from the fact that there is no clear consensus on the underlying mechanism applicable across a wide range of taxa, climates or geographic locations linking latitude with body size. Environmental temperature is undoubtedly strongly correlated with latitude providing rationale to argue for an effect of temperature on the metabolism and temperature regulation of homeotherms, and consequently, on their body size. However, a given individual's habitat and biotic context may modulate the effect of temperature on body size, which may be highly variable across species and geographic locations. For example, interspecific competition is known to drive the community size structure of co-existing species of rodents, which may override the underlying effect of temperature on body size (Guisan and Thuiller 2005, Freilich and Connolly 2015, Wood et al. 2016). Intraspecific competition also varies with latitude; populations at higher, colder latitudes are occurring at lower densities than those at lower, warmer latitudes, thereby facing a smaller competitive pressure. The key to better understanding body size variation in mammals will lie in the understanding of the strength and interaction between abiotic and biotic factors of a population at a given place and time. Despite decades of work on body size variation with a multitude of scientific publications and sets of empirical data, we still "don't know why mammals have the size they do" (Van Valen 1973).

By conducting an empirical comparative study like ours, we may not be able to offer a general hypothesis for the underlying mechanism driving body size variation in mammals, nor make any firm conclusions on the validity and generality of Bergmann's rule, but we can provide some objective insight into the patterns of body size variation across species' ranges. In this study on Bergmann's rule, we collected empirical data for several species of mammals using various body size traits, in contrast with previous meta-analyses whose results and conclusions rely on literature reviews based on work that is not readily comparable. In the context of rapid climate warming, there is a need for better quality data that reviews the body size variation for many species, which is especially critical for species in temperate zones whose plastic responses in morphological traits and possible northward distributional shifts may have knock-on effects on community dynamics. For the mammalian hosts of Lyme disease, the inclusion of biotic drivers, such as body size variation, in species distribution models will increase their predictive power and determine which species are moving at a faster rate northward into southern Canada, thereby helping to predict the future extent and risk of Lyme disease in these emergent regions.

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Wood, C. M., J. W. Witham, M. L. Hunter, and D. P. C. Peters. 2016. Climate-driven range shifts are stochastic processes at a local level: two flying squirrel species in Maine. Ecosphere **7**:e01240.

SUPPLEMENTARY MATERIAL

Appendix 1. List of references for museum collections which were a part of the database extractions from VertNet for which body masses were used.

- AMNH Mammal Collections 2016
- CHAS Mammalogy Collection 2016
- CRCM Vertebrate Collection 2016
- CUMV Mammal Collection 2016
- DMNS Mammal Collection 2016
- LACM Vertebrate Collection 2016
- MSB Mammal Collection 2016
- NCSM Mammals Collection 2016
- NMU Mammal Collection 2017
- UAZ Mammals 2016
- UCLA Donald R. Dickey Bird and Mammal Collection 2015
- UConn Mammals 2016
- UCM Mammals Collection 2016
- UWBM Mammalogy Collection 2015
- WNMU Mammal Collection 2016

Appendix 2. Range of adult body masses for each species found in the literature (Desrosiers et al. 2002, Kays and Wilson 2010, various pages Animal Diversity Web).

	BODY MASS RANGES		
	Desrosiers et al. 2002	*Kays and Wilson 2010*	*Animal Diversity Web*
B. brevicauda	11-30 g	11-30 g	18-30 g
D. virginiana	-	300-6500 g	1900-6000 g
M. monax	-	3000-4000 g	2000-6000 g
M. mephitis	-	1200-6300 g	700-6300 g
M. pennsylvanicus	20-70 g	33-65 g	33.75-50.49 g
M. gapperi	13-42 g	6-42 g	6-42 g
N. insignis	15-34 g	15-30 g	17-35 g
P. gossypinus	-	17-46 g	17-46 g
P. leucopus	10-43 g	15-25 g	15-25 g
P. maniculatus	10-35 g	10-30 g	10-24 g
P. lotor	-	4000-15800 g	1800-10400 g
S. cinereus	2.4-7.8 g	2-5 g	2.5-4 g
S. floridanus	-	800-1500 g	800-1530 g
T. hudsonicus	-	80-150 g	66-115 g
T. striatus	-	140-250 g	197.3-282.2 g
V. vulpes	-	3000-6000 g	3000-14000 g
Z. hudsonius	10-28 g	15-30 g	11.15-30 g

Appendix 3. Results of the GLM between the slope coefficients from the linear regressions of the log-transformed size-latitude relationship with the interaction between latitude and trait.

B. brevicauda	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	4.06	4.06	503.84	**< 0.001**
Trait	3	220.55	73.52	9125.44	**< 0.001**
*Latitude*Trait*	3	0.28	0.09	11.55	**< 0.001**

D. virginiana	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	157.80	157.77	2717.03	**< 0.001**
Trait	3	592.20	197.41	3399.66	**< 0.001**
*Latitude*Trait*	3	0.10	0.03	0.46	0.712

M. monax	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	79.40	79.44	3500.67	**< 0.001**
Trait	3	947.70	315.90	13920.22	**< 0.001**
*Latitude*Trait*	3	0.00	0.01	0.55	0.647

M. mephitis	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	0.88	0.88	66.15	**< 0.001**
Trait	3	291.55	97.18	7346.25	**< 0.001**
*Latitude*Trait*	3	0.10	0.03	2.48	0.062

M. pennsylvanicus	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	0.00	0.00	0.23	0.630
Trait	3	214.81	71.60	5784.26	**< 0.001**
*Latitude*Trait*	3	0.19	0.06	5.00	**0.002**

M. gapperi	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	4.45	4.45	86.34	**< 0.001**
Trait	3	244.92	81.64	1583.51	**< 0.001**
*Latitude*Trait*	3	0.16	0.05	1.06	0.363

N. insignis	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	0.06	0.06	6.74	**0.010**
Trait	3	240.00	80.00	8618.79	**< 0.001**
*Latitude*Trait*	3	0.06	0.02	1.98	0.117

P. gossypinus	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	1.45	1.45	187.53	**< 0.001**
Trait	3	205.77	68.59	8852.75	**< 0.001**
*Latitude*Trait*	3	0.13	0.04	5.47	**0.001**

P. leucopus	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	49.20	49.21	1384.05	**< 0.001**
Trait	3	514.40	171.48	4823.31	**< 0.001**
*Latitude*Trait*	3	0.10	0.05	1.34	0.260

P. maniculatus	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	2.60	2.63	136.62	**< 0.001**
Trait	3	427.00	142.34	7396.58	**< 0.001**
*Latitude*Trait*	3	0.50	0.16	8.31	**< 0.001**

P. lotor	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	58.10	58.10	1907.91	**< 0.001**
Trait	3	1114.50	371.50	12196.73	**< 0.001**
*Latitude*Trait*	3	1.30	0.40	13.97	**< 0.001**

V. vulpes	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	13.30	13.31	1689.34	**< 0.001**
Trait	3	326.20	108.74	13802.47	**< 0.001**
*Latitude*Trait*	3	0.00	0.01	1.18	0.319

S. cinereus	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	0.28	0.28	21.03	**< 0.001**
Trait	3	220.96	73.65	5493.57	**< 0.001**
*Latitude*Trait*	3	0.04	0.01	0.93	0.424

Z. hudsonius	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	0.47	0.47	43.84	**< 0.001**
Trait	3	135.69	45.23	4229.45	**< 0.001**
*Latitude*Trait*	3	0.02	0.01	0.70	0.550

S. floridanus	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	56.30	56.27	7130.23	**< 0.001**
Trait	3	642.80	214.28	27152.62	**< 0.001**
*Latitude*Trait*	3	0.10	0.02	2.42	0.067

T. hudsonicus	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	2.60	2.63	725.09	**< 0.001**
Trait	3	546.60	182.19	50286.62	**< 0.001**
*Latitude*Trait*	3	0.00	0.00	0.58	0.628

T. striatus	*df*	*Sum Sq.*	*Mean Sq.*	*F value*	*P-value*
Latitude	1	3.80	3.83	672.90	**< 0.001**
Trait	3	410.80	136.94	24037.69	**< 0.001**
*Latitude*Trait*	3	0.10	0.04	6.65	**< 0.001**

Appendix 4. The effect of latitude, year, species and sex on each of the four log-transformed morphological traits (SL, SW, TRL, BM). The model used for each trait was Size ~ Latitude + Year + Species +Sex + Species x Latitude + Species x Year + Species x Sex + Latitude x Year + Latitude x Year x Species.

Skull Length	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	34.80	34.80	14791.22	< **0.001**
Year	1	15.10	15.14	6434.46	< **0.001**
Species	16	539.50	33.72	14332.23	< **0.001**
Sex	1	0.00	0.00	1.12	0.291
*Latitude*Species*	16	0.30	0.02	8.56	< **0.001**
*Year*Species*	16	0.00	0.00	1.30	0.187
*Species*Sex*	16	0.20	0.01	5.11	< **0.001**
*Latitude*Year*	1	0.00	0.01	2.73	0.099
*Latitude*Year*Species*	16	0.10	0.01	3.58	< **0.001**

Skull Width	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	45.60	45.57	16794.24	< **0.001**
Year	1	20.80	20.82	7671.42	< **0.001**
Species	16	598.60	37.41	13787.89	< **0.001**
Sex	1	0.00	0.01	3.49	0.062
*Latitude*Species*	16	0.50	0.03	12.05	< **0.001**
*Year*Species*	16	0.10	0.00	1.63	0.055
*Species*Sex*	16	0.40	0.02	8.28	< **0.001**
*Latitude*Year*	1	0.00	0.00	1.29	0.256
*Latitude*Year*Species*	16	0.20	0.01	4.50	< **0.001**

Tooth Row Length	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	38.00	37.95	16996.12	**< 0.001**
Year	1	19.60	19.64	8794.59	**< 0.001**
Species	16	992.60	62.04	27782.30	**< 0.001**
Sex	1	0.00	0.00	1.46	0.228
*Latitude*Species*	16	0.50	0.03	13.28	**< 0.001**
*Year*Species*	16	0.10	0.01	3.44	**< 0.001**
*Species*Sex*	16	0.10	0.01	2.60	**< 0.001**
*Latitude*Year*	1	0.00	0.00	0.09	0.762
*Latitude*Year*Species*	16	0.10	0.01	3.47	**< 0.001**

Body Mass	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	991.00	990.60	17392.22	**< 0.001**
Year	1	2104.00	2103.60	36932.38	**< 0.001**
Species	16	4893.00	305.80	5369.01	**< 0.001**
Sex	1	0.00	0.00	0.03	0.866
*Latitude*Species*	16	3.00	0.20	2.86	**< 0.001**
*Year*Species*	16	2.00	0.10	2.59	**< 0.001**
*Species*Sex*	16	4.00	0.20	3.93	**< 0.001**
*Latitude*Year*	1	0.00	0.10	2.32	0.128
*Latitude*Year*Species*	16	3.00	0.20	3.26	**< 0.001**

Appendix 5. The effect of latitude, year, and size category on each of the four log-transformed morphological traits (SL, SW, TRL, BM). The model used for each trait was Size ~ Latitude + Year + Size Category + Sex + Size Category x Latitude + Size Category x Year + Size Category x Sex + Latitude x Year + Latitude x Year x Size Category.

Skull Length	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	34.80	34.80	635.24	**< 0.001**
Year	1	15.10	15.10	276.34	**< 0.001**
Size Category	1	439.30	439.30	8020.45	**< 0.001**
Sex	1	0.10	0.10	2.37	0.124
Latitude Size Category*	1	0.10	0.10	2.13	0.144
Year Size Category*	1	2.00	2.00	36.09	**< 0.001**
*Size Category*Sex*	1	0.10	0.10	0.95	0.330
*Latitude*Year*	1	1.30	1.30	23.28	**< 0.001**
*Latitude*Year*Size Category*	1	0.60	0.60	10.92	**< 0.001**

Skull Width	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	45.60	45.60	594.18	**< 0.001**
Year	1	20.80	20.80	271.42	**< 0.001**
Size Category	1	461.10	461.10	6011.76	**< 0.001**
Sex	1	0.10	0.10	1.38	0.240
Latitude Size Category*	1	0.30	0.30	3.51	0.06107
Year Size Category*	1	2.10	2.10	27.25	**< 0.001**
*Size Category*Sex*	1	0.10	0.10	0.68	0.40848
*Latitude*Year*	1	2.30	2.30	30.54	**< 0.001**
*Latitude*Year*Size Category*	1	0.50	0.50	6.92	**0.009**

Tooth Row Length	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	38.00	38.00	369.99	**< 0.001**
Year	1	19.60	19.60	191.45	**< 0.001**
Size Category	1	785.40	785.40	7656.97	**< 0.001**
Sex	1	1.80	1.80	17.55	**< 0.001**
Latitude Size Category*	1	4.00	4.00	39.41	**< 0.001**
Year Size Category*	1	3.90	3.90	38.13	**< 0.001**
*Size Category*Sex*	1	0.10	0.10	1.42	0.233
*Latitude*Year*	1	1.00	1.00	9.81	**0.002**
*Latitude*Year*Size Category*	1	1.10	1.10	11.13	**< 0.001**

Body Mass	Df	Sum of Squares	Mean Square	F-value	P-value
Latitude	1	991.00	991.00	2576.89	**< 0.001**
Year	1	2104.00	2104.00	5472.03	**< 0.001**
Size Category	1	3826.00	3826.00	9951.62	**< 0.001**
Sex	1	1.00	1.00	1.48	0.224
Latitude Size Category*	1	1.00	1.00	2.46	0.117
Year Size Category*	1	23.00	23.00	59.84	**< 0.001**
*Size Category*Sex*	1	1.00	1.00	1.33	0.250
*Latitude*Year*	1	6.00	6.00	16.59	**< 0.001**
*Latitude*Year*Size Category*	1	4.00	4.00	10.88	**< 0.001**

Appendix 6. The calculated K statistic and λ values with their associated p-values from the tests of phylogenetic signal. For each morphological trait, the slope coefficient of the linear regression between a given log-transformed trait and latitude and a phylogenetic tree extracted from Bininda-Emonds et al. (2007) supertree were used to calculate phylogenetic signal.

LATITUDE

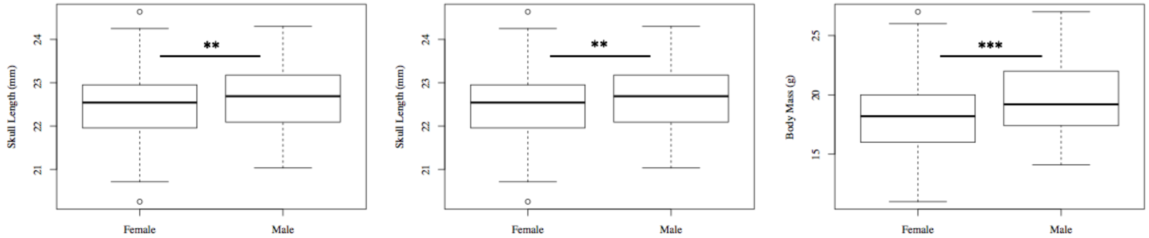
Slope coefficient	*K statistic*	*P-value*	*λ value*	*Log-likelihood*	*Log-likelihood for λ = 0*	*P-value*
Skull length	0.513	0.208	7.18E-05	68.7565	68.7567	1.000
Skull width	0.589	0.106	4.41E-05	67.1032	67.1033	1.000
Tooth row length	0.368	0.505	7.18E-05	68.6633	68.6636	1.000
Body mass	0.252	0.785	7.18E-05	38.7155	38.7157	1.000

TIME

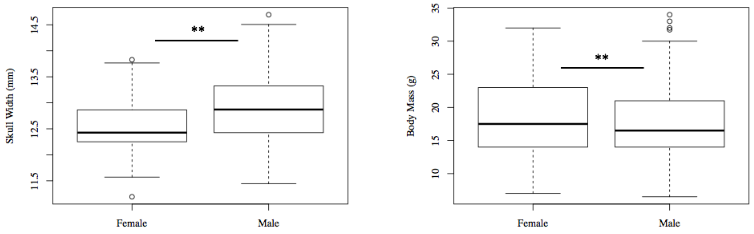
Slope coefficient	*K statistic*	*P-value*	*λ value*	*Log-likelihood*	*Log-likelihood for λ = 0*	*P-value*
Skull length	0.487	0.176	0.351	118.6221	118.5375	0.681
Skull width	1.448	0.004	0.929	114.2258	111.5016	0.020
Tooth row length	0.733	0.025	0.790	114.197	113.1752	0.153
Body mass	0.405	0.365	7.18E-05	76.54866	76.54886	1.000

Appendix 7: Detailed plots of the sexual dimorphism exhibited by certain species where a significant difference is the value of the morphological traits is found between the males and females.

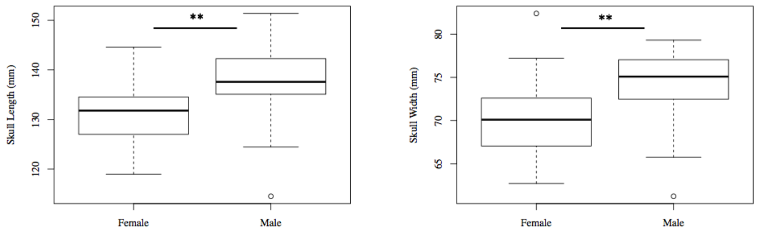
Blarina brevicauda
Sexual dimorphism



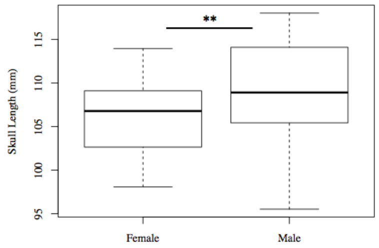
Myodes gapperi
Sexual dimorphism



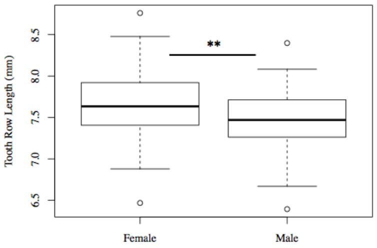
Vulpes vulpes
Sexual dimorphism



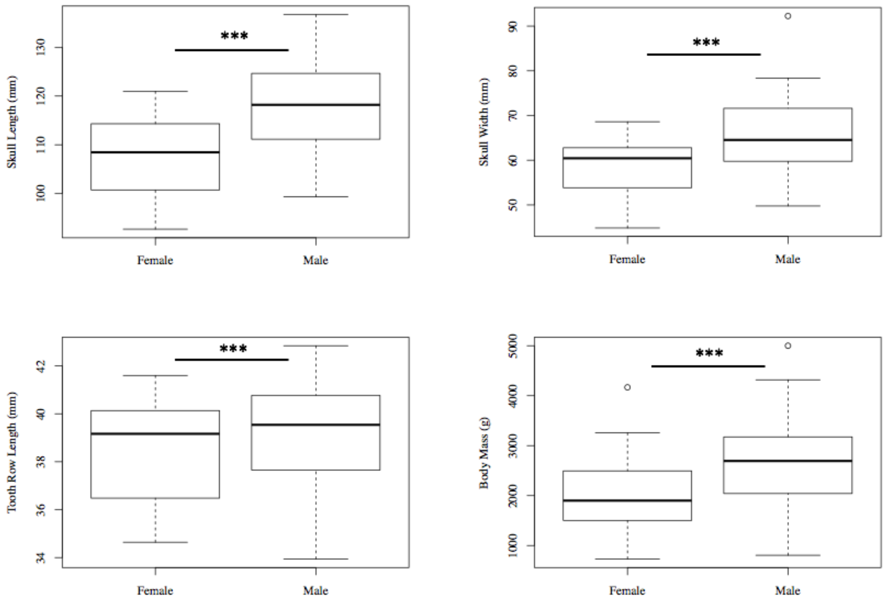
Procyon lotor
Sexual dimorphism



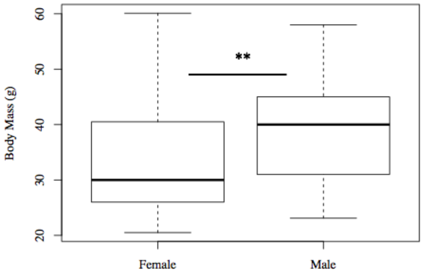
Tamiasciurus hudsonicus
Sexual dimorphism



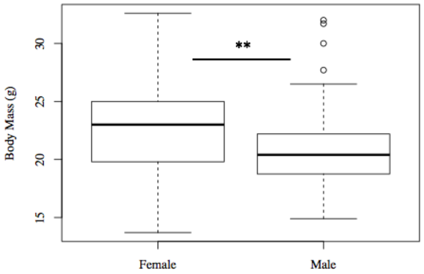
Didelphis virginiana
Sexual dimorphism



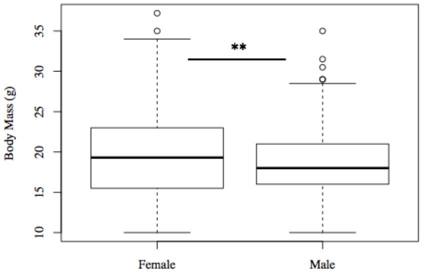
Microtus pennsylvanicus
Sexual dimorphism



Napaeozapus insignis
Sexual dimorphism



Peromyscus leucopus
Sexual dimorphism



Appendix 8. The p-values associated with each of GLM model run for each morphological trait for a given species. All significant values after a Bonferroni correction are bolded. The abbreviations are SL (skull length), SW (skull width), TRL (tooth row length), and BM (body mass).

B. brevicauda	*SL*	*SW*	*TRL*	*BM*
Latitude	**< 0.001**	**< 0.001**	0.054	**< 0.001**
Year	**0.004**	0.818	0.086	0.660
Sex	**0.006**	**0.002**	0.235	**< 0.001**
Lat*Sex	-	-	-	**< 0.001**
Lat*Year	-	-	0.045	-

D. virginiana	*SL*	*SW*	*TRL*	*BM*
Latitude	0.095	**< 0.001**	**< 0.001**	**< 0.001**
Year	0.917	0.687	0.272	0.583
Sex	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Lat*Sex	-	-	-	**< 0.001**

M. monax	*SL*	*SW*	*TRL*	*BM*
Latitude	**< 0.001**	**< 0.001**	**< 0.001**	0.129
Year	0.318	0.106	0.105	0.500
Sex	0.982	0.628	0.195	0.741

M. mephitis	*SL*	*SW*	*TRL*	*BM*
Latitude	0.058	0.035	0.050	0.773
Year	0.754	0.131	0.036	0.476
Sex	0.128	0.338	0.151	0.338
Lat*Year	-	-	0.047	-

M. pennsylvanicus	*SL*	*SW*	*TRL*	*BM*
Latitude	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Year	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
Sex	0.122	0.166	0.345	**0.008**
Lat*Year	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**

M. gapperi	*SL*	*SW*	*TRL*	*BM*
Latitude	**0.002**	**< 0.001**	**< 0.001**	**0.006**
Year	**0.002**	**< 0.001**	0.199	**< 0.001**
Sex	0.031	**0.001**	0.876	**0.002**
Lat*Year	**0.002**	**0.001**	-	-

N. insignis	*SL*	*SW*	*TRL*	*BM*
Latitude	**0.003**	**< 0.001**	**0.008**	0.303
Year	0.795	0.445	0.134	0.311
Sex	0.259	0.053	0.193	**0.002**
Lat*Sex	-	0.045	-	**0.001**
Lat*Year	-	-	-	0.301
Year*Sex	-	-	-	**0.002**
Lat*Year*Sex	-	-	-	**0.001**

P. gossypinus	*SL*	*SW*	*TRL*	*BM*
Latitude	0.769	0.641	0.500	0.196
Year	0.338	0.613	0.772	0.768
Sex	0.447	0.526	0.260	0.103

P. leucopus	*SL*	*SW*	*TRL*	*BM*
Latitude	0.056	0.949	0.522	0.150
Year	0.571	0.065	0.016	0.722
Sex	0.582	0.376	0.525	**0.002**

P. maniculatus	*SL*	*SW*	*TRL*	*BM*
Latitude	0.231	**< 0.001**	0.026	**< 0.001**
Year	**0.003**	**< 0.001**	0.072	0.530
Sex	0.194	0.763	0.159	0.019
*Lat*Sex*	-	-	-	0.023
*Lat*Year*	-	**< 0.001**	0.031	-

P. lotor	*SL*	*SW*	*TRL*	*BM*
Latitude	0.115	0.172	**0.003**	**< 0.001**
Year	0.324	0.155	0.560	**< 0.001**
Sex	**0.010**	0.190	0.068	0.553
*Lat*Sex*	-	-	0.029	-
*Lat*Year*	-	-	-	**< 0.001**

S. cinereus	*SL*	*SW*	*TRL*	*BM*
Latitude	0.315	**< 0.001**	0.020	0.021
Year	0.019	0.059	0.046	0.020
Sex	0.233	0.028	0.029	0.211
*Lat*Year*	-	-	-	0.020

S. floridanus	*SL*	*SW*	*TRL*	*BM*
Latitude	0.260	**0.003**	0.177	0.022
Year	0.949	0.761	0.097	0.115
Sex	0.757	0.818	0.983	0.310

T. hudsonicus	*SL*	*SW*	*TRL*	*BM*
Latitude	0.134	0.969	0.384	0.279
Year	0.114	0.115	0.304	0.148
Sex	0.022	0.475	**0.009**	0.776
*Lat*Sex*	0.020	-	-	-
*Lat*Year*	0.134	-	-	-
*Sex*Year*	0.022	-	-	-
*Lat*Year*Sex*	0.020	-	-	-

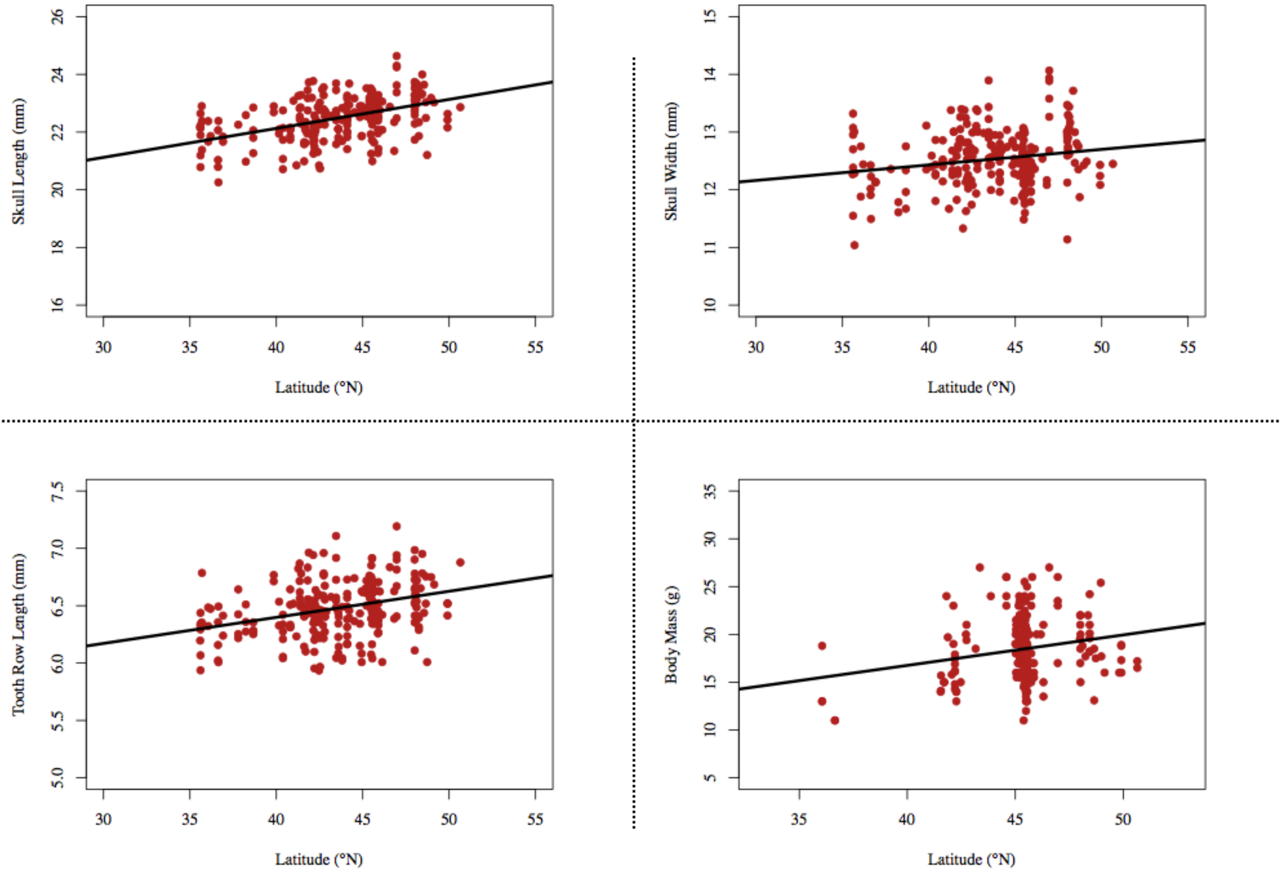
T. striatus	*SL*	*SW*	*TRL*	*BM*
Latitude	0.014	0.051	**< 0.001**	0.087
Year	0.015	0.049	0.697	0.856
Sex	0.801	0.772	0.871	0.317
*Lat*Year*	0.015	0.050	-	-

V. vulpes	*SL*	*SW*	*TRL*	*BM*
Latitude	0.739	**0.004**	0.890	0.365
Year	0.775	**0.005**	0.360	**< 0.001**
Sex	**0.006**	**0.002**	0.103	0.322
*Lat*Year*	-	**0.004**	-	-

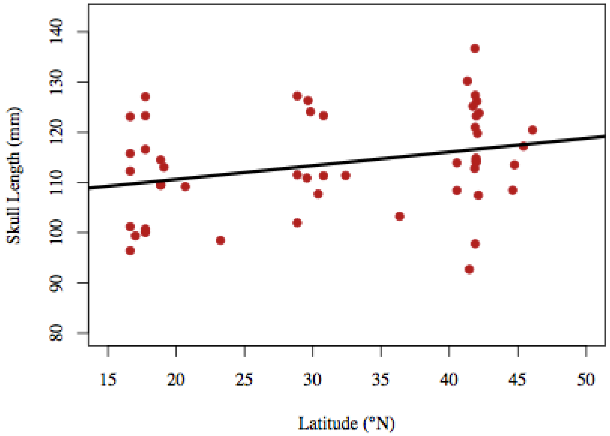
Z. hudsonius	*SL*	*SW*	*TRL*	*BM*
Latitude	0.146	**0.012**	0.337	0.832
Year	0.093	0.205	0.371	0.107
Sex	0.326	0.578	0.189	0.983

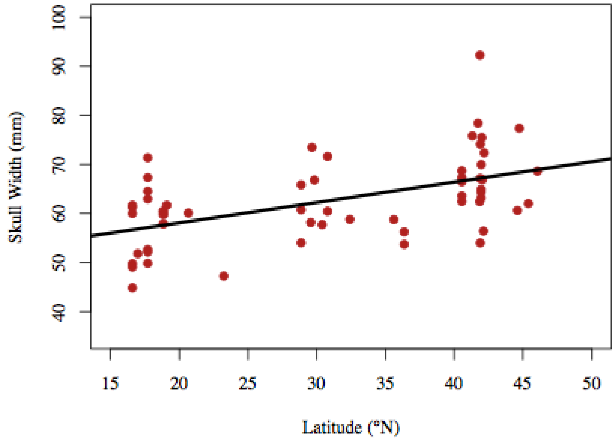
Appendix 9. Raw data points values for each morphological trait of a given specimen with a linear regression of the relationship between the given morphological trait and latitude. Four plots are found per species with museum specimens including the skull length (top left), skull width (top right), tooth row length (bottom left), and body mass (bottom right).

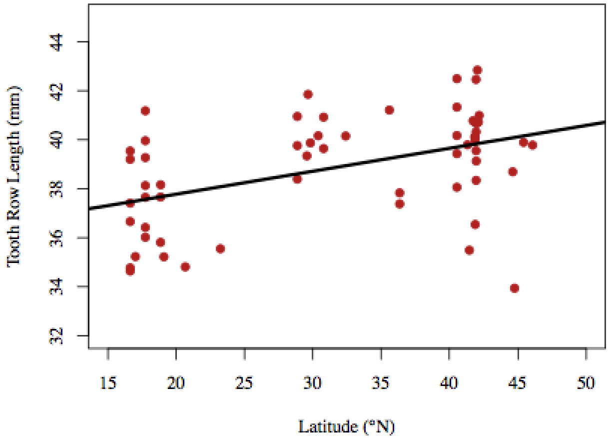
Blarina brevicauda

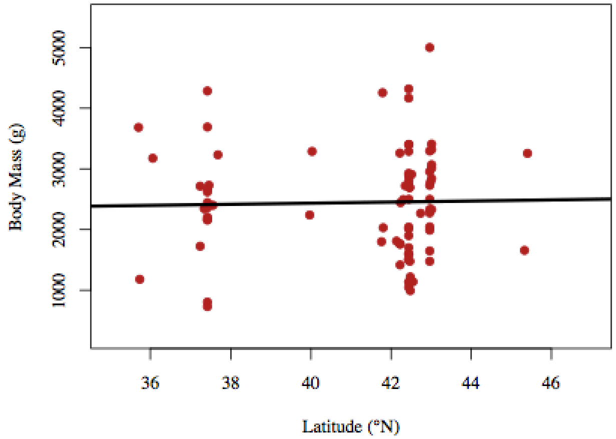


Didelphis virginiana

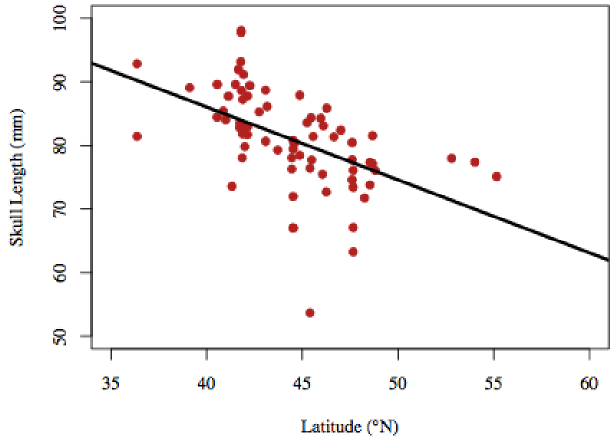


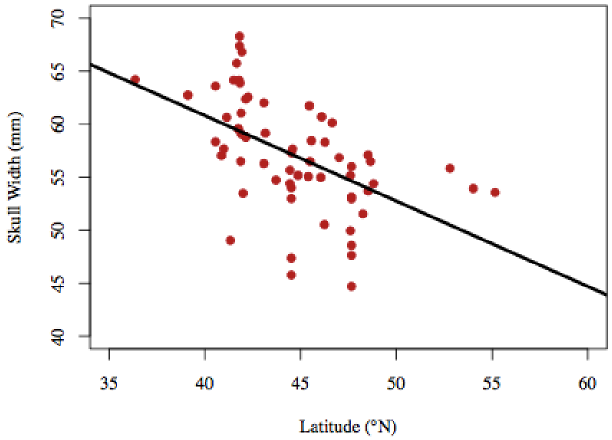


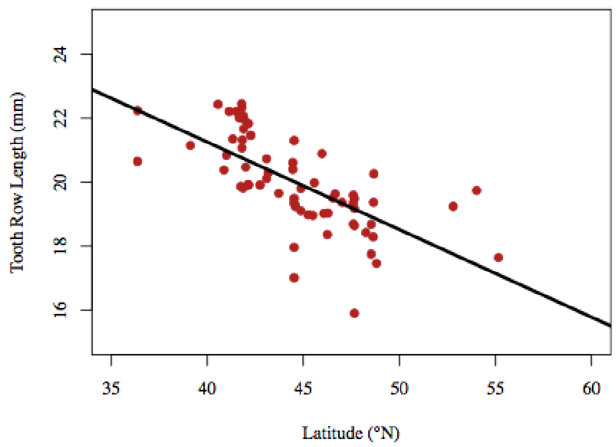


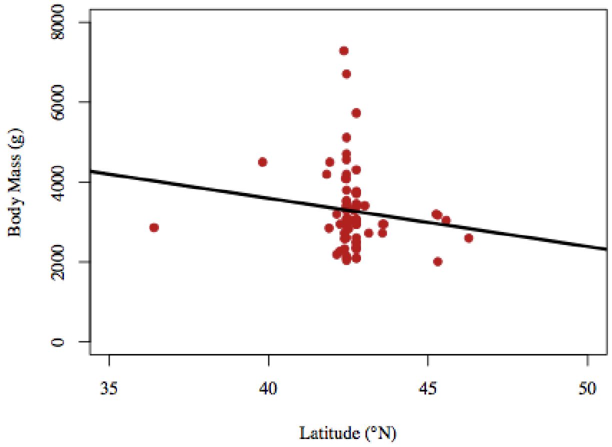


Marmota monax

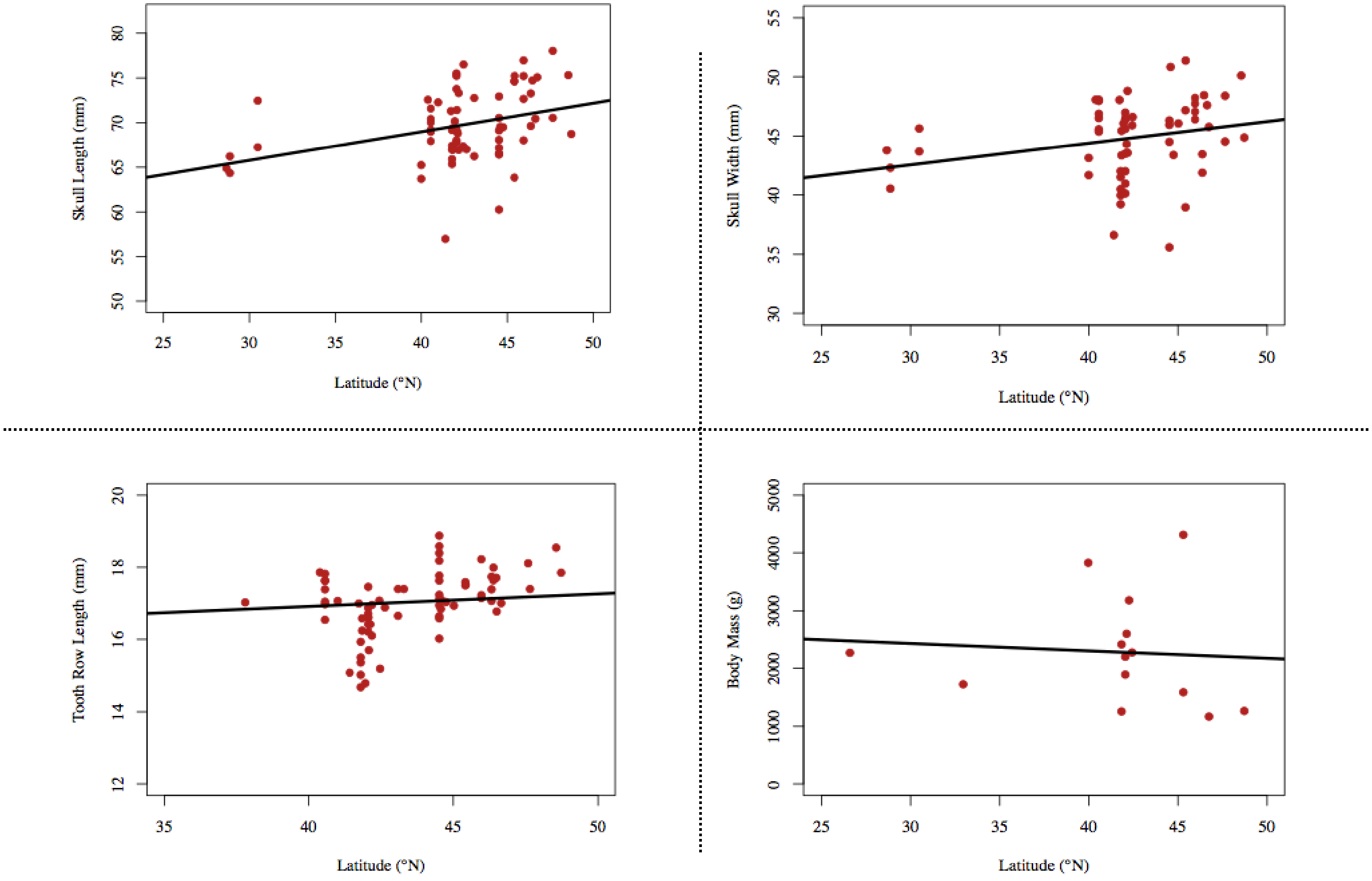




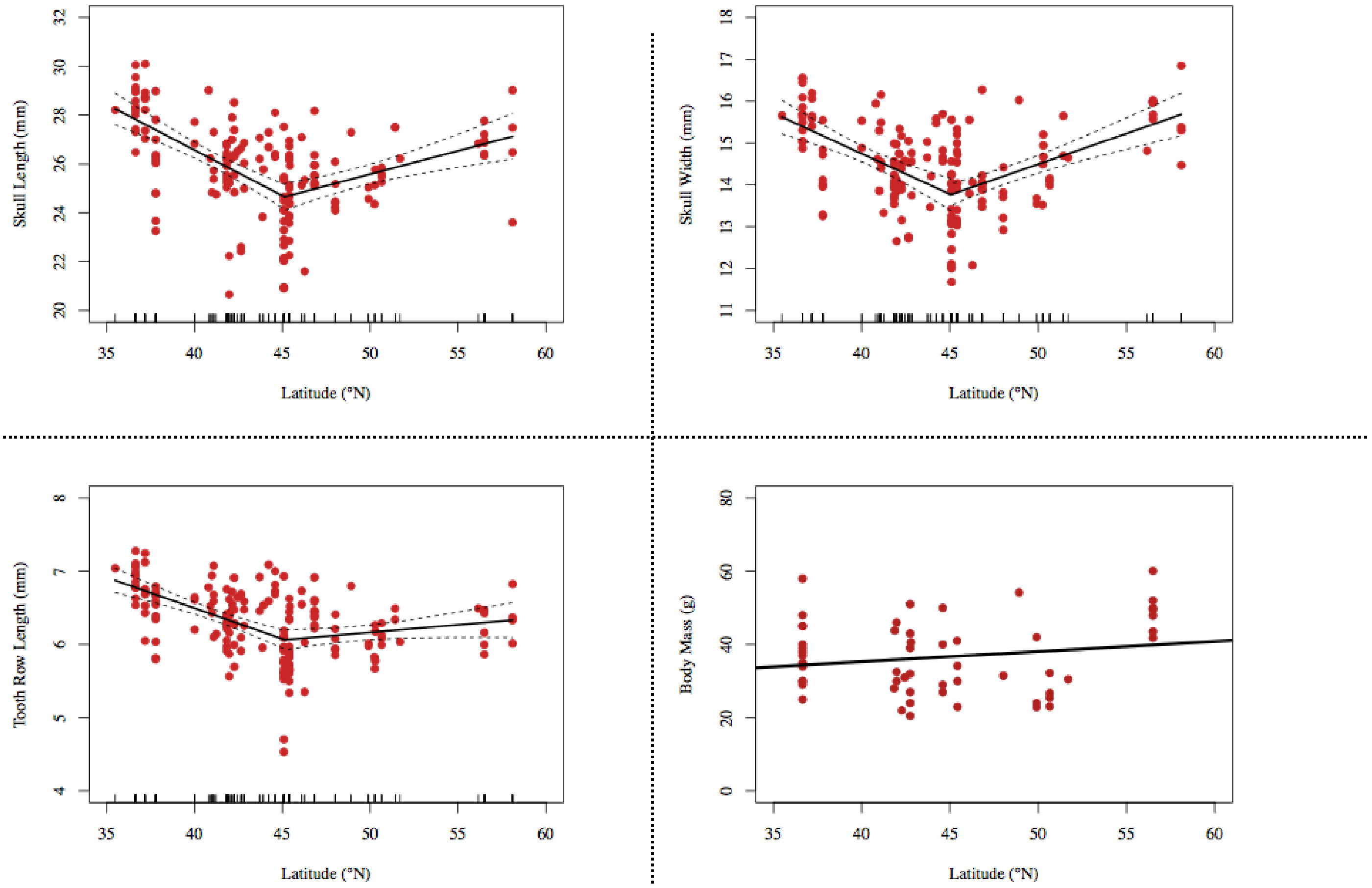




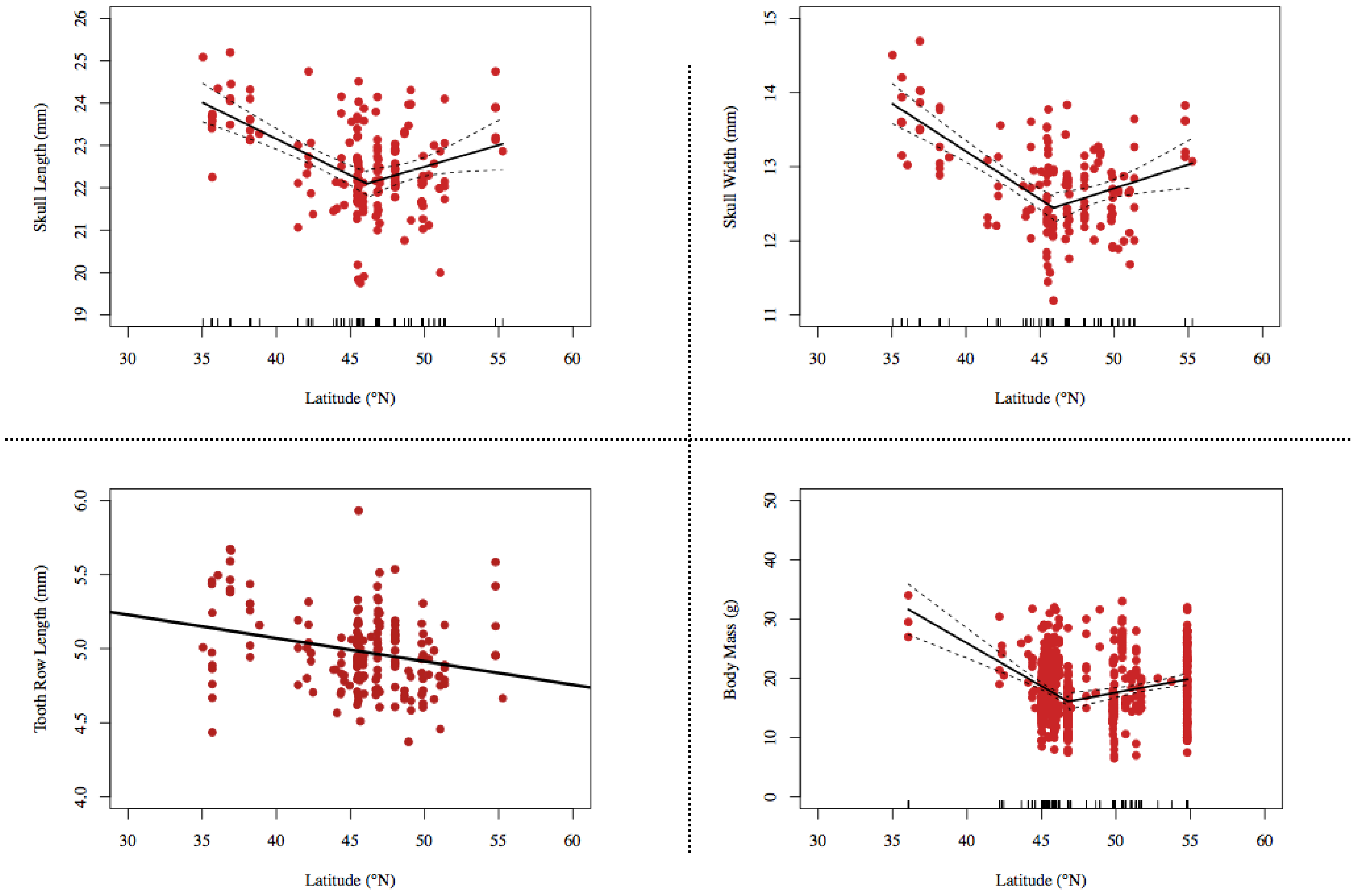
Mephitis mephitis



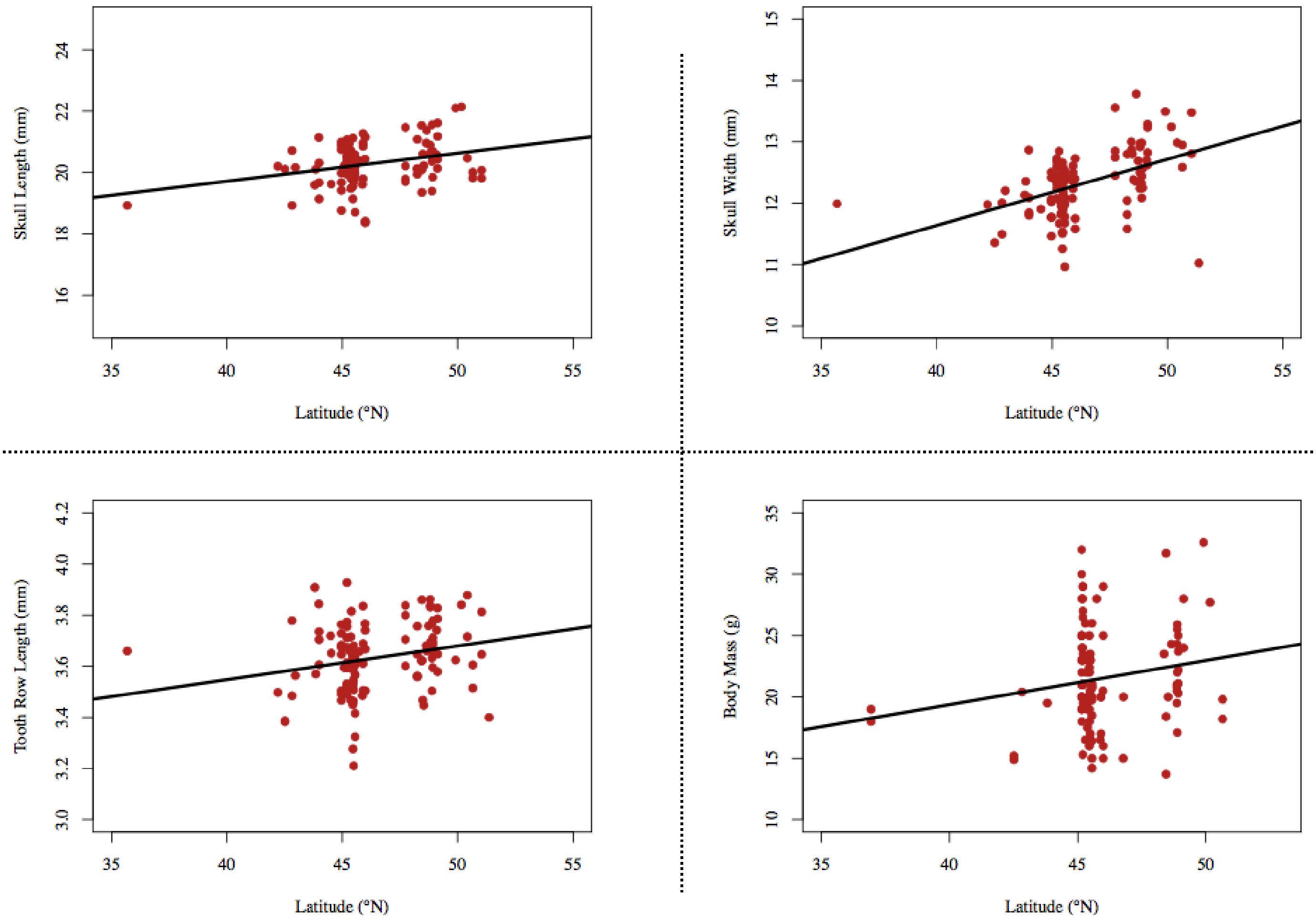
Microtus pennsylvanicus



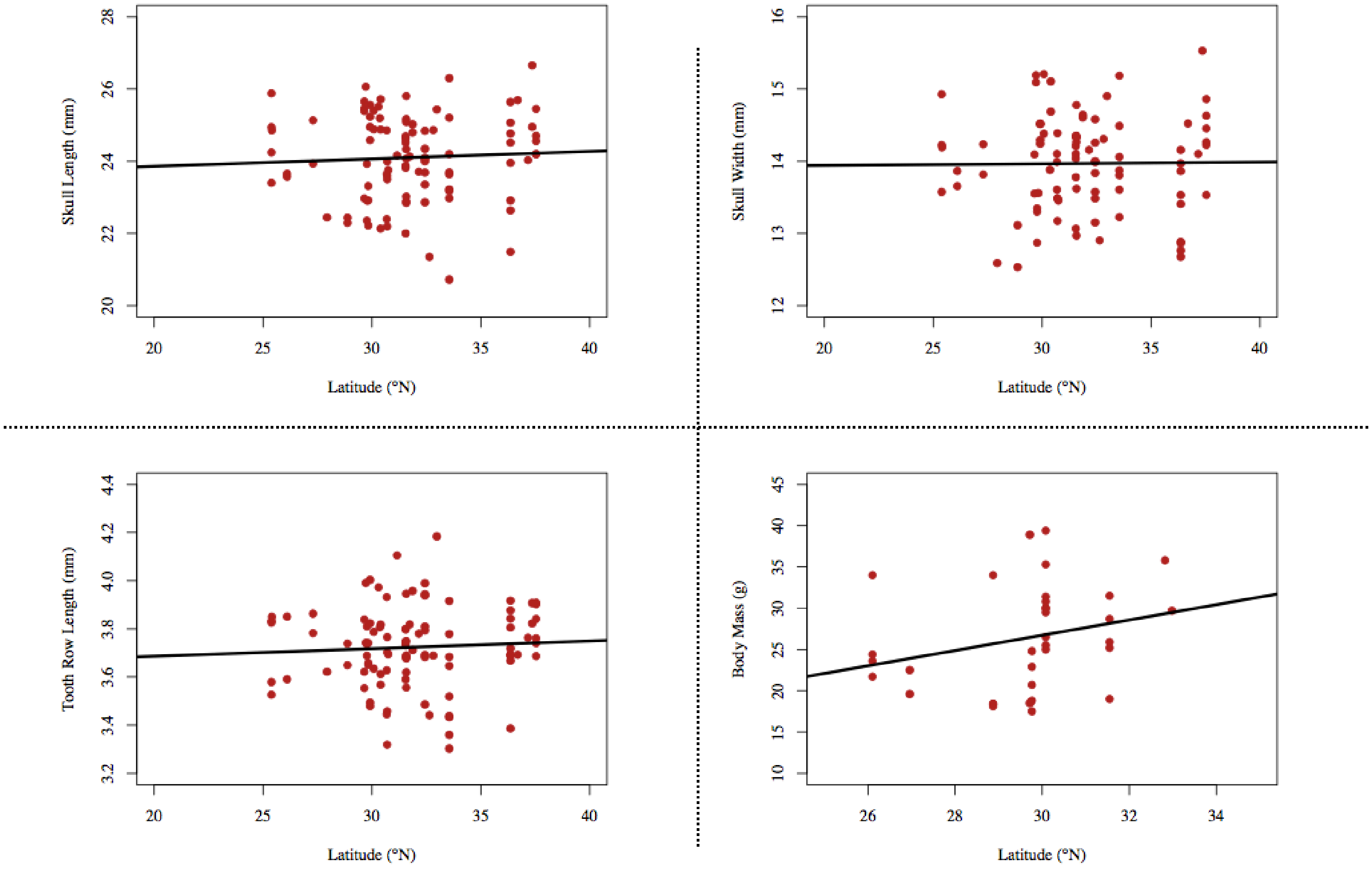
Myodes gapperi



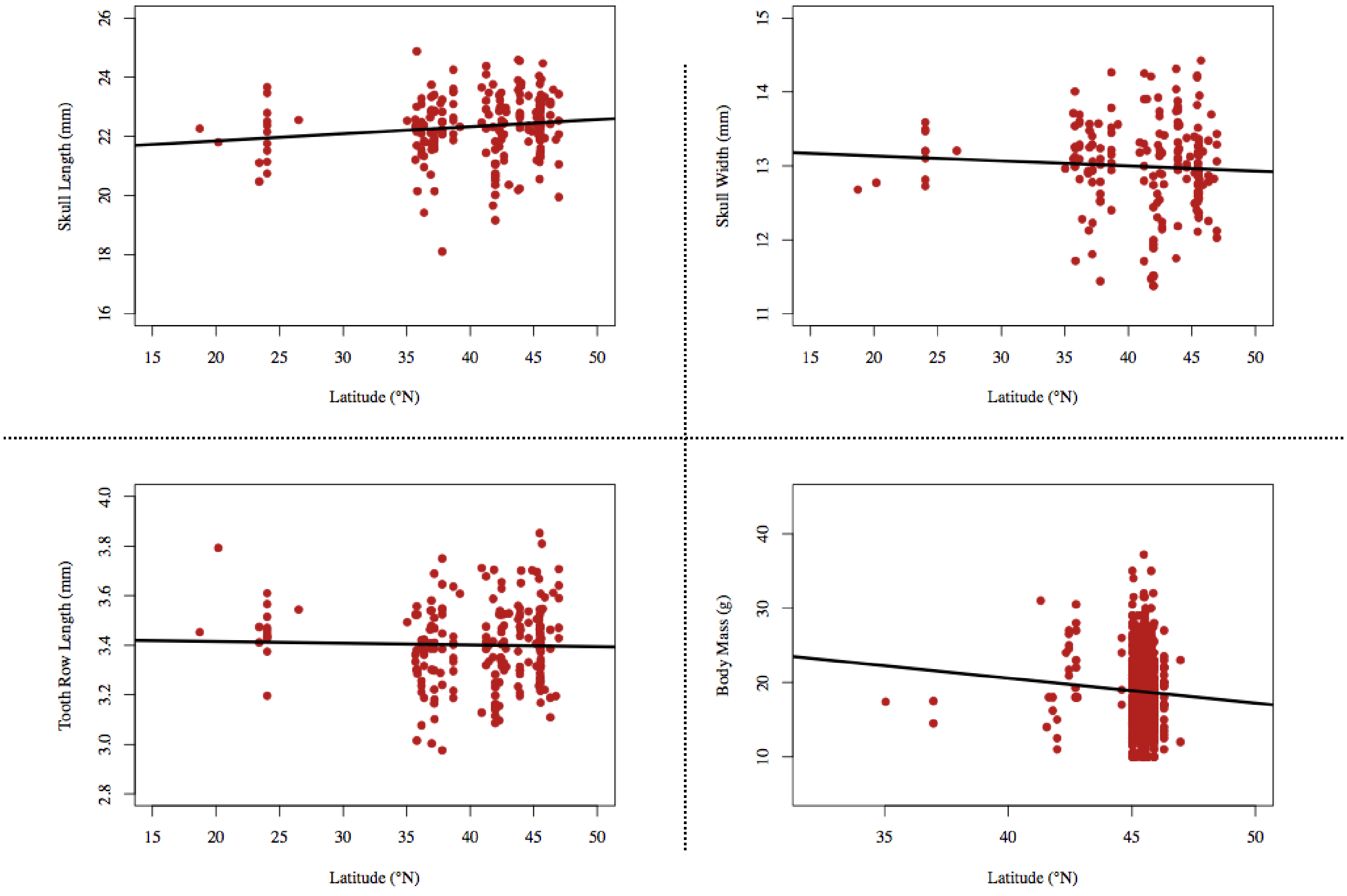
Napaeozapus insignis



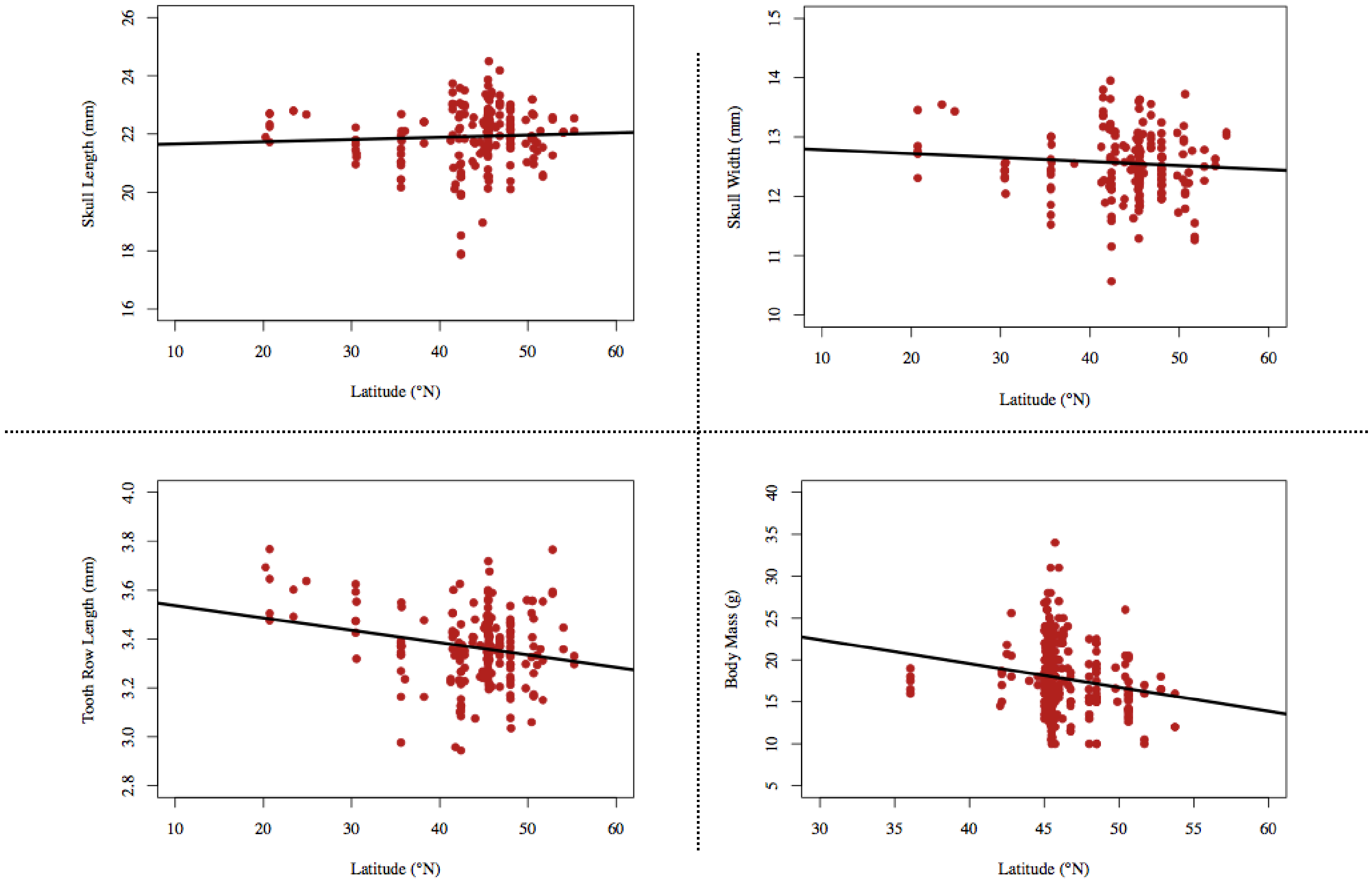
Peromyscus gossypinus



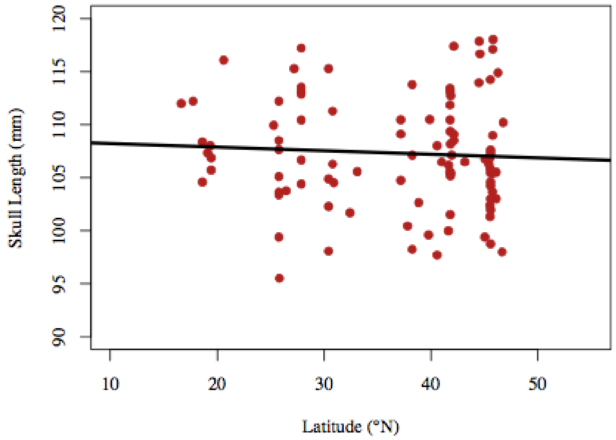
Peromyscus leucopus

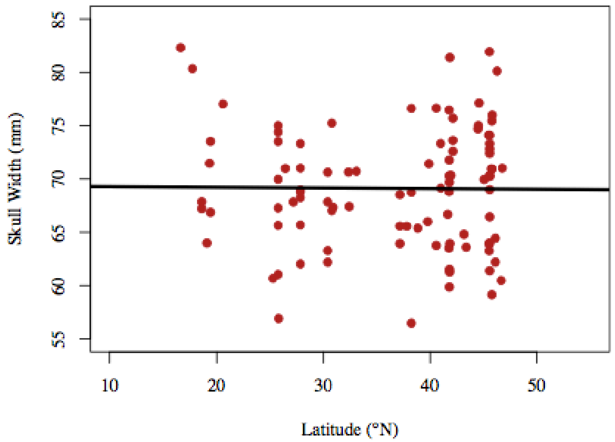


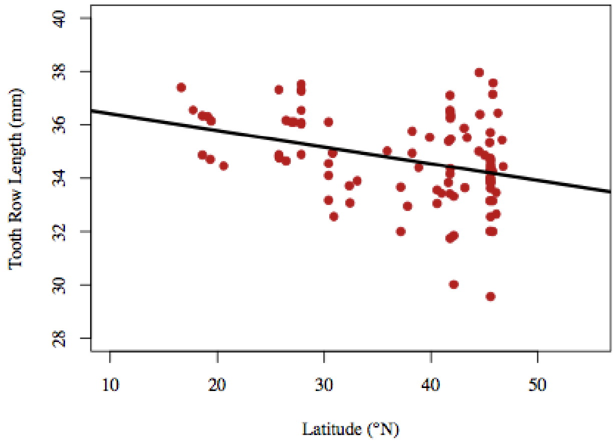
Peromyscus maniculatus

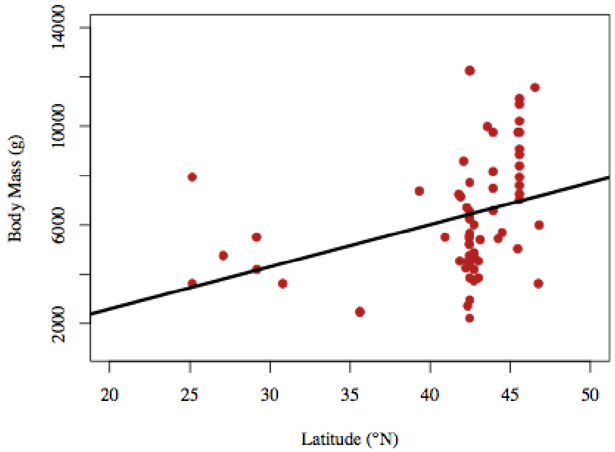


Procyon lotor

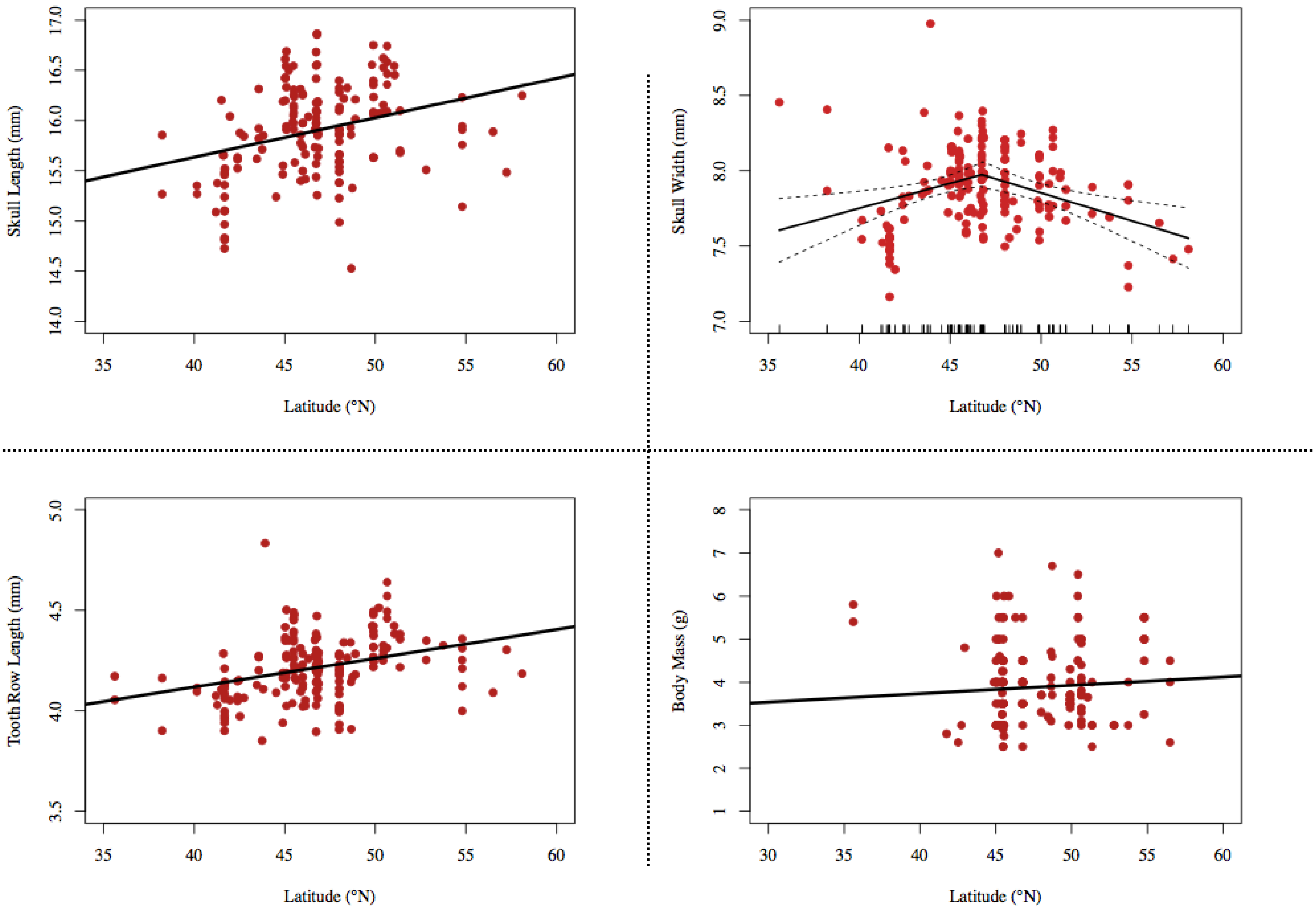




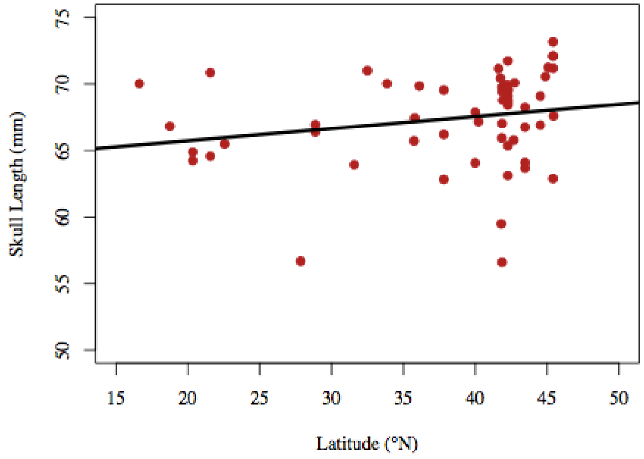


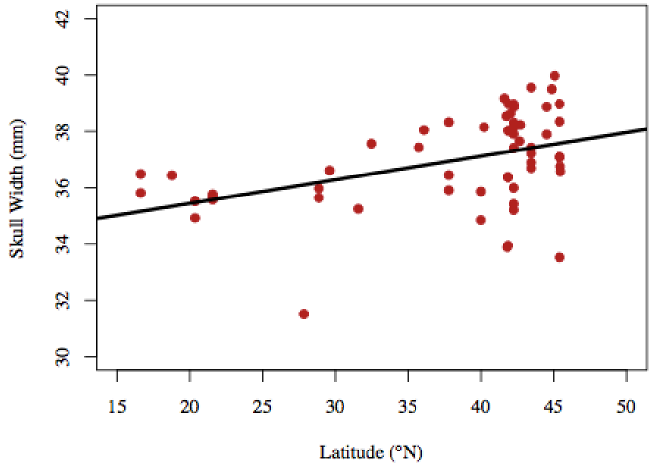


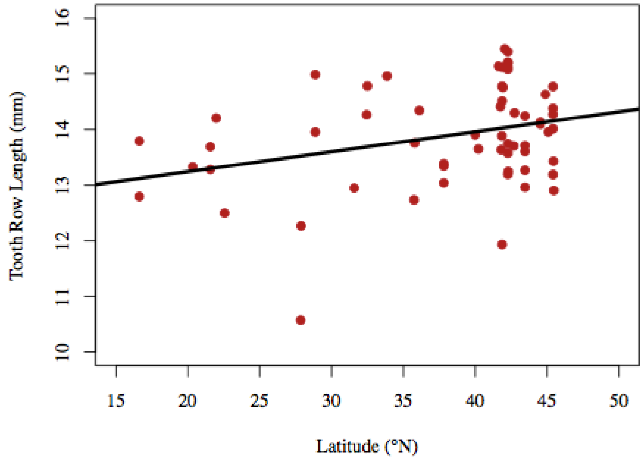
Sorex cinereus

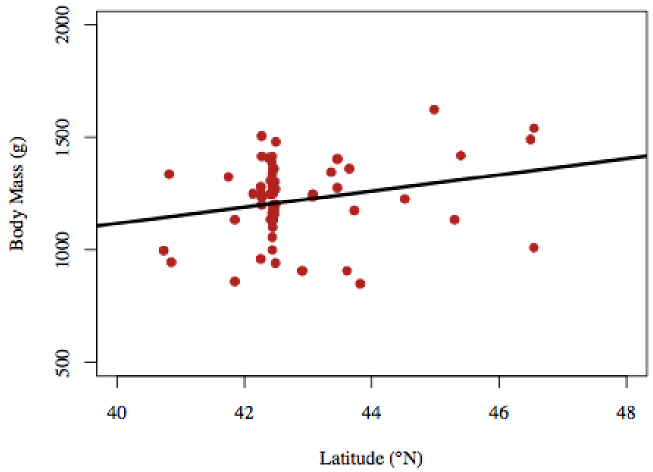


Sylvilagus floridanus

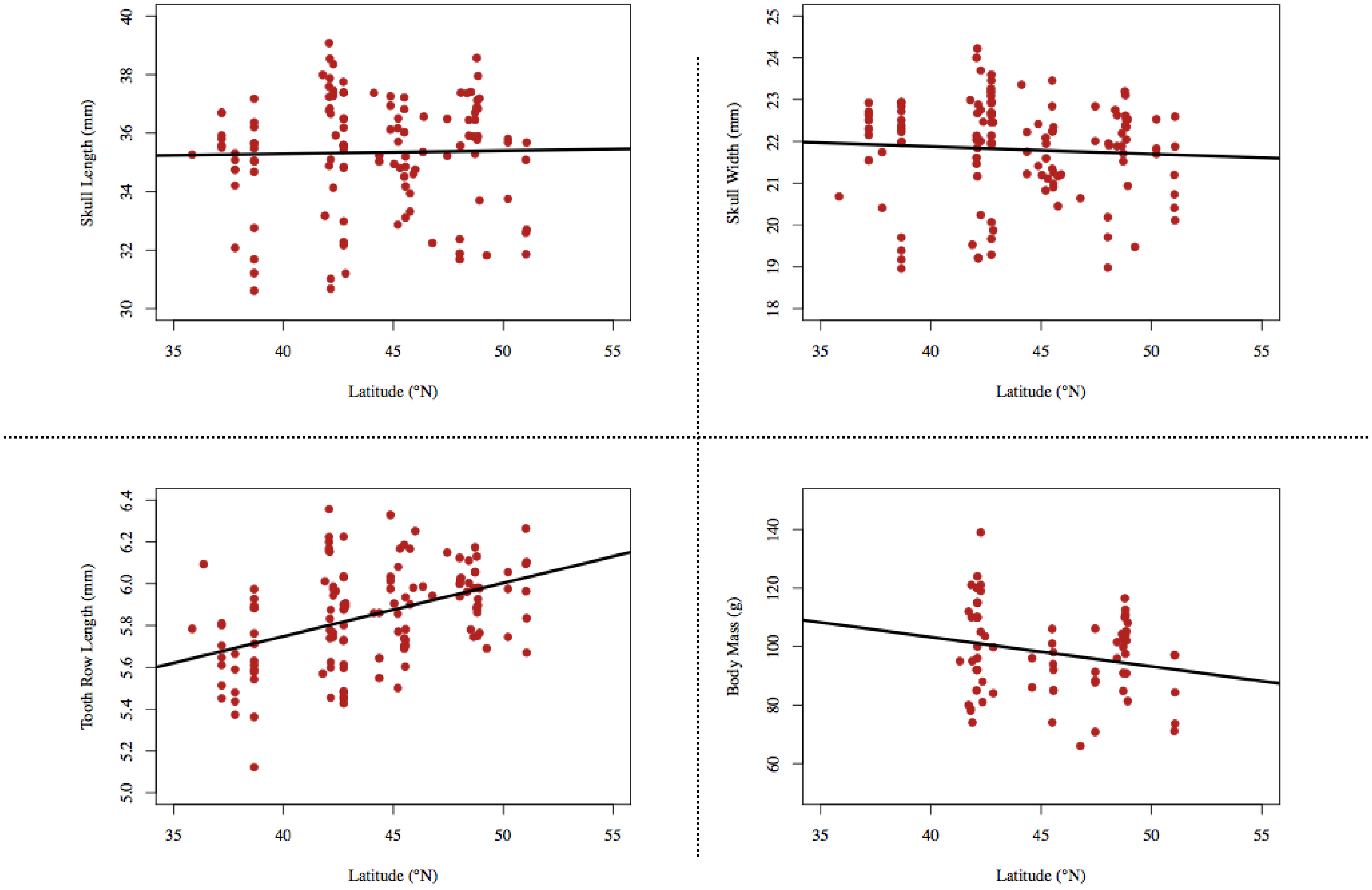




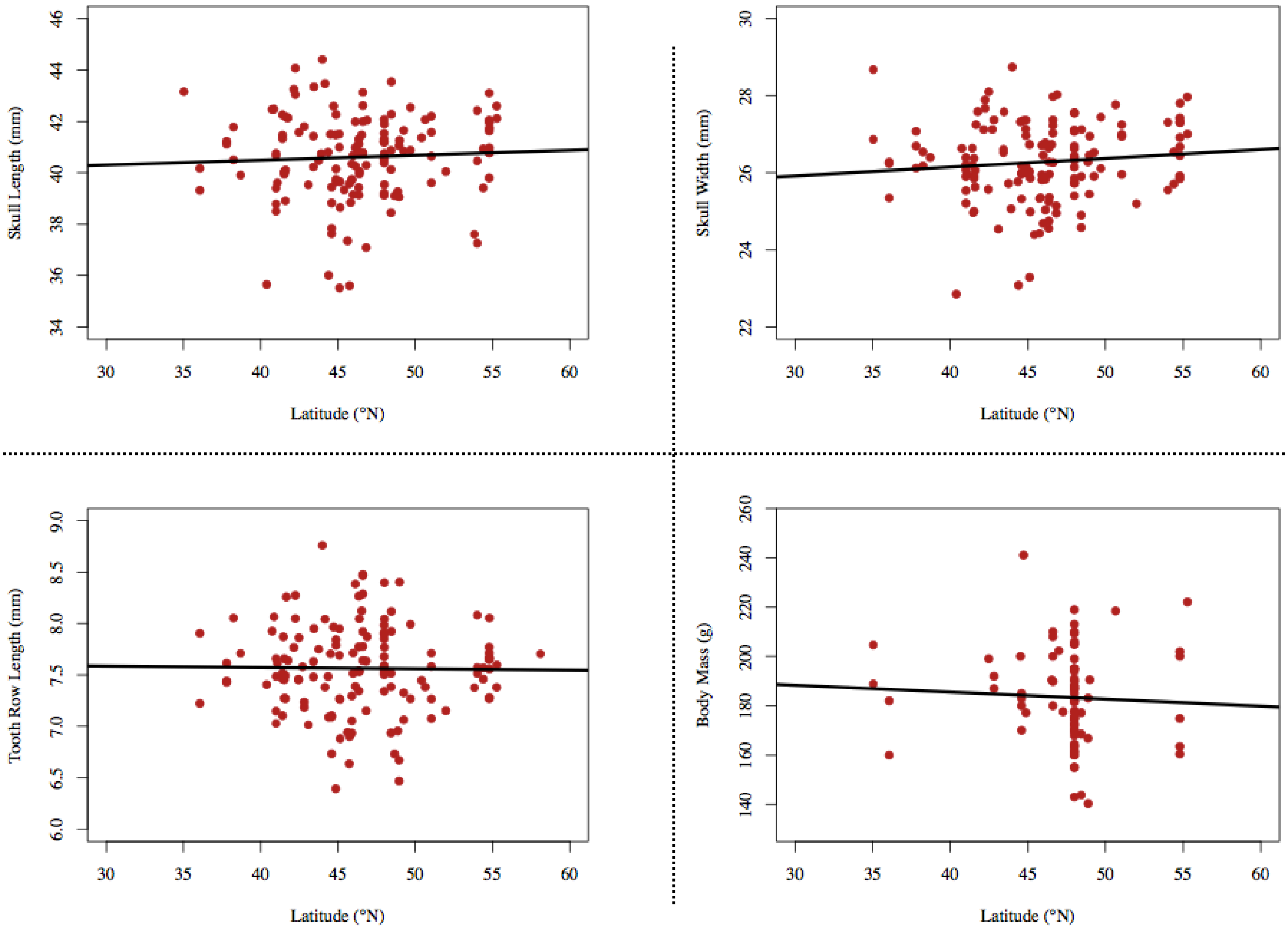




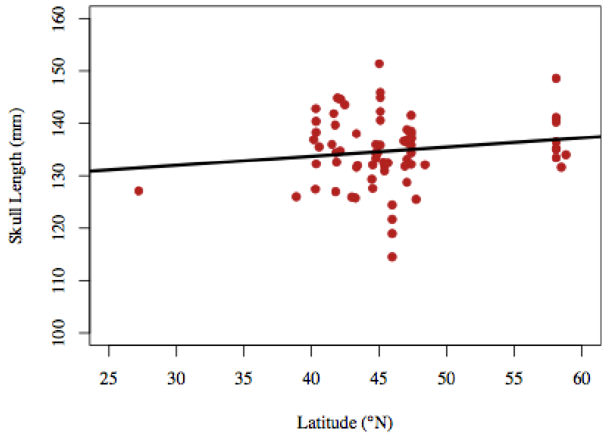
Tamias striatus

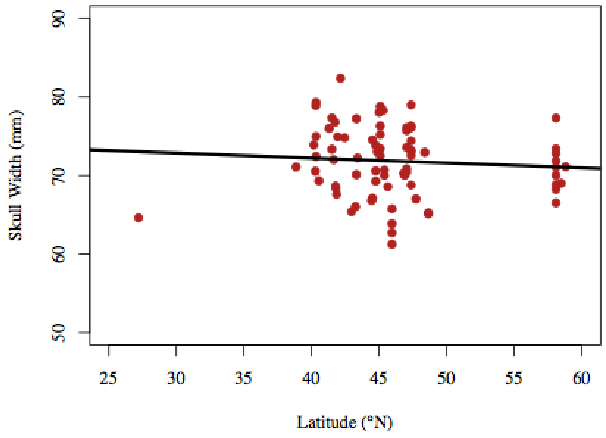


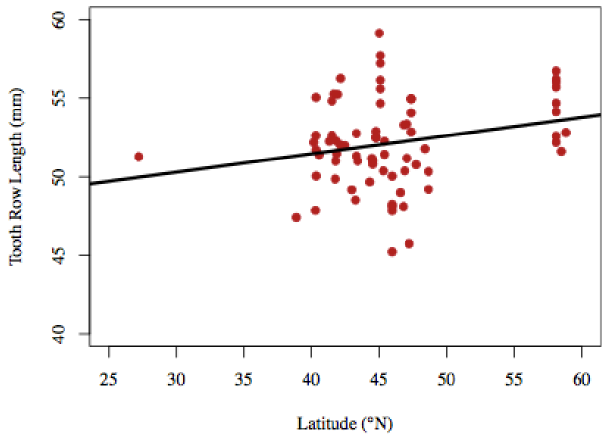
Tamiasciurus hudsonicus

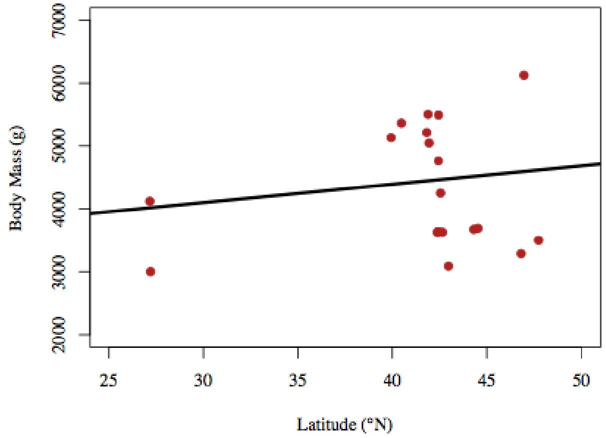


Vulpes vulpes









Zapus hudsonius