



## Latitudinal body-mass trends in Oligo-Miocene mammals

John D. Orcutt and Samantha S. B. Hopkins

**Abstract.**—Paleoecological data allow not only the study of trends along deep-time chronological transects but can also be used to reconstruct ecological gradients through time, which can help identify causal factors that may be strongly correlated in modern ecosystems. We have applied such an analysis to Bergmann's rule, which posits a causal relationship between temperature and body size in mammals. Bergmann's rule predicts that latitudinal gradients should exist during any interval of time, with larger taxa toward the poles and smaller taxa toward the equator. It also predicts that the strength of these gradients should vary with time, becoming weaker during warmer periods and stronger during colder conditions. We tested these predictions by reconstructing body-mass trends within canid and equid genera at different intervals of the Oligo-Miocene along the West Coast of North America. To allow for comparisons with modern taxa, body mass was reconstructed along the same transect for modern *Canis* and *Odocoileus*. Of the 17 fossil genera analyzed, only two showed the expected positive relationship with latitude, nor was there consistent evidence for a relationship between paleotemperature and body mass. Likewise, the strength of body-size gradients does not change predictably with climate through time. The evidence for clear gradients is ambiguous even in the modern genera analyzed. These results suggest that, counter to Bergmann's rule, temperature alone is not a primary driver of body size and underscore the importance of regional-scale paleoecological analyses in identifying such drivers.

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### Introduction

Diversity and body-size clines have been observed along a number of ecological gradients: two of ecology's foundational studies analyzed trends along elevational (Humboldt and Bonpland 1807) and latitudinal transects (Bergmann 1847), and modern researchers have traced patterns along climatic (e.g., Bradshaw and Holzapfel 2010), water depth (e.g., Smith and Brown 2002), chemical (e.g., Hollister et al. 2010), and other gradients. Such research lays the foundation for the formulation of ecological models: by observing how organisms respond to a wide range of environmental conditions in modern ecosystems, it is possible to predict how the same organisms will respond to environmental changes in the future. These models are critically important to anticipating and mitigating the effects of anthropogenic climate change, but in some cases lack predictive power (as is the case, for example, with ecological niche models of range shifts; Guralnick and Pearman 2010; Davis et al.

2014). This is partially because of the complexity of ecological interactions, in which several factors may influence biotic variables. It is also due in part to the complexity of the ecosystems themselves, in which many biotic and abiotic variables influence and are influenced by one another, making it difficult to tease out which variables are most important in shaping biotic patterns (Bertheaux et al. 2006). Finally, models of future responses to environmental change based on neontological research are, of necessity, based on biotic variability across environmental regimes for which there is a historical precedent. Even the most conservative estimates of future warming indicate a rapidly increasing divergence from the climatic conditions that have characterized the Holocene (Intergovernmental Panel on Climate Change 2014), meaning that any prediction of biotic responses to this change requires extrapolating well beyond the range of modern data.

These last two concerns can be addressed by not only examining biotic clines within modern

ecosystems but by using the fossil and paleo-environmental records to trace chronoclines, following ecological change through time. By applying a four-dimensional perspective to ecology, biotic responses to environmental conditions that do not exist in modern ecosystems can be observed and potential causal factors that are currently tightly tied to one another can be teased apart as they vary through time. This approach has historically played a small part in our understanding of ecological drivers of biological trends, in large part because of the perceived incompleteness of the fossil record and inaccuracy of paleo-environmental reconstructions. However, many taxa are represented by very large fossil samples, and many regions have been the subject of rigorous paleoecological study, allowing robust reconstructions of trends along chronological transects and, at least in certain cases, the identification of causal factors. A great deal of paleontological research along these lines has focused on Cenozoic fossil mammals of North America, which are represented by an extremely rich fossil record that has been extensively collected for well over a century. These studies have, for the most part, tracked either mammal diversity (Lillegraven 1972; Alroy et al. 2000; Prothero 2004) or body size (Koch 1986; Alroy 1998; Gingerich 2003; Smith et al. 2010; Orcutt and Hopkins, 2013; Saareinen et al. 2014) through time. Others have examined patterns within the same variables at different intervals through time (Rose et al. 2011; Lyons et al. 2013; Fraser et al. 2014).

Chronocline analysis is especially well suited to address one of the longest-standing ecological questions: What drives mammal body-size evolution? This question was first raised by Bergmann (1847), who observed that latitudinal body-size gradients were visible within most mammal taxa at several taxonomic levels, with larger taxa or individuals tending to live at higher latitudes and smaller taxa or individuals living at lower latitudes. However, trying to tie body size to any other biotic or climatic variable has proven difficult. Bergmann himself suggested that the gradients he observed were a product of temperature, as large animals are better able to retain heat due

to their small surface area-to-volume ratio, while smaller animals are more effective at shedding it. Some analyses, most notably that of Geist (1987), have suggested that not only is Bergmann's rule *sensu stricto* invalid but that the monotonic latitudinal body-mass gradients on which it is based do not exist. However, other studies have confirmed the patterns observed by Bergmann, finding body-size gradients within most mammal taxa (Ashton et al. 2000; Meiri and Dayan 2003; Blackburn and Hawkins 2004) and faunas (Rodríguez et al. 2008). While some authors have supported Bergmann's rule *sensu stricto*, others have suggested that other ecological variables play a more direct role than temperature in driving body-size evolution. Some of the proposed mechanisms posit biotic drivers. Primary productivity may limit the size to which herbivores can grow (Rosenzweig 1968), while the size and abundance of prey may influence body size in predators (McNab 1970; Erlinge 1987). Size trends in island taxa suggest that competition may play an important role in shaping body-mass patterns, but the effects of competition appear to vary between size classes (Damuth 1993), while predation pressure may select for larger prey taxa (Korpimäki and Norrdahl 1989). Besides temperature, two other climatic variables have been posited to play a major role in body-size evolution: precipitation (large animals have a greater capacity for storing water and will be selected for in arid climates; James 1970) and seasonality (large animals have a greater capacity for fat reserves and will be selected for in seasonal climates; Millar and Hickling 1990).

Several paleontological studies have tested Bergmann's rule, either explicitly or indirectly (Gingerich 2003; Smith et al. 2010; Meachen and Samuels 2012; Lovegrove and Mowoe 2013; Lyons and Smith 2013; Orcutt and Hopkins, 2013; Saareinen et al. 2014). These studies have ranged from local to global in scope and, as with neontological analyses, have reached divergent conclusions. Gingerich (2003) examined condylarth and perissodactyl body-mass trends across the Paleocene/Eocene Boundary in Wyoming's Bighorn Basin, finding that all the taxa in question showed body-mass spikes during the Paleocene–Eocene Thermal Maximum (PETM).

However, Gingerich notes that the magnitude of these increases was too great to be explained solely by elevated temperatures, instead suggesting that dwarfing in Bighorn Basin mammals was due to a decrease in the nutritional value of plants, itself driven by the same rise in CO<sub>2</sub> levels that drove an increase in global temperature during the PETM. Orcutt and Hopkins (2013) detail the results of a study of body mass in three families of Oligo-Miocene mammals in the northwest United States. No evidence was found of a causal relationship between any climatic variable and body mass. Instead, different body-mass profiles were observed within each family, suggesting that, for most of the Cenozoic, climate alone had little effect on body-size evolution and that the factors that do shape body-mass trends are complex and vary between taxa. Similarly, in analyses of Pleistocene and Holocene predators, Meachen et al. (2014b) and Meachen and Samuels (2012) showed no negative relationship between temperature and body size in wolves and *Smilodon* and a change in body size that did not correlate with climate in coyotes. A correlation between body mass and mean annual temperature was observed in Cenozoic mammals at the global scale by Smith et al. (2010) and Saarinen et al. (2014), seemingly supporting Bergmann's rule *sensu stricto*. However, a correlation between global temperature and body size does not necessarily imply a straightforward causal relationship. This point is underscored by Lovegrove and Mowoe (2013), who examined mammal body-size trends through time within different ecological categories based on locomotor modes. Their results support a model in which unguligrade herbivores and digitigrade carnivores increased in size as the result of the spread of grasslands after the Eocene, while plantigrade mammals generally remained small, constrained by the presence of larger predatory mammals. The rise of grasslands was coincident with, and likely tied to, a cooling and drying climate (Retallack 2001). This close connection between climate and ecosystem change means that the Lovegrove and Mowoe (2013) model, in which body size is driven by a complex set of interactions with the physical environment and with other organisms, might yield body-mass data that would be

correlated with temperature despite the absence of a direct causal relationship.

One way to test whether temperature alone can explain trends in mammal body-size evolution is to examine body-size patterns at various points through time. Most previous paleontological work on Bergmann's rule has focused on body-size change through time within a region, though the size of those regions has varied from individual basins to the entire planet. Lyons and Smith (2013) conducted such a test when they examined body-mass distributions among mammals at different intervals between the Cretaceous and today, finding that a unimodal size distribution at the end of the Mesozoic gave way to a bimodal distribution by the Eocene that has remained remarkably stable throughout the Cenozoic. Conspicuously lacking from the paleontological study of mammalian body-size evolution are similar analyses of geographic trends through time. To perform such an analysis, we have reconstructed body-size trends along the West Coast of North America, both among Oligo-Miocene equids and canids and among modern analogues for each family. These data are used to test the assertion of Bergmann (1847), supported by Smith et al. (2010) and Saarinen et al. (2014), that body size in modern and Cenozoic mammals is driven primarily by temperature. Taking Bergmann's rule *sensu stricto* as a working hypothesis, two predictions can be made. First, body size should be positively correlated with latitude and negatively correlated with mean annual temperature for a majority of taxa during any given interval, as environments closer to the poles are always expected to be cooler than those near the equator. Second, as climatic gradients vary through time, the steepness of body-mass gradients should vary, with steeper slopes during cooler intervals with high lapse rates and shallower slopes during warm intervals with low lapse rates. The increasing strength of these gradients during cool intervals should also lead to their appearance in a larger number of taxa. Because modern temperature is lower today than at any point during the Oligo-Miocene (Zachos et al. 2001), body-size gradients should be especially prevalent in Recent taxa relative to their fossil analogues.

## Methods

The first hypothesis was tested by reconstructing body-size trends along a transect running along the West Coast of North America from Washington to Oaxaca (Fig. 1). Specimens from sites dating to the Arikareean–Hemphillian (Oligocene–Miocene, 30–5 Ma; Tedford et al. 2004) North American Land Mammal Ages (NALMAs) were included. This interval and region was chosen because of the remarkably rich fossil record available (Carrasco et al. 2005). The West Coast of the United States (encompassing, for the purposes of this study, the states of Washington, Oregon, Idaho, Nevada, and California) has an extensively sampled fossil record that has been collected for well over a century. While Mexican faunas have been the subject of less

study historically, recent research has uncovered several diverse faunas, particularly from the states of Chihuahua, Guanajuato, and Oaxaca. Besides being extremely well sampled, the Arikareean–Hemphillian interval encompasses several important climatic events (Zachos et al. 2001), making it an ideal natural laboratory in which to examine the influence of temperature on biotic variables. The late Oligocene is characterized by relatively cool temperatures, the onset of which was concurrent with the beginning of continental glaciation in Antarctica. The early Miocene was characterized by markedly warmer temperatures, which culminated in the mid-Miocene Climatic Optimum (MMCO; 16–14 Ma), a brief but significant warming spike representing the warmest period in Earth's history since the Eocene. Climate cooled steadily in the late Miocene, approaching the cold global temperatures seen today by 5 Ma.

The huge size of the Oligo-Miocene fossil record in North America makes an analysis of body-size evolution in all mammals impractical, so this study focuses on trends within two representative families: equids and canids. These two families are distinct from one another in body size, diet, and ecology, and both are well represented in the fossil record (Carrasco et al. 2005). Besides being common, equids and canids have historically been the focus of a great deal of research, and this extensive study has led to the construction of robust and well-resolved phylogenies for both (Mac Fadden 1992; Wang 1994; Wang et al. 1999; Tedford et al. 2009). Crucially for the aims of this project, robust approximations of body mass exist for each family. For canids, body mass is approximated using the length of the first lower molar (Van Valkenburgh 1990). Several dental proxies for mass exist for equids, including the lengths of all lower cheek teeth and the second upper molar (Janis 1990). The majority of the dental measurements used in this study were obtained from specimens in museum collections, though these were supplemented by some previously published measurements for faunas that were underrepresented in the collections visited. These collections were the American Museum of Natural History, Idaho Museum of Natural



FIGURE 1. Map of study area. Circles represent formation included in this study. Scale bar, 500 km.

History, John Day Fossil Beds National Monument, Natural History Museum of Los Angeles County, Raymond Alf Museum, San Bernardino County Museum, Sierra College Museum of Natural History, San Diego Natural History Museum, South Dakota School of Mines and Technology, Universidad Nacional Autónoma de México, University of California Museum of Paleontology, University of Oregon Condon Fossil Collection, and University of Washington Burke Museum.

Body-mass data for fossil taxa were analyzed within genera. Most studies of body-size evolution in extant animals have focused on trends at the species level (Ashton et al. 2000), but a higher taxonomic level was used in this study for two reasons. Bergmann's rule, as it was originally formulated, was meant to explain genus-level trends (Watt et al. 2010). Bergmann (1847) found the strongest body-size gradients within genera, with large species toward the poles and small species toward the equator. As such, any test of Bergmann's rule *sensu stricto* should be conducted at the generic level. In addition, an examination of species-level patterns in body size is necessarily short in duration; the average mammalian species duration is approximately two million years (Foote and Raup 1996; Alroy 2000; Vrba and DeGusta 2004) and would not permit a long-term analysis of size evolution. The Oligo-Miocene fossil record makes species-level analyses impractical. While the Arikarean–Hemphillian record is outstanding in its quality, it is not complete, and at the lower the taxonomic level, fewer specimens are available. Several genera are represented by sufficient numbers of individuals to make robust analyses possible, but few species are present in large enough numbers or over a large enough range to make them suitable subjects for body-mass research. Besides this, few groups of Oligo-Miocene mammals have been the subject of intensive, large-scale taxonomic studies (though canids are an exception to this rule; Wang 1994; Wang et al. 1999; Tedford et al. 2009), and as such the diversity of named species may not reflect a taxon's true species diversity. Only in the case of the equid genus *Merychippus* was body size examined at other taxonomic levels. *Merychippus* is a

paraphyletic genus that includes species of basal equines, hipparionins, and equines (MacFadden 1992). In the interest of including only monophyletic taxa, equin and hipparionin *Merychippus* were considered as two separate genera; only the latter was present along a large enough portion of the transect to be included here.

Due to the nature of the data sampled here, which in many cases are dominated by specimens from a small number of localities, a nonparametric test of the relationship between latitude and body size is more appropriate than least-squares regression. We performed a Spearman rank correlation test on body size and paleolatitude binned into NALMA subdivisions (Tedford et al. 2004). Biostratigraphic units were used instead of million-year intervals due to the imprecision of dating for many West Coast sites, the vast majority of which are dated using relative rather than absolute methods (Carrasco et al. 2005). For all NALMA subdivisions for which data were available, body mass was regressed against latitude, a proxy for temperature during intervals in which no paleoclimatic estimates exist. Faunas from the relatively static North American Plate were deposited at paleolatitudes roughly comparable to the modern latitude at which they have been uncovered. However, a number of sites in Southern California lie on the Pacific Plate and have moved northward significantly since the Oligocene. For these localities, paleolatitude was calculated using the rates of plate movement estimated by Atwater and Stock (1998). While there is a long tradition in the study of Bergmann's rule of using latitude as a proxy for temperature, it is reasonable to expect that temperature might vary between sites at similar latitudes but at differing distances from the coast. This is particularly a concern in California and Nevada, where sites from the Great Basin and Mojave Desert sit at the same latitude as sites from the San Francisco Bay Area and the Los Angeles Basin, respectively. Without more paleoclimatic work, it is impossible to quantitatively assess the magnitude of the difference in temperature between these regions, but it is likely that, just as today, coastal temperatures were mediated by the ocean and were likely lower than those



of inland sites. However, due to the richness of the fossil record in the region, it is possible to test whether or not such differences affected mammal body size. For genera found in both coastal and inland localities at comparable latitudes, mean body size and 95% confidence intervals for those means were calculated to test for significant differences in mass between the coast and the continental interior.

While the bulk of this analysis uses latitude as a proxy for mean annual temperature, extensive research on Oregon paleosols allows climate for most NALMA intervals to be reconstructed there (Retallack 2007), and early Barstovian floras in central Nevada and California's San Joaquin valley have been used to estimate temperature in those regions (Yang et al. 2011; Table 1). This allows body mass to be compared directly to temperature in early Barstovian genera present in Oregon, Nevada, or the San Joaquin valley. For both sets of correlations, the probability that a significant relationship existed between temperature or latitude and body size was calculated. Because it posits a positive relationship with latitude and a negative relationship with temperature, only significant relationships that meet this criterion were taken to support Bergmann's rule.

In order to test the second hypothesis, that body-size gradients should be more prevalent during cooler intervals such as those that characterize Recent ecosystems, the data set was expanded to include body masses of extant taxa from along the same transect (which was extended to include available data from British Columbian and Alaskan specimens). As with the fossil data, Recent data were compared with both latitude and mean annual temperature for the site at which they

were collected using a Spearman rank correlation test. This was preferable to using existing studies of Bergmann's rule as a basis, because it provided a higher degree of control, both analytically (both modern and fossil trends could be observed at the genus level, while most modern studies of body-size focus on species-level trends) and geographically (both modern and fossil trends could be observed along a West Coast transect rather than extrapolating from continent-wide patterns). Data were gathered from the online databases of the National Museum of Natural History, University of Alaska Museum of the North, University of California Museum of Vertebrate Zoology, University of New Mexico Museum of Southwest Biology, and University of Washington Burke Museum. The taxon chosen as a comparison for canids was the genus *Canis*. No truly wild equids are currently extant in North America, so the cervid *Odocoileus* was used as a proxy. Deer are more common in most collections than other potentially analogous taxa, such as *Antilocapra* and *Bison*. While deer are browsers and thus ecologically not comparable to living horses, they are good analogues for Oligo-Miocene equids, many of which likely retained a much higher percentage of browse in their diet than modern taxa (MacFadden et al. 1999; Janis et al. 2000).

## Results

The first series of tests was to determine whether or not latitudinal or climatic body-size gradients were present in Oligo-Miocene mammals. Of the 17 genera for which latitudinal trends could be analyzed, only four were found to have a significant ( $p < 0.05$ ) relationship between latitude and body size (Fig. 2 and 3,

TABLE 1. Sources of early Barstovian paleoclimatic data and estimated mean annual temperatures (MAT) in degrees Celsius.

Locality	Proxy	Region	MAT	Source
49 Camp	Paleobotanical	Central Nevada	9.4	Yang et al. 2011
Buffalo Canyon	Paleobotanical	Central Nevada	7.5	Yang et al. 2011
Eastgate	Paleobotanical	Central Nevada	9	Yang et al. 2011
Fingerrock	Paleobotanical	Central Nevada	8.6	Yang et al. 2011
Goldyke	Paleobotanical	Central Nevada	8.7	Yang et al. 2011
Mascall Ranch	Paleopedological	Columbia Plateau	14	Retallack 2007
Middlegate	Paleobotanical	Central Nevada	8.9	Yang et al. 2011
Temblor	Paleobotanical	San Joaquin Valley	17.3	Yang et al. 2011

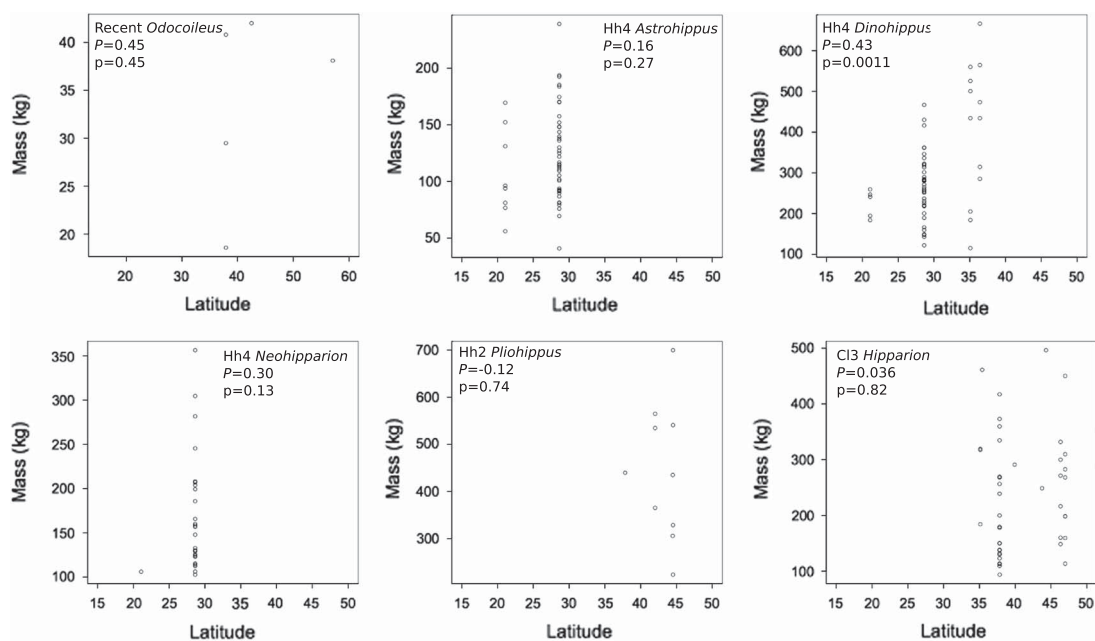


FIGURE 2. Latitudinal body-mass gradients in modern *Odocoileus* and fossil equids. Land mammal age subdivisions are denoted by abbreviations (Ba, Barstovian; Cl, Clarendonian; Hh, Hemphillian). Spearman's rho ( $P$ ) and  $p$ -value are indicated for each relationship.

Table 2). Of these, only two equids, early Barstovian hipparionin *Merychippus* ( $p=0.0005$ ) and late late Hemphillian *Dinohippus* ( $p=0.00009$ ), show the significant positive relationship with latitude predicted by Bergmann's rule. In total, five early Barstovian genera were present in sufficient numbers from localities for which climate could be reconstructed to directly analyze the relationship between temperature and body mass. In only one of these taxa (hipparionin *Merychippus*) was a significant ( $p=0.0007$ ) negative correlation present (Figs. 4 and 5, Table 3).

Ten genera (nine horses and one canid) have been found at both coastal and inland sites from the same interval and at the comparable latitudes, and these were used to test for differences in body size between marine-mediated and rain shadow climates (Table 4). In only one case (middle Clarendonian *Pliohippus* from the San Francisco Bay Area and the San Joaquin valley) is there a significant difference between body mass between the two regions.

The second series of analyses tested for a relationship between climate and body size by reconstructing body-mass trends in modern

taxa from colder climates than were represented at any point in the Oligo-Miocene and by directly comparing body mass to mean annual temperature. Of the two Recent genera analyzed, *Canis* shows a significant relationship between latitude and body mass ( $p=0.0006$ ) but *Odocoileus* does not (Figs. 2 and 3, Table 2). Likewise, neither genus showed a significant relationship between mean annual temperature and body mass (Figs. 4 and 5, Table 3). In total, two early Barstovian genera and one Recent genus showed the predicted positive relationship with latitude (Figures 2 and 3, Table 2), while only one early Barstovian genus (and no modern genera) showed the expected negative relationship with temperature.

## Discussion

### Hypothesis Tests

The findings of this study do not support Bergmann's rule in either modern or Oligo-Miocene ecosystems. The first prediction derived from Bergmann's (1847) model suggests that, in any given interval, body size

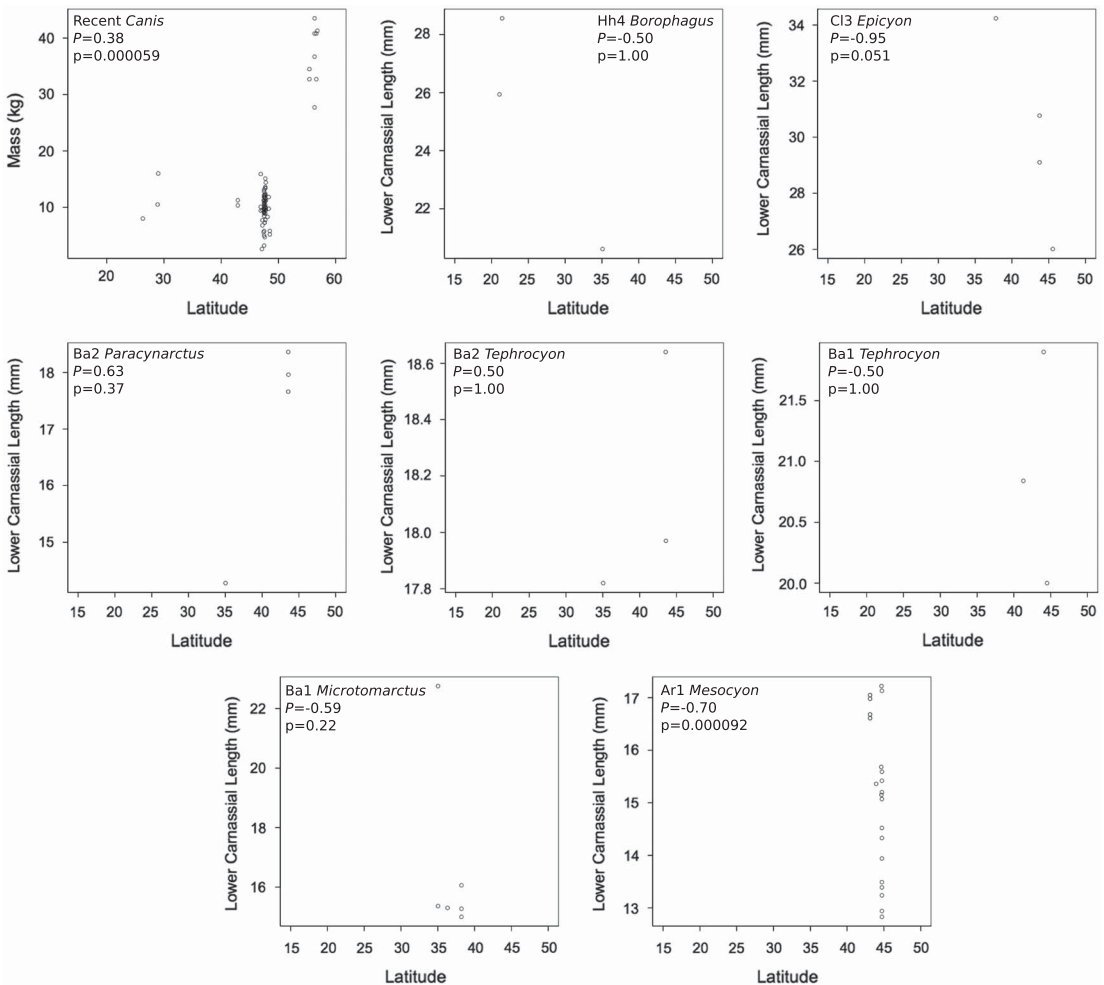


FIGURE 3. Latitudinal body-mass gradients in modern and fossil canids. Land mammal age subdivisions are denoted by abbreviations (Ar, Arikareean; Ba, Barstovian; Cl, Clarendonian; Hh, Hemphillian). Spearman's rho ( $P$ ) and  $p$ -value are indicated for each relationship.

should be positively correlated with latitude and negatively correlated with temperature. With the exception of only a small number of taxa, this is not the case in this study. In an earlier examination of Bergmann's rule, Mayr (1966) suggested that a biological rule should apply to 50% or more of taxa. The taxa examined here come nowhere close to this benchmark, with 14 out of 19 showing no evidence of directional latitudinal trends in body mass and with only three genera showing the expected positive relationship with latitude. Likewise, only one of the seven taxa compared directly to temperature shows a significant relationship between body mass and climate.

While the slope of such relationships might be expected to vary with time, their near absence within the genera analyzed in this study suggests they are the exception rather than the rule, falsifying the first prediction tested here.

The second prediction derived from Bergmann's rule—that the strength and frequency of latitudinal gradients should vary with climate—is likewise unsupported. Of the three genera with significant positive relationships between body size and latitude, two (late Hemphillian *Dinohippus* and Recent *Canis*) do occur during cooler intervals, seemingly supporting Bergmann's rule. However, other taxa from cool intervals show no such



TABLE 2. Comparison of latitude and body mass between fossil and modern genera. NALMA subdivision, sample size, Spearman's rho (P), and probability that a significant relationship exists between latitude and body size are shown for each sample. Shaded cells indicate samples for which significant relationships exist.

Genus	Age	<i>n</i>	P	<i>p</i>
<i>Odocoileus</i>	Modern	5	0.45	0.45
<i>Astrohippus</i>	Hh4	49	0.16	0.27
<i>Dinohippus</i>	Hh4	56	0.43	0.0011
<i>Neohipparion</i>	Hh4	27	0.30	0.13
<i>Pliohippus</i>	Hh2	10	-0.12	0.74
<i>Hipparion</i>	Cl3	43	0.036	0.82
<i>Hypohippus</i>	Ba1	19	-0.21	0.37
<i>Archaeohippus</i>	Ba1	13	0.20	0.50
<i>Desmatippus</i>	Ba1	12	-0.020	0.95
<i>Acritohippus</i>	Ba1	36	-0.46	0.0043
<i>Merychippus</i>	Ba1	102	0.34	0.00052
<i>Canis</i>	Modern	77	0.38	0.00059
<i>Borophagus</i>	Hh4	3	-0.50	1.0
<i>Epicyon</i>	Cl3	4	-0.95	0.051
<i>Paracynarctus</i>	Ba2	4	0.63	0.37
<i>Tephrocyon</i>	Ba2	3	0.50	1.0
<i>Tephrocyon</i>	Ba1	3	-0.50	1.0
<i>Microtomarctus</i>	Ba1	6	-0.59	0.22
<i>Mesocyon</i>	Ar1	25	-0.70	0.000092

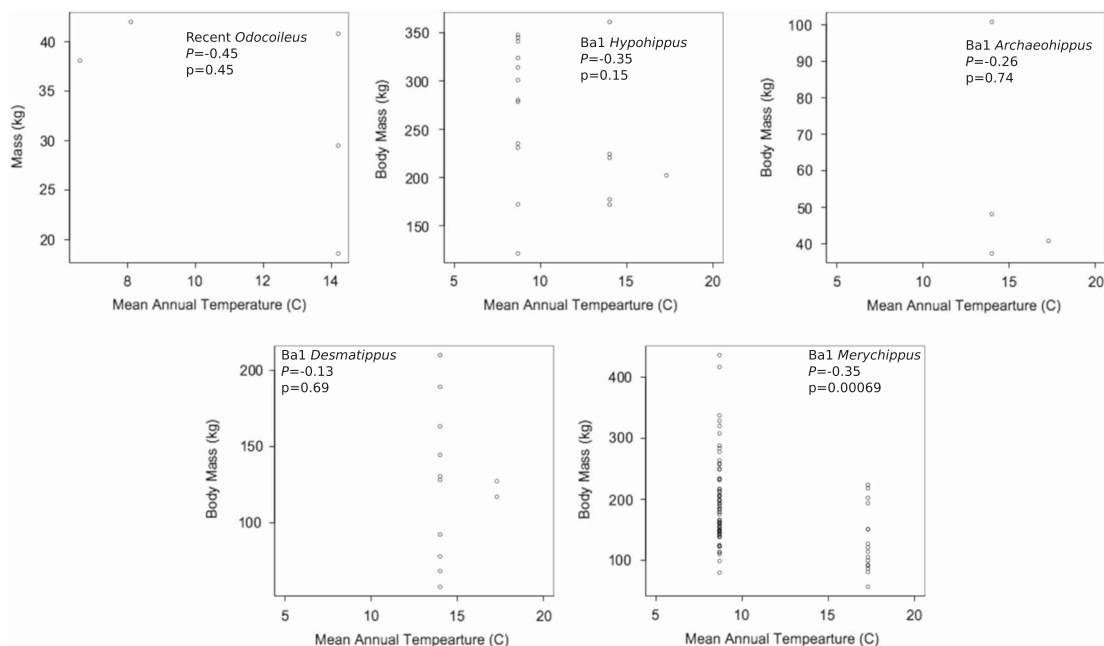


FIGURE 4. Climatic body-size gradients in Recent *Odocoileus* and early Barstovian (Ba1) equids. Spearman's rho (P) and *p*-value are indicated for each relationship.

relationship, and in one case (early early Arikareean *Mesocyon*) a significant negative relationship exists. A further refutation of Bergmann's rule is *Merychippus*, an extremely well-sampled taxon that shows a clear positive

relationship with latitude but occurs in the early Barstovian during the MMCO, the warmest interval of the Neogene (Zachos et al. 2001) and the NALMA subdivision that should have the lowest prevalence of

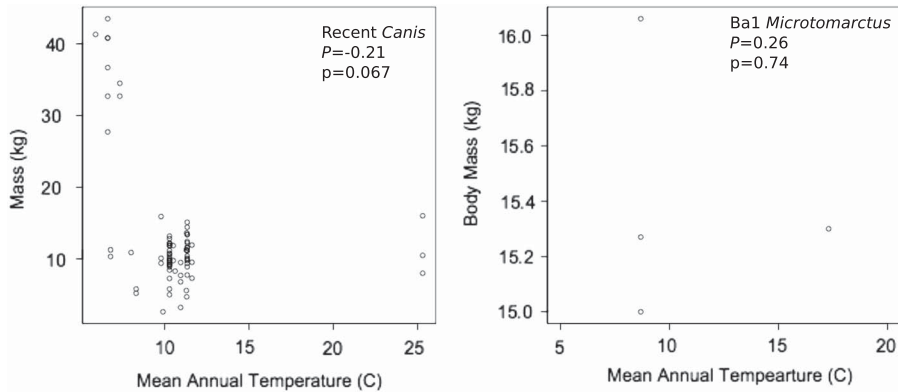


FIGURE 5. Climatic body-size gradients in modern and early Barstovian canids. Spearman's rho ( $P$ ) and  $p$ -value are indicated for each relationship.

TABLE 3. Comparison of temperature and body mass between early Barstovian and modern genera. NALMA subdivision, sample size, Spearman's rho ( $P$ ), and probability that a significant relationship exists between temperature and body size are shown for each sample. Shaded cells indicate samples for which significant relationships exist.

Genus	Age	$n$	$P$	$p$
<i>Odocoileus</i>	Recent	5	-0.45	0.45
<i>Hypohippus</i>	Ba1	14	-0.35	0.15
<i>Archaeohippus</i>	Ba1	4	-0.26	0.74
<i>Desmatippus</i>	Ba1	12	-0.13	0.69
<i>Merychippus</i>	Ba1	93	-0.35	0.00069
<i>Canis</i>	Recent	77	-0.21	0.067
<i>Microtomarctus</i>	Ba1	4	0.26	0.74

latitudinal gradients. It is also the only taxon to show a significant negative relationship with temperature; the absence of such relationships in all other genera examined further underscores the disjunction between climate change and the strength and frequency of body-size gradients.

#### Sampling and Taphonomic Bias

The results obtained in this study have thus far been considered to represent genuine ecological signals, but as is always the case in paleontology, taphonomic bias and analytical limitations must be considered. One potential confounding factor in this study is the scarcity of paleoclimatic data from the southern end of the transect (particularly California and Mexico). Floras from which paleoclimate can be reconstructed are scarce south of Nevada, and paleoclimatic reconstructions based on

paleopedological or isotopic proxies are non-existent, even for extremely productive and well-studied localities and faunas (the most striking example being the Barstow Fauna of Southern California, a fauna that has been so well studied that it has lent its name to a NALMA but has never been the subject of a rigorous, quantitative paleoclimatic analysis). This dearth of climatic data was the rationale for using latitude as a proxy for temperature during most intervals. Climatic data from the U.S. National Oceanic and Atmospheric Administration for sites yielding the extant material included in this analysis show that temperature and latitude are tightly correlated ( $R^2 = 0.67$ ,  $p < 0.0001$ ) in modern ecosystems, but the relationship is not perfect. In particular, it is worth considering local variations in climate and whether these variations and their effects are obscured by using latitude as the sole proxy for climate. However, the comparison of specimens from coastal and inland sites failed to show consistent differences in size. This suggests that small-scale climatic differences are not being obscured by large-scale latitudinal patterns and that latitude is an appropriate proxy for temperature when no direct measurement is available.

Similarly, it is possible that the evolutionary response of body size to climatic change occurs on a short timescale that is obscured by the relatively large temporal bins used here. While several of the biostratigraphic units into which specimens have been sorted represent long periods of time (5Ma in the case of the late

TABLE 4. Comparison of body-mass data from coastal and inland sites. Mean mass (in kg) and 95% confidence intervals are shown for each genus (samples in which  $n = 1$  do not include confidence intervals). Bay Area, San Joaquin valley, and transverse ranges biogeographic regions are considered coastal; western Nevada and Mojave Desert biogeographic regions are considered inland.

Taxon	Bay Area	San Joaquin valley	Transverse ranges	Western Nevada	Mojave Desert
Ba1 <i>Microtomarctus</i>		15.30		15.44 ± 0.62	19.06 ± 7.25
Ba1 <i>Hypohippus</i>		202.22		274.26 ± 40.70	207.42
Ba1 <i>Archaeohippus</i>		40.78	46.26 ± 20.17		46.90
Ba1 <i>Scaphohippus</i>			148.70 ± 24.71		174.85 ± 29.61
Ba1 <i>Acritohippus</i>			169.73 ± 50.60		168.04 ± 58.98
Cl2 <i>Hipparion</i>	226.08 ± 107.57				319.81
Cl2 <i>Pliohippus</i>	409.23 ± 190.89		196.82 ± 36.53	234.26	336.29 ± 88.21
Cl3 <i>Hipparion</i>	202.86 ± 40.65	273.69 ± 87.78		290.95	461.21
Cl3 <i>Neohipparion</i>	126.46 ± 56.07			476.10 ± 355.57	
Cl3 <i>Pliohippus</i>	395.37 ± 136.50	492.17 ± 61.75			404.70

early Arikareean), the NALMA subdivisions that contained sufficient material to reconstruct latitudinal gradients were all relatively short (Ar1, 2 Ma; Ba1, 1.2 Ma; Ba2, 2.3 Ma; Cl3, 1 Ma; Hh2, 0.7 Ma; Hh4, 1 Ma; Tedford et al. 2004). These units are shorter in time than the subepochs used as bins in the studies by Smith et al. (2010) and Saarinen et al. (2014), both of which found a correlation between body size and temperature, and are comparable in duration to the million year bins widely used in paleobiological analyses (e.g., Hunt and Roy 2006; Hopkins, 2007; Liow et al. 2008). As discussed above, the comparison between coastal and inland sites in California and Nevada suggests that the effects of small-scale environmental differences between localities are minimal compared with those of large-scale climatic trends. While having precise dates and paleoclimatic reconstructions for a larger number of localities would certainly allow for a more robust analysis, the length of the temporal bins used in this analysis should be sufficient for observing macroecological trends through time.

A constant concern in paleontology is the quality of the fossil record. Not only are whole ecosystems rarely preserved, but an already incomplete record is often further biased by differential preservation, collection (Behrensmeyer et al. 2000), and description (Davis and Pyenson 2007), creating taphonomic noise that can obscure true biological signals if insufficiently large samples are considered. This is especially a concern for taxa such as canids and other carnivores that

are well sampled and extensively studied but are generally rare within ecosystems and for taxa such as rodents that are common within ecosystems but are either infrequently preserved or undercollected. Sample size is demonstrably driving at least one signal in this study: late Clarendonian *Epicyon* shows a strong (though not significant) negative correlation with latitude, but this is almost certainly the result of an incomplete sample. Wang et al. (1999) note that two species of *Epicyon* are present at late Clarendonian sites throughout North America: the giant *E. haydeni* and the smaller *E. saevus*. Both are present in the Juntura Formation of Oregon (Orcutt and Hopkins, 2011), but only *E. haydeni* is represented by dental material from the coeval Contra Costa Group of the San Francisco Bay Area. Were the sample size from this site larger, it would almost certainly include *E. saevus*, likely obscuring the seemingly strong latitudinal gradient. The small sample size of many other canid taxa makes it possible, or even likely, that many of the patterns observed here do not reflect biological trends. However, sample size cannot be invoked to explain every body-size gradient—or lack thereof—observed in Oligo-Miocene canids. *Mesocyon* is both extremely common and extremely well sampled in Arikareean faunas (Wang 1994) and is present in large numbers in the latitudinally distant John Day ( $n = 16$ ) and Otay formations ( $n = 9$ ). While the Arikareean is one of the coldest intervals of the Oligo-Miocene, there is no evidence of a significant difference in *Mesocyon*

size between Southern California and Oregon. Likewise, sample size cannot explain most of the patterns observed in equids, which are both common and well sampled. Even the most poorly sampled equid in the database (late early Hemphillian *Pliohippus*) has a sample size of 10, and *Merychippus* is represented by more than 100 specimens. Significant results such as the positive correlations between body mass and latitude in hipparionin *Merychippus* ( $n = 102$ ) and *Dinohippus* ( $n = 56$ ) are likely not taphonomic artifacts but can be interpreted as ecological trends. The same is true, though, for the patterns observed in other well-sampled taxa such as *Acritohippus* ( $n = 36$ ), *Hipparion* ( $n = 43$ ), and *Astrohippus* ( $n = 49$ ), in which no latitudinal gradient is visible. Taphonomic bias is also unlikely to affect these patterns too strongly; in many cases, taxa sampled in similar numbers and from the same sites (e.g., *Dinohippus* and *Astrohippus*) show different patterns.

Perhaps the most striking result of this study is the absence of latitudinal gradients among the modern genera examined. A negative correlation with temperature and a positive correlation with latitude, both in keeping with Bergmann's rule, are visible in *Odocoileus*, but the sample is insufficiently large to establish whether or not the trend is significant (while deer are common, they also often lack body-mass data in collections, as individuals tend to be large and difficult to measure accurately). Only within *Canis* are significant trends apparent. However, these patterns are likely a sampling artifact: specimens from the contiguous United States and southern Canada are almost exclusively coyotes (*C. latrans*), while specimens from northern Canada and southeast Alaska are almost all wolves (*C. lupus*). While neither of these species shows a significant relationship with temperature or latitude, wolves are larger than coyotes, and their presence at the north end of the transect accounts for the negative correlation with temperature and positive correlation with latitude. At first glance, this seems to support Bergmann's rule *sensu stricto*, as it is a case of larger species within a genus occupying colder climates. However, it is unlikely that this is a truly natural signal, as wolves have been

extirpated over large areas of the contiguous United States, and many of these extirpations took place before systematic specimen collecting had taken hold or at the hands of individuals with no scientific interest in preserving data about the animals they had killed. Were reliable data to exist for wolf populations along the southern end of the coastal transect, they would very likely obscure the trend currently visible in the data. In fact, previous analyses of geographic trends within extant canid species, all of which include at least one species of *Canis*, show that these species do not show monotonic relationships with latitude (McNab 1970; Geist 1987; Thurber and Peterson 1991) or temperature (Meachen and Samuels 2012). If, as these studies suggest, modern latitudinal transects in *Canis* are shaped by extirpation rather than by climate, both Recent genera included in this study would fail to conform to the predictions made by Bergmann's rule, and one of the few lines of evidence obtained in this analysis that seemingly supports Bergmann's rule would disappear.

#### Drivers of Body-Mass Gradients

Many neontological studies of Bergmann's rule have shown evidence of latitudinal body-mass gradients (Ashton et al. 2000), which our results do not support. This may be due in part to the level at which the studies were conducted: almost all recent research on body-size evolution has focused on patterns within species. It may be that temperature and body mass interact at a very fine scale and that geographic trends become obscured at higher taxonomic levels. This would run counter to Bergmann's (1847) observation of body-mass gradients within genera and would contradict his suggestion that the forces driving trends within genera should drive similar trends at all taxonomic levels. Another possibility is that the source of the data for these studies is influencing the patterns observed in them. Bergmann's research, and several landmark studies in the field since (e.g., Erlinge 1987; Korpimäki and Norrdahl 1989), focused on mammals in Europe. As is the case with wolves in North America, many large animals have long since been extirpated from the southern, temperate parts of Europe and, if they survive

at all, are present only in the more inaccessible regions of the continent. These regions tend to be cold and are, for the most part, located far to the north, and this alone could explain the appearance of latitudinal gradients and of a negative correlation between temperature and body size. Studies of Bergmann's rule have, of course, been conducted in other areas as well, but the example of the wolves suggests that even on relatively "wild" continents such as North America, extirpation and extinction can strongly influence body-mass patterns.

If mean annual temperature has not been the primary driver of mammalian body size through time, what factor or factors have been? Precipitation and seasonality are the two climatic variables besides temperature that have been proposed to influence body-mass evolution (James 1970; Millar and Hickling 1990). Unlike temperature, precipitation and seasonality should not be expected to vary predictably with latitude. Rather, the prevalence of arid, seasonal environments in continental interiors suggests that tracking body-size trends along longitudinal gradients would be a more appropriate test of the effect of these variables. The comparison of coastal and inland sites conducted as part of this analysis is a small-scale longitudinal analysis and suggests that significant differences in body size between marine-mediated and rain shadow sites are unlikely to be found. However, a larger-scale analysis of longitudinal trends from the Pacific Coast, across the Western Cordillera, and onto the Great Plains might reveal trends that could prove useful in identifying the role precipitation and seasonality have played in driving body-size evolution. As with temperature, paleoclimatic reconstructions for a wider range of localities would allow for direct comparisons between climate and body size through time.

A majority of neontological analyses indicate a biotic driver of body-size trends. The biotic interactions most frequently hypothesized to have a causal relationship with body mass are competition (Damuth 1993, McNab 1970), predation (Korpimäki and Norrdahl 1989), and food supply (Rosenzweig 1968; McNab 1970; Geist 1987; Erlinge 1987; Thurber and

Peterson 1991). While biotic interactions can be difficult to quantify in paleoecosystems, the fossil record does provide opportunities for testing the influence of biotic interactions. Analyses of morphological change through time in Pleistocene and Holocene coyotes (Meachen and Samuels 2012; Meachen et al. 2014a) represent an example of such a test. These analyses suggest that while *Canis latrans* did not go extinct along with several other Pleistocene megafauna, the ecological reorganization brought about by these extinctions had a major influence on coyote size and morphology. Similar analyses linking size with morphological traits associated with biotic variables (e.g., using relative blade length as a proxy for carnivory; Van Valkenburgh 1988) along chronoclines could be useful in identifying the influence of these variables on body-size evolution.

Lovegrove and Mowoe (2013) present another chronocline analysis of body size and suggest that, rather than being driven by one ecological variable, body-size evolution is the product of complex interactions between variables that affect some taxa differently than others. Orcutt and Hopkins (2013) reached a similar conclusion, showing that three families of mammals from the same age and region showed very different body-size trends through the Oligo-Miocene. The data presented here suggest that biotic patterns can vary considerably even between closely related genera; *Merychippus* and *Acritohippus*, for instance, are both *Merychippus*-grade equids, but while the former shows a strong latitudinal gradient, the latter does not. The same is true of *Dinohippus* and its close (but smaller) relative *Astrohippus*. Not only do body-size patterns vary between coeval taxa, but they also often vary between closely related taxa through time. The late Miocene hipparionins *Hipparion* and *Neohipparion*, for example, are both likely descended from the hipparionin merychippines of the mid-Miocene (MacFadden 1992), but whereas *Merychippus* exhibits a strong latitudinal gradient, its probable descendants do not. Bergmann's "rule," then, not only does not apply to most taxa examined here, but it does not apply to related taxa at different points in time.



The lack of support for Bergmann's rule in this analysis is at odds with the findings not only of Bergmann (1847) but also with the more recent research on body-size trends through time by Smith et al. (2010) and Saarinen et al. (2014). This discrepancy can likely be explained in part by methodological differences. Smith et al. (2010) and Saarinen et al. (2014) examined maximum body-size trends through time on a global scale, in both cases finding a correlation between temperature and body mass. As discussed above, the large-scale relationship between climate and environmental change over the course of the Cenozoic means that any analysis carried out at the global scale could yield results that seemingly support Bergmann's rule *sensu stricto*, when in fact a more complex model, such as the one proposed by Lovegrove and Mowoe (2013), might better explain any patterns observed. It is important to supplement such analyses with studies of trends at a smaller scale in order to more directly observe the degree to which climate has driven body-size evolution. Our analysis of body-size trends along the West Coast of North America within genera from three families suggests that temperature alone likely does not drive body-size evolution. This may not be true for all taxa at all times and in all places. Lovegrove and Mowoe (2013), for example, find some support for Bergmann's rule in cold-adapted taxa such as castorids and marmots, and it is possible that temperature and other climatic variables play a more important role in shaping body-size patterns in colder climates, such as those characterizing the Pliocene and Pleistocene, or in different regions. While this study does not support a simple relationship between climate and body size, determining whether there are conditions under which such a relationship does exist, or whether body size in certain taxa is more tightly correlated with temperature, is certain to remain a major focus of ecological research. While the research detailed here is by no means the final word on the subject, it demonstrates, along with the research of Gingerich (2003), Smith et al. (2010), Lovegrove and Mowoe (2013), and Saarinen et al. (2014), that paleontology provides a unique and invaluable perspective on a very old debate and that paleoecology should play a

major role in future tests of Bergmann's rule and its corollaries.

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