A STATISTICAL EXAMINATION OF THE CHANGE IN BODY SIZE OF MAMMALIAN COMMUNITIES ACROSS THE EOCENE-OLIGOCENE BOUNDARY

By

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ABSTRACT

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The body mass change of mammals across the Eocene-Oligocene Boundary (EOB) and the potential relationship with global climate change was studied. Global climate went through a period of dramatic cooling and drying during the Eocene-Oligocene Transition. The effects on the environments of North America were dramatic, causing a shift from abundant, dense rainforest canopy in the Eocene to open savannah environment in the Oligocene. Mammal faunas from the White River Group of the continental interior of North America were investigated. Statistical surveys of large mammal faunas (> 1 kg) from the Douglas, Wyoming, and surrounding area and small mammal fauna (< 1 kg) from northwestern Nebraska were performed to assess three hypotheses regarding body mass change: (1) climate change has no effect on body mass, (2) climate cooling increases mammalian body mass, and (3) climate cooling decreases mammalian body mass. Mass of large mammals was estimated from the length of skulls and the width of occipital condyles. Mass of small mammals was estimated based on the size of the first lower molar. The Eocene fauna studied here contains some of the largest and smallest mammals of all time; body mass estimates in this study ranged from as small as 4.5 g in the insectivore genus *Oligoryctes* up to titanotheres massing 1,589 kg. Large mammals were found to decrease in body mass across the EOB, whereas body mass of small mammals increased. This phenomenon of extreme body masses approaching the middle of the range of body masses is likened to the Island Effect, where large mammals decrease in body size and small mammals increase in body size to accommodate a decrease in available habitat and resources. The change in body mass was attributed to environmental degradation brought on by climate change. Lower

body mass evolved in large, herbivorous mammals as they adapted to diminished food resources. Small mammals likewise responded to climate change by adapting to the prevalence of open environments, and granivorous diets evolved as tropical vegetation waned.

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CHAPTER I. INTRODUCTION

The purpose of this thesis is to study the effect of climate change across the Eocene-Oligocene Boundary (EOB) on different mammalian faunas. Study of modern mammals has resulted in the many rules that explain how environment changes mammalian body mass, but Bergmann's rule (Bergmann, 1847) is the most well-known explanation for the effect of climate on body mass. The rule, simply put, states that mammals at higher latitudes (colder climates) have greater body mass than their counterparts in lower latitudes (warmer climates). The relationship between climate and mammalian body mass is hotly contested for both the fossil record (e.g., Prothero and Heaton, 1996; Clyde and Gingerich, 1998; Gingerich, 2003) and modern faunas (e.g., Blackburn et al., 1999; Beatty, 2007). The goal of this study was to investigate the body masses of a range of different sizes, ranging from as small as a shrew to larger than a rhinoceros, to determine what effect, if any, climate change had on them and, furthermore, if the change was homogeneous (all mammals respond in the same proportional manner) or heterogeneous (did climate change affect different mammals in different ways). We tested three hypotheses during the course of the study: (1) mammalian body mass decreases as climate cools, (2) mammalian body mass increases as climate cools, and (3) climate cooling has no effect on mammalian body mass. This thesis is intended to reconcile the different hypothesis of the controls of mammalian body size.

Considerable attention has been paid to estimation of body mass of extinct mammals and the ways to estimate it (e.g., Damuth and MacFadden, 1990). The use of allometric relationships in the changes of skeletal elements—using a model that compares linear changes in single dimensions of bones to the exponential increase of body mass—has proven the most reliable way of studying body mass (Gingerich and Smith, 1985). Teeth have been used successfully to study the body mass distributions of fauna across the Paleocene-Eocene Boundary (Clyde and Gingerich, 1998; Gingerich, 2003). Study of the Eocene-Oligocene Transition should prove especially interesting in this regard, as the smallest known mammal occurred in the Eocene of North America (Bloch et al., 1998) and the largest known terrestrial mammal occurred in the Oligocene of Asia (Fortelius and Kappelman, 1993).

This thesis consists of the statistical analysis of body mass data generated from skeletal measurements of fossil mammals. Two datasets were constructed as part of this thesis: a set of cranial measurements was compiled from fossil mammals from the Douglas, Wyoming, area and a set of measurements of the lower first molar (m1) of mammals from the Toadstool Park and Raben Ranch localities of northwest Nebraska. Chapter II is concerned with the mammals from the Douglas, Wyoming, data set that were estimated to have mass > 1 kg. Chapter III deals with the entire set of measurements from the second data set, which is composed entirely of small rodents and other insectivorous mammals < 1 kg in mass. Chapter IV summarizes the overall hypothesis that links the results of the studies in chapters II and III, most significantly the invoking of the Island Effect Hypothesis for explanation of seemingly inconsistent conclusions of the two studies.

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CHAPTER II. REDUCTION IN BODY MASS OF MAMMALIAN COMMUNITIES ACROSS THE EOCENE-OLIGOCENE BOUNDARY NEAR DOUGLAS, WYOMING: A STATISTICAL ANALYSIS

Currently in review as:

Reduction in body mass of mammalian communities across the Eocene-Oligocene Boundary near Douglas, Wyoming: A statistical analysis. PALAIOS.

ABSTRACT

The link between global climatic cooling and change in body mass of mammals across the Eocene-Oligocene Boundary from White River Formation of Douglas, Wyoming (WY), and the surrounding areas was investigated. The Eocene-Oligocene Transition was a time of dramatic global cooling and is thought to be the cause for extinction of some mammalian groups. Three hypotheses were tested during this study: mammalian body mass decreased due to global cooling; mammalian body mass increased due to global cooling; and global cooling had no effect on mammalian body mass. Previous studies have demonstrated that mammalian body mass decreased during global warming events, and mean body mass in mammals is hypothesized to increase during global cooling events as canopy cover decreased and open environments became available. The lengths and widths of more than 200 skulls from mammal remains collected from Douglas, WY, and the surrounding areas were used to generate body mass estimates of the mammalian fauna from the late Eocene to middle Oligocene. The Eocene fauna was statistically compared with the Oligocene fauna using a two-sample Kolmogorov-Smirnov test to determine differences in the body mass of the mammals from the two epochs. Different groups of

mammals were tested to determine if some groups are affected by climate change differently. We demonstrate with high statistical confidence that the body mass of the mammalian community was overall smaller during the Oligocene compared to the Eocene, but body masses of a few groups (oreodonts and carnivores) did not vary significantly across the boundary.

INTRODUCTION

The purpose of this paper is to test the link between global climate change and mammalian body mass across the Eocene-Oligocene Boundary (EOB) from the White River Formation (WRF) of Douglas, Wyoming (WY). Three hypotheses concerning the response of mammalian body mass to global cooling were tested: (1) body mass reduced during global cooling, (2) body mass increased during global cooling, or (3) body mass was unaffected by global cooling. Measurements gathered from mammal skulls from the WRF were used to produce body mass estimates, which were then statistically evaluated to test these hypotheses. Research conducted on the mammalian response to transient warming during the Paleocene-Eocene Thermal Maximum (PETM), demonstrated that mammalian body mass decreased from 50–60% as a result of global warming of 4–8°C (Clyde and Gingerich, 1998; Gingerich, 2003). Mammalian body mass is hypothesized to increase in response to cooling climate, but the relationship between global cooling and mammalian body mass evolution is less well understood. This research will supplement the understanding of the (1) response of ancient mammals to climate change and contribute to the discussion of the overall controls of mammalian physiology, and (2) possible responses of mammals to future climate change.

The Eocene–Oligocene Transition (EOT) was one of the most dramatic climate change events of the Cenozoic (Fig. 1). Marine records demonstrate that deep-sea temperature dropped

~4°C (from ~5°C to ~1°C) at the beginning of the Oligocene (Zachos et al., 2001). Change in continental environments was even more dramatic, as mean annual temperature dropped ~8°C (from ~21°C to ~13°C) (Zanazzi et al., 2007). Records generated from paleosols corroborate this evidence, showing that continental environments went through a rapid cooling and drying period across the EOT (Retallack, 1983, 1992, 2007). Dense forest environments dominated during the Eocene, whereas open environments with limited forest canopy characterized the Oligocene (Retallack, 1983). Studies of forest vegetation show an increase of vegetation relying on wind pollination rather than insect pollination during the Oligocene (Wolfe, 1992)—evidence that the environments began to open significantly. The Douglas, WY, area transitioned from a dense woodland during the late Eocene to an open woodland during the earliest Oligocene, then to open bushland during the mid to late Oligocene, based on the change in paleosol character from fluvial to eolian environments and the change from a wet-to a dryland snail fauna (Evanoff et al., 1992). Carbon dioxide concentration in the atmosphere also decreased markedly across the EOT (Pagani et al., 2005). Antarctic ice sheets formed for the first time in the Cenozoic during the Oligocene (Zachos et al., 2001), likely as a result of the development of vigorous circumpolar ocean currents that began as the Drake Passage opened up (Lawver et al., 1992; Lawver and Gahagan, 2003). The Oligocene is noted as the beginning of more modern global ecological conditions (Prothero, 1994a). If there is a strong relationship between climate and mammalian body mass, it therefore should be detectable across the EOT.

Mammalian body mass is controlled by numerous factors. Mass is controlled primarily by intake of food and metabolism (Kleiber, 1932; Peters, 1986; Campbell et al., 1999). Viewed at larger scales, mass is dependent on environment and relates to organism behavior (McNab, 1990). Climate, therefore, affects the mass of mammals. In such ectothermic groups of terrestrial animals as insects, amphibians, and reptiles, temperature has a direct effect on body mass. Ectothermic animals, reptiles in particular, benefit from larger sizes as a way of controlling body temperature; modeling indicates that large reptiles maintain constant high body temperature despite daily temperature fluctuations (Spotila et al., 1973; Stevenson, 1985; Seebacher, 1999). There is some discussion as to whether temperature-imposed constraints on the upper size limit of reptiles exist (O'Connor and Dodson, 1999). Endothermic animals, however, maintain constant body temperature by using their own metabolic heat (Campbell et al., 1999). Mammals, therefore, tend not to increase in mass as temperature increases. The smallest mammal on record in fact existed during the Eocene (Bloch et al., 1998), the warmest time during the Cenozoic (Zachos et al., 2001).

Changes in mammalian body mass are predicted by three rules: Cope's rule, Bergmann's rule, and Allen's rule. Cope's rule states that lineages increase in body mass through time (Stanley, 1973; Brown and Maurer, 1986; Alroy, 1998; Hone and Benton, 2005). This rule has been invalidated several times (e.g. MacFadden, 1986), but may hold at a large scale for early mammals that arose from extinction-resistant insectivorous lineages (Stanley, 1973). The two other rules put forward a relationship between climate and body mass; Bergmann's rule states that mammals in colder climates have overall larger mass (Bergmann, 1847; Rensch, 1938; Ashton et al., 2000), whereas Allen's rule states that mammals in colder climates have shorter limbs than their equivalents in warmer climates (Allen, 1877; Harrison, 1960; Serrat et al., 2008). These rules are both highly disputed and are not likely valid in a broad scope (Blackburn et al., 1999; Beatty, 2007), but they represent two explanations for the change in body mass observed in the fossil record of mammals. The first explanation is that larger body mass is more advantageous as climate cools in order to maintain constant body temperature. The second suggests that mammals grow larger in response to decreasing forest cover as a predation defense or as a physiological response to the change in their food supply or quality. This paper will test the explanatory power of these hypotheses on the faunal change in the mammalian communities of the WRF across the EOT.

METHODS AND MATERIALS

Measurements were taken from mammal skulls collected from the WRF of Douglas, WY, and the surrounding area, including material from northern Colorado and western Nebraska. Populations in which these mammals lived are assumed not to have been geographically isolated from one another, and likely existed as a large community. Skulls were measured from the vertebrate fossil collections housed at the University of Kansas Natural History Museum, the University of Wyoming, the University of Colorado at Boulder, the Tate Geological Museum, and the collection of Dr. Kent Sundell (Table 1;Supplemental data). Rodents and other insectivorous mammals were excluded from this study and will be treated separately in an upcoming study. Only adult skulls were used in this analysis in order to prevent error caused by ontogenetic variation. Fossil remains from the Douglas area were only collected from carbonate nodules in order to keep with the isotaphonomic method advocated by Clyde and Gingerich (1998). Remains from other areas (western Nebraska and northern Colorado) were used to fill in where taxa were underrepresented.

The following measurements were collected (Fig. 2). Skull length is the maximum anterior to posterior length of the skull, measured from the eruption of the first upper incisor (I1) to the furthest point at the posterior end of the skull. The proxy for skull width is the maximum distance between the outside edges of the occipital condyles. This measurement is used because it consistently scales with body mass in many types of mammals and is less prone to taphonomic bias than skull length (Martin, 1980). Both of these measurements were not available from every skull because of taphonomic loss (i.e., incomplete skulls). Stratigraphic information was collected for each specimen, but specific stratigraphic levels were not available for all specimens. Mammals were determined, therefore, to belong either to the late Eocene or early to mid-Oligocene, and the statistical analysis compares those two assemblages. Measurements for skull width were converted into body mass estimates using the Group II equation from Martin (1980), and the skull length measurements were converted into body mass estimates using the greatest skull length regression calculated by Janis (1990).

Cumulative relative frequency curves were generated for the Eocene and Oligocene data sets. The two data sets were statistically compared using a two-sample Kolmogorov-Smirnov (K-S) test as described in Sokal and Rohlf (1995). The Eocene sample size (N_E), Oligocene sample sizes (N_O), greatest unsigned difference (D), and p-values are reported. The test was performed six times, for each of the following six subsets of the data: all mammals, all mammals excluding titanotheres, all ungulates, all ungulates excluding titanotheres, oreodonts, and carnivores.

RESULTS

All mammals

K-S testing of all specimens demonstrates an overall decrease in body mass (N_E=31, N_O=179, D=0.4997, p=3.715 x 10^{-6}). The hypothesis that the Eocene and Oligocene curves come from the same distribution is rejected at the 0.001 level (i.e., not the same curve), giving great statistical confidence (99.9%) that the body mass of the mammals in the Oligocene is lower than those of the Eocene (Fig. 3). This test falsifies the hypotheses that global cooling either increased body mass or caused no change in body mass in mammals. Minimum estimated body mass of the Eocene fauna is 2.61 kg (5.74 lbs), and maximum estimated body mass is 1,589.11 kg (3,503.39 lbs). Minimum estimated body mass of the Oligocene fauna is 0.05 kg (0.12 lbs), and maximum estimated body mass is 527.10 kg (1,162.06 lbs).

All mammals excluding titanotheres

K-S testing of the sample excluding titanotheres demonstrates a decrease in body mass (N_E=28, N_O=179, D=0.4928, p=1.352 x10^{-5}), the same conclusion as the previous test. The hypothesis that the Eocene and Oligocene curves come from the same distribution is rejected at the 0.001 level, reinforcing the results of the previous test. This test falsifies the hypotheses that global cooling either increased body mass or caused no change in mammalian body mass in mammals. This test also demonstrates with high statistical confidence (99.9%) that mammals became smaller in the Oligocene (Fig. 4). Minimum estimated body mass of the Eocene fauna is 2.61 kg (5.74 lbs), and maximum estimated body mass is 1,321.13 kg (2,912.59 lbs). Minimum estimated body mass of the Oligocene fauna is 0.05 kg (0.12 lbs), and maximum estimated body mass is 527.10 kg (1,162.06 lbs).

All ungulates

K-S testing of the ungulates alone demonstrates a decrease in body mass (N_E=23, N_O=91, D=0.3569, p=1.861 x 10^{-2}). The hypothesis that the two curves come from the same distribution is rejected at the 0.05 level. Ungulates clearly became smaller in the Oligocene (Fig. 5). This test also falsifies the hypotheses that global cooling either increased body mass or caused no change in mammalian body mass. Minimum estimated body mass of the Eocene fauna is 6.88 kg (15.16 lbs), and maximum estimated body mass is 1,589.11 kg (3,503.39 lbs). Minimum estimated body mass of the Oligocene fauna is 3.12 kg (6.88 lbs), and maximum estimated body mass is 527.10 kg (1162.06 lbs).

All ungulates excluding titanotheres

K-S testing of the ungulates excluding the titanotheres demonstrates there was no change in body mass (N_E=20, N_O=91, D=0.2852, p=0.1173). The hypothesis that the two curves come from the same distribution cannot be rejected. This test falsifies the two hypotheses that global cooling caused an increase or decrease in body mass change in mammals (Fig. 6). Minimum estimated body mass of the Eocene fauna is 6.88 kg (15.16 lbs), and maximum estimated body mass is 1,321.13 kg (2,912.59 lbs). Minimum estimated body mass of the Oligocene fauna is 3.12 kg (6.88 lbs), and maximum estimated body mass is 527.10 kg (1,162.06 lbs).

Oreodonts

This sample included all *Agriochoerus* estimates with the rest of the estimates made from oreodonts. The test indicated that body mass did not change (N_E=15, N_O=66, D=0.2091, p=0.6869). The hypothesis that the two curves come from the same distribution cannot be rejected. This test falsifies the two hypotheses that global cooling caused an increase or decrease in body mass change in mammals (Fig. 7). Minimum estimated body mass of the Eocene fauna is 6.88 kg (15.16 lbs), and maximum estimated body mass is 24.98 kg (55.07 lbs). Minimum estimated body mass of the Oligocene fauna is 3.12 kg (6.88 lbs), and maximum estimated body mass is 44.25 kg (97.55 lbs).

Carnivores

This sample included all the Carnivora and the entelodonts that were sampled. K-S testing of the sampled carnivores indicated no difference between the two samples (N_E=10, N_O=20, D=0.3, p=0.6024). The hypothesis that the curves come from the same distribution cannot be rejected. The lack of difference between the two curves falsifies the hypotheses that mammals became smaller or large in response to global cooling (Fig. 8). Minimum estimated body mass of the Eocene fauna is 13.73 kg (30.30 lbs), and maximum estimated body mass is 1,321.13 kg (2,912.59 lbs). Minimum estimated body mass of the Oligocene fauna is 0.53 kg (1.17 lbs), and maximum estimated body mass is 527.10 kg (1,162.06 lbs).

Potential sources of error

The error attributed to the use of these two different body mass estimation methods—occipital condyle widths using the Martin (1980) equation and skull lengths using the Janis (1990) equation—is not responsible for any significant error in the result. Estimates using these methods are found in both the Eocene and Oligocene curves, so the error would bias both curves in the same fashion (J. Kelly personal communication, 2010).

The sample size of the Oligocene distribution (n=191) is much greater than the sample size of the Eocene distribution (n=33). There is potential error due to the possibility that data is missing from the Eocene curve. This is inconsequential, however, due to the high confidence (p<0.001) with which we accept the results of the K-S test. This potential error is further acceptable, because there are more fossils recovered from the Oligocene than the Eocene of the WRF of Douglas, WY. Mammal fossils from the Eocene are more difficult to prepare, because the matrix is not easily removed from the bones. These Eocene fossils, therefore, not only occur less frequently, but they also are less likely to be prepared intact and useful for measurement. The K-S two-sample test also retains its power despite the sample-size difference, because it is a non-parametric test—ranks are compared rather than data itself (Sokal and Rohlf, 1995).

There is some error that can be attributed to the mass estimation equations. The Martin (1980) equation produced smaller mass estimates for most animals, but for the largest animals—*Hyaenodon*, *Archaeotherium*, and titanotheres in particular—the Janis (1990) equation produced smaller estimates. Some mass estimates appear to be grossly overestimated: the estimates for titanothere body mass using the Martin (1980) equation generates estimates in excess of 13,300 kg (29,000 lbs), far greater than the estimated 10,000 kg (~22,000 lbs) mass of the largest bull elephant on record (Owen-Smith, 1988)! The sample used to generate the estimation method did not include large ungulate mammals with antlers or horns, so titanotheres—which had large occipital condyles as a result of large body mass and the need to hold up a large head laden with horns and bony projections—would appear excessively large using that method. The mass estimates generated by the Martin (1980) equation for the largest *Archaeotherium* and the titanotheres of the Eocene were, therefore, replaced with estimates generated from the Janis (1990) equation. Large disagreements in body mass were observed for estimates for some camels and oreodonts, which were determined to be a result of taphonomic bias in skull length. There is, otherwise, reasonably good agreement between the two approximation methods.

DISCUSSION

Interpretations of the K-S tests of the specimens used in this study demonstrate that body mass of the entire mammalian community decreased from the late Eocene to the middle

Oligocene. The first three tests encompassed a wide variety of mammalian groups, ranging from the Leporidae (rabbits) to the giant titanotheres. The high statistical significance with which we accept the results of the first two tests are likely due to the presence of rabbits in the Oligocene sample, which are very small in comparison to all other taxa investigated (< 1 kg in size), very abundant (70 measured), and not present in the Eocene because no intact skull material was available. The fact that the result of the third test corroborates the first two tests, despite the exclusion of rabbits, confirms the conclusion that the community overall is becoming smaller and is not merely a statistical artifact. The change in overall body mass may be attributed to the sudden change in climate that may have drastically changed or limited the food supplies of the herbivorous mammal groups. The mammals best suited to survive in these conditions would have been those generalists who could tolerate a range of vegetation types (succulents and grasses), as well as those that consumed smaller amounts of vegetation. Such specialized animals as rhinoceroses were affected adversely, and titanotheres became completely extinct. Oreodonts, which were likely generalists, appear to have done well across the transition, as these taxa persisted across the EOB with little change (Prothero, 1994b; Prothero and Heaton, 1996).

The range of body masses within individual taxa increased in addition to the overall decrease in body mass. The Eocene and Oligocene oreodont body-mass distributions were not statistically different from one another (test 5), but the dramatic increase in the observed range of body mass suggests that oreodonts in particular diversified into a range of body sizes across the EOT. The body-mass minimum of the Oligocene oreodonts is less than half of that of those oreodonts from the Eocene, whereas the body mass maximum of the Oligocene oreodonts is nearly twice that of the Eocene oreodonts. Oreodonts diversified into two new body-size classes, likely as a result of changes in behavior. The larger oreodonts may have adapted a larger body mass to deal with a grazing lifestyle, a possibility suggested by stable isotope analysis of their diet (Zanazzi and Kohn, 2008). The smaller oreodonts, however, may have adopted burrowing behavior. Some oreodonts from the WRF of WY have been interpreted to be communal, den-dwelling animals (Sundell, 2004, 2006). Mammal fossils in the Brule Member of the WRF of Douglas, WY, are frequently found in oblong nodules interpreted as burrows. Rodents, rabbits, and oreodonts are the mammals most frequently reported from such nodules.

Global cooling provided an opportunity for smaller mammals to conserve their small size by adapting to burrowing life styles. Burrows may have been used as a method of thermoregulation in order to maintain specific temperature and humidity conditions (Groenewald et al., 2001; Hasiotis et al., 2004), or they may otherwise have been used as hiding structures, as small mammals would no longer have been able to escape onto small tree branches during the Oligocene. The body-mass change across the EOT supports the hypothesis that the Oligocene was the beginning of a new widespread mammalian burrowing community.

The lack of change in carnivorous mammals is an unexpected result. The mass of carnivores should depend on the mass of their prey; a decrease in prey body mass should be mirrored by a decrease in carnivore body mass. A study of canid evolution in North America through the last 50 million years has shown that canids tend to increase in mass through the course of their lineages as a result of selective pressure for hypercarnivory (Van Valkenburgh et al., 2005). Large predators cannot rely on smaller prey for consistent nutrition (Carbone et al., 1999). Hypercarnivory is also positively correlated with large body mass in mammalian carnivores (Van Valkenburgh, 1999; Van Valkenburgh et al., 2005), so larger predators are also better adapted to eating large prey. The K-S tests on the mammals that would have been prey items demonstrate a clear decrease in body mass (aside from the oreodonts), but the body mass of predators appears unchanged. Modern carnivores are known to shift prey sources during harsh periods—drought, changing prey vulnerability, etc. (Owen-Smith and Mills, 2008). Some carnivores may have remained unchanged because they preyed on vulnerable megafauna—sick, elderly, or very young—during the Eocene, but relied on adult individuals of smaller bodied prey during the Oligocene so that the total mass preyed upon remained relatively unchanged. If this shift in predatory behavior occurred, then the body mass of carnivores could remain essentially unchanged across the EOT.

The lack of body mass change may also indicate such omnivorous behavior as that of modern bears and warthogs. For example, the diet of enteledonts has been in question, as they have been variously suspected of being browsing omnivorous, browsers, scavenging browsers, and carnivores (see Joeckel, 1990, for summary). Joeckel (1990) concluded that enteledonts were likely primarily carnivorous based on tooth wear, tooth arrangement, and jaw architecture. These animals, however, may have relied on foraging and scavenging to supplement their food supply as predatory pigs (see Meehan, 1998, for ecomorph classification). Entelodonts, however, do decrease in body mass at this interval, which may suggest that their predatory lifestyle was negatively affected by the environmental change at the EOB in a way unlike that of the other carnivorous mammals of the time.

The body-mass change reported here is similar to body-mass change reported from the Paleocene-Eocene Boundary. Gingerich (2003) demonstrated that the mammal fauna underwent a dwarfing trend of approximately 50–60%. The results from the EOB also demonstrate a dwarfing of the overall community, although the magnitude of body mass change at the EOB is less, ~28-41% based on comparison of the medians of the ungulates and ungulates excluding megafauna tests. These results suggest two things: either climate may have no serious long-term effect on body mass, or that at all times of dramatic climatic and environmental change body mass tends to decrease. Prothero and Heaton (1996) reported that the mammal taxa that persisted across the EOB throughout WY and the surrounding states did not undergo notable mass change or speciation. The presence of such gigantic mammals as titanotheres in the Eocene indicates that the metabolic limits on body mass are not much different than those for the mammals that live today, despite the fact that the Eocene was as much as 12°C warmer than the present (Zachos et al., 2001). The fact that the largest mammals do tend to track the colder times of the Cenozoic—the presence of the giant indricotheres in the Oligocene of Asia (e.g., Fortelius and Kappelman, 1993) and the giant mammalian fauna of the Pleistocene (Prothero, 2006)—undermines the hypothesis of Prothero and Heaton (1996) that climate change has no effect on body mass, however.

The results of our study indicate that body mass decreases during times of dramatic climatic and environmental change. This is perhaps a response to changing nutritional quality and availability of vegetation. The increased presence of C4 plant mass in the Oligocene (Fox and Koch, 2003) was not a substantial portion of the diet of any ungulate groups at that time (Zanazzi and Kohn, 2008), but conditions in the Oligocene would still have hindered the overall nutritional quality of the plants at the time. Plant nutritional quality is decreased as a consequence of the following factors: plants conserve shoot growth in drier conditions and instead favor root growth in an attempt to obtain water and other nutrients; photosynthetic rates are higher in greater pCO_2 concentrations; and C:N ratio decreases as pCO_2 concentration decreases (Field et al., 1992). Climatic drying and decreasing pCO_2 across the EOT, therefore, could have limited plant nutrition. Nonruminant ungulate mammals (e.g., perissodactyls) adapted to grazing lifestyles by evolving greater body mass to process larger amounts of food, so that they could overcome the lower quality of the vegetation by consuming a greater amount (Demment and Van Soest, 1985). Results presented here demonstrate a decrease in body mass across taxonomic groups despite a decline of vegetative quality. In the timeframe investigated here smaller body masses were more adaptive for the mammals of the Oligocene to accommodate lower quality vegetation. Furthermore, our results suggest that incredibly large body masses likely require longer periods of time (>10 million years) to evolve.

The extinction of titanotheres at the end of the Eocene is the primary explanation for the magnitude of the body-mass decrease reported here. The three titanotheres and one rhinoceros measured from the Eocene are all an order of magnitude larger than the largest animals present in the Oligocene sample. The extinction of the titanotheres can likely be attributed to climate. Titanothere dentition consisted of low-crowned teeth that were easily abraded but were, however, highly specialized for consuming succulent vegetation (i.e., browse) (Mader, 1998). The contraction of forested areas at the end of the Eocene due to climatic cooling and drying would have limited their food supply and driven them to extinction. The extinction of this group at the end of the Eocene does not invalidate the hypothesis that mammalian body mass increases as result of climatic cooling, rather it is an example of a lineage going extinct without enough time to be replaced. *Indricotherium*, the largest known terrestrial mammal, occurred during the Oligocene (Fortelius and Kappelman, 1993), but many millions of years must have passed with abundant food resources for such an animal to evolve. Analysis of the increase in the mass of mammals according to Cope's rule at the family level suggests that the average amount of time required for a family to evolve from relatively small size to giant size is on the order of 20 million years and no less than 5 million years (Bonner, 1968). The lack of giant forms in the

Oligocene sample may merely indicate that evolutionary constraints on body mass increase require tens of millions of years or more for mammals to become that large.

The results of this investigation may also be attributed to a specific environmental change observed in the area of Douglas, WY. The environment of the late Eocene portion of the WRF would have been akin to a tropical rain forest, entirely dominated by canopy cover (Retallack, 1983; Prothero, 2006). The Oligocene environment did not immediately become an open grassland as the climate cooled. The early Oligocene environment was still dominantly covered by canopy, with only small open areas dispersed among the forests. Not until the early late and mid-late Oligocene did the canopy cover begin to thin and open environments become more prevalent. Even at this time, however, the environments of the North American midcontinent were still considered to be forests rather than grasslands or steppes (Retallack, 1983; Hembree and Hasiotis, 2007). The prevalence of leafy vegetation, then, may explain why small browsing ungulates would have been able to persist in the colder climate as opposed to the large titanotheres and rhinoceroses, which were also browsers but required greater amounts for sustenance. Large body mass has been suggested as an adaptation for the ability to move over long distances in the search of food (Pennycuick, 1979; Janis and Wilhelm, 1993). If this is the case, the prevalence of trees in early Oligocene environments may have undermined the advantage of large body mass.

Our results clearly undermine the hypothesis that metabolic requirements are responsible for the shift in mammalian body mass during climate change events. The global cooling event that occurs at the EOB is widely accepted from both marine (Zachos et al., 2001) and continental records (Retallack, 1983, 1992, 2007; Zanazzi et al., 2007). Temperature change in continental environments at this interval is estimated to be on the order of 2–4°C (Retallack 2007). If mammals needed to insulate their bodies against dramatic climatic cooling, global cooling across the EOT would have been significant enough change to necessitate body mass increase. Scholander (1956) suggested that the exceptions to Bergmann's and Allen's rules were all related to specific ecological requirements imposed on organisms; that is, there may be selective pressure on animals to respond to changes in temperature, but some particular physiological requirements (i.e., food consumption) trump those pressures. The results of this study appear to confirm that observation. The statistically significant decrease in body mass across the EOT we report here, therefore, necessitates reexamination of the controls and response of mammalian body mass to changes in global climate.

CONCLUSIONS

Body mass estimates generated from over 200 skulls collected from Douglas, WY, and the surrounding area were compared using K-S two sample tests. The tests indicate with high confidence that the overall community of mammals decreased in body mass across the EOT based on tests of the entire fauna, the entire fauna excluding the megafauna, and the ungulate fauna. The hypotheses that body mass increased or went unchanged in response to global cooling is rejected for the overall herbivorous mammalian fauna of the WRF of Douglas, WY. Such large mammalian groups as titanotheres went extinct at the end of the Eocene and were not replaced in the portion of the Oligocene sampled in this study, indicating that mammals with exceptionally large body mass may take many millions of years to evolve. Smaller body mass was likely a selective pressure for the remaining herbivorous mammals because of the dramatic changes in vegetation that took place at that time. The body mass of the overall mammalian community decreased 28–41% based on comparison of the medians of the sampled populations of ungulate mammals.

Tests of the oreodont and carnivorous mammal faunas indicated no statistically significant change. The body mass of carnivorous mammals did not change significantly, because they were likely able to change their predation habits to cope with environmental stresses. Entelodonts may have increasingly relied on scavenging behavior in the Oligocene, which may account for observed smaller body mass, as compared to the rest of the carnivores.

Changes in body mass in mammals do not behave according to Cope’s rule, but rather appear to be more closely controlled by changes in specific environmental parameters. Climate change is the major driving mechanism for changes in mammalian body mass, as changing climate affects the environmental parameters that determine mammalian body mass. The hypothesis that changes in temperature alone are responsible for changes in mammalian body mass, as is predicted by Bergmann’s or Allen’s rules, is rejected. The change in availability and quality of vegetation instead appears to be the primary control on mammalian body mass, as the body mass of herbivorous mammals appeared to fluctuate more with climate change. The dietary needs of herbivores appear to depend more on the environment than the dietary needs of carnivores. The increased availability is a less significant, but nonetheless important, factor in body mass development of mammalian communities. A similar decrease in mammalian body mass was observed at the EOT as was observed at the PETM, which suggests that vegetation quality is a delicate balance controlled by a variety of factors that is easily disturbed during rapid climate change events. The combination of decreasing forest canopy and vegetation quality was likely for the overall decreased body mass during the Oligocene. The limited opening of the forest canopy during the Oligocene was a factor that prompted several mammalian taxa, oreodonts most significantly, to begin burrowing. Decreased body mass is seen as an adaptation for a burrowing lifestyle. Results of this study also contradict previous hypotheses that predict that the opening of the environment causes mammalian taxa across-the-board to increase in body mass.

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FIGURES

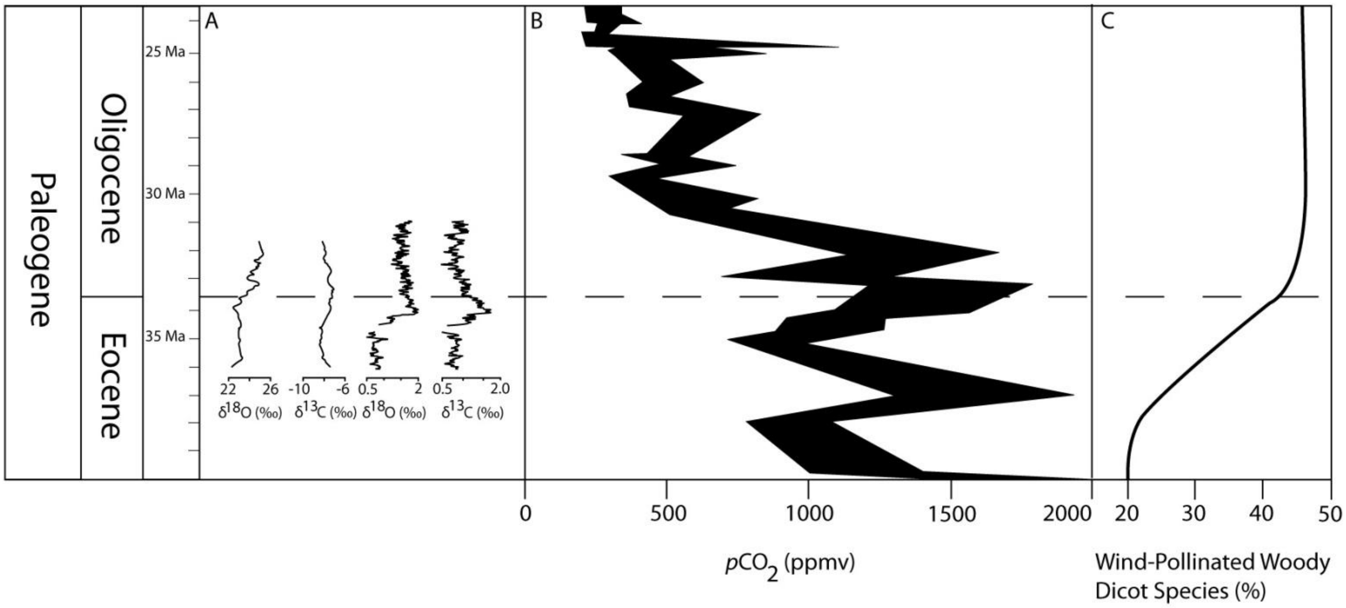

FIGURE 1—Graphs illustrating climatic and environmental changes that occurred across the EOT. A) Climatic cooling is inferred from the changes in $\delta^{13}C$ and $\delta^{18}O$ from continental (left) and deep marine records (right). Continental $\delta^{18}O$ curve generated using VSMOW standard, continental $\delta^{13}C$ and marine curves generated using VPDB standard (modified from Coxall et al., 2005; Zanazzi et al., 2007). B) Intermediate estimates of global atmospheric carbon dioxide concentrations during the EOT. Atmospheric carbon dioxide concentrations fell dramatically at the EOB and continued to decline into the middle Oligocene (modified from Pagani et al., 2005). C) The amount of forest vegetation that relied on wind pollination as opposed to insect pollination rose substantially during the EOT (modified from Wolfe, 1992).

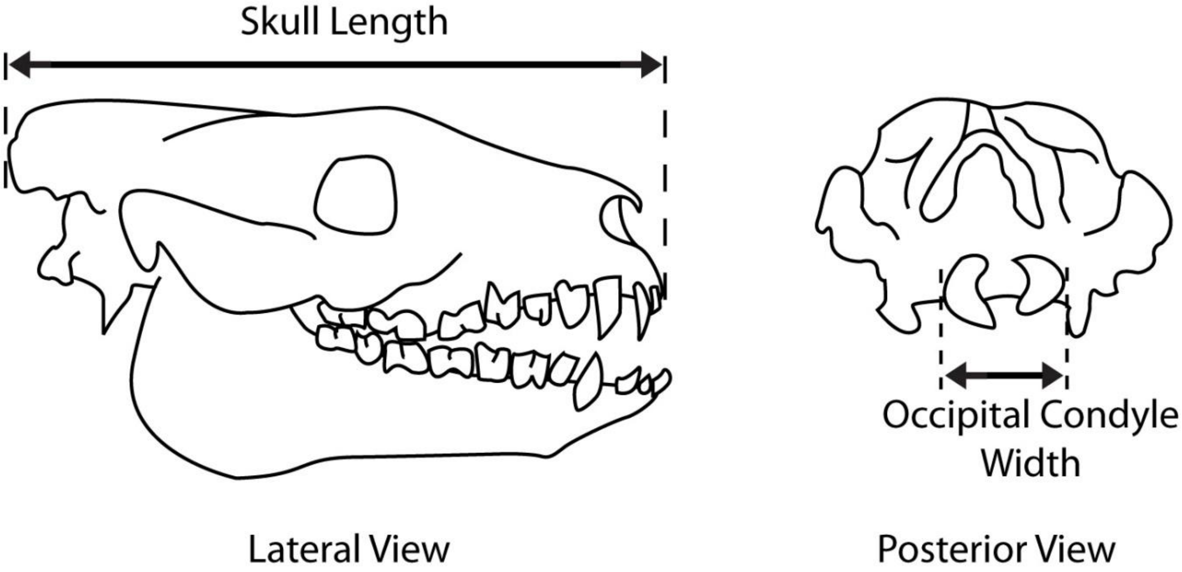

FIGURE 2—Illustration of measured skull elements. Skull length is the distance between from the eruption of the first upper incisor (I1) to the posterior end of the skull. Width of the occipital condyle was measured between the outermost edges.

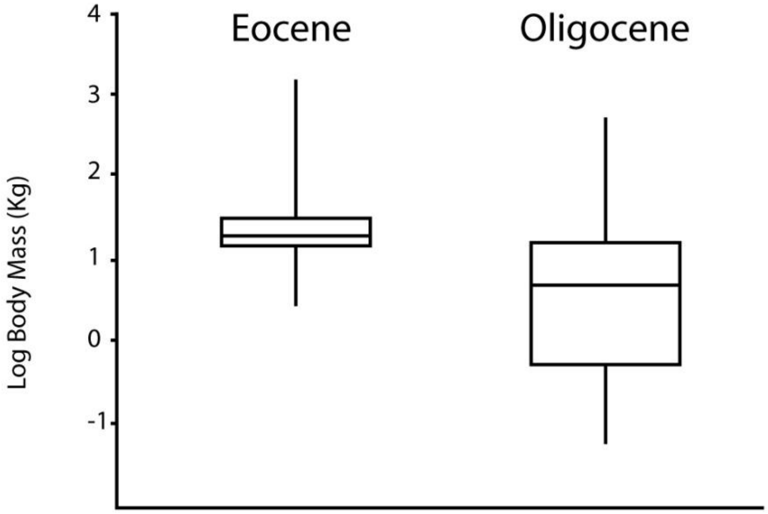

FIGURE 3—Box and whisker plot comparing the body masses of all mammals from the Eocene and Oligocene.

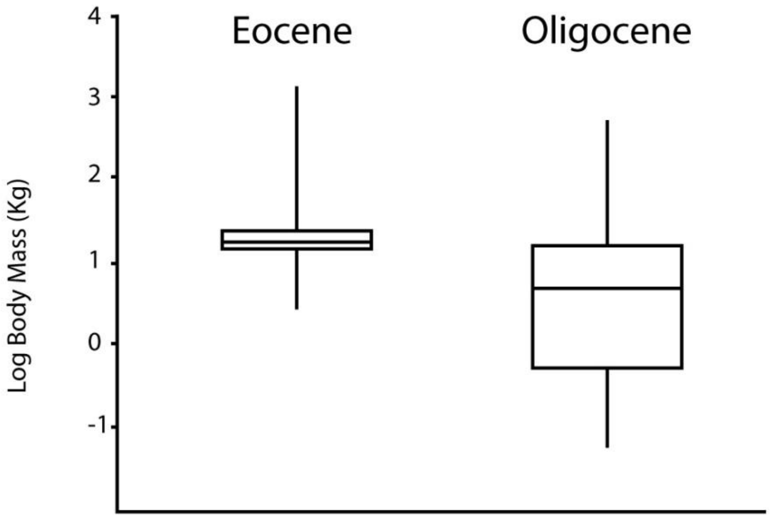

FIGURE 4—Box and whisker plot comparing the body masses of all mammals excluding titanotheres from the Eocene and Oligocene.

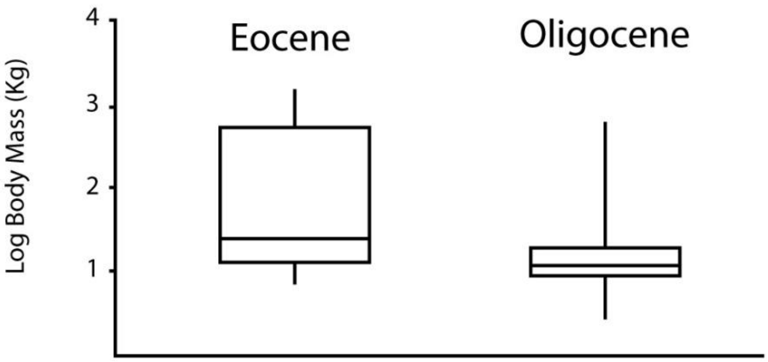

FIGURE 5—Box and whisker plot comparing the body masses of all ungulates from the Eocene and Oligocene.

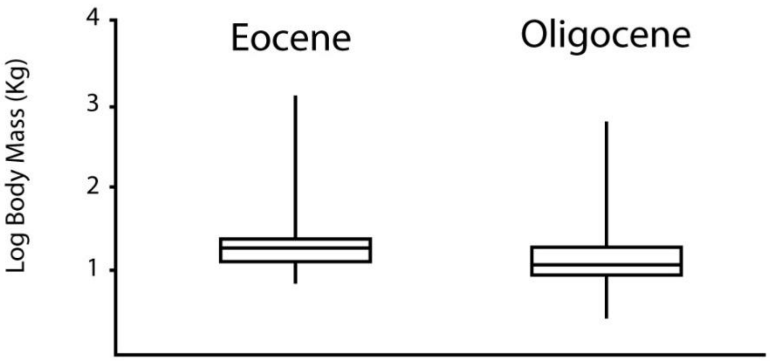

FIGURE 6— Box and whisker plot comparing the body masses of all ungulates excluding titanotheres from the Eocene and Oligocene.

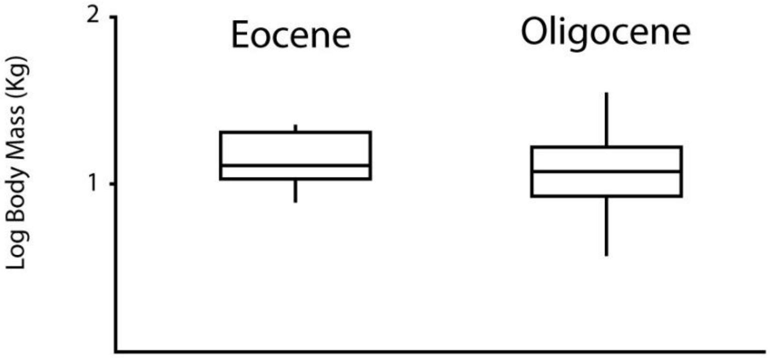

FIGURE 7— Box and whisker plot comparing the body masses of all oreodonts from the Eocene and Oligocene.

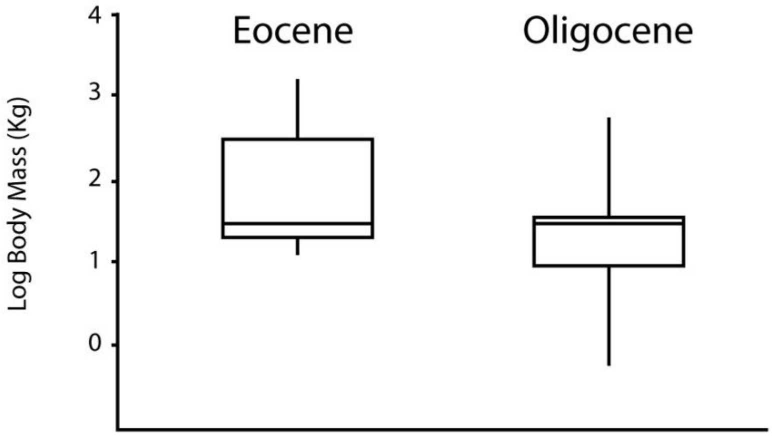

FIGURE 8— Box and whisker plot comparing the body masses of all carnivorous mammals from the Eocene and Oligocene.

TABLES

Museum	Number	Taxa	Epoch	SL (mm)	OC (mm)	Body mass (kg)	LOG body mass	Method	Tests
UW	V-76023; 11033	Leptomeryx	Eocene	0	20	2.605379402	0.415870975	OC	1,2,3,4
Boulder	UCM 17754	Merycoidodon gracile	Eocene	132	26	6.877987446	0.837461379	OC	1,2,3,4,5
UW	V-76023; 12895	Merycoidodontidae	Eocene	169	28	9.047835735	0.956544707	OC	1,2,3,4,5
UW	V-76025; 12863	Merycoidodontidae	Eocene	150	28	9.047835735	0.956544707	OC	1,2,3,4,5
Sundell	DF 2658	oreodont	Eocene	162	29	10.30226184	1.012932584	OC	1,2,3,4,5
Boulder	UCM 17757	Poebrotherium	Eocene	182	29	10.30226184	1.012932584	OC	1,2,3,4
Sundell	DF 2523	oreodont	Eocene	155	30	11.67908001	1.067408634	OC	1,2,3,4,5
Sundell	DF 2821	oreodont	Eocene	146	0	13.18104206	1.119949746	SL	1,2,3,4,5
UW	V-76023; 11355	Miniochoerus cf. chacronensis	Eocene	182	31	13.18555026	1.120098259	OC	1,2,3,4,5
Boulder	UCM 67344	Hoplophoneus	Eocene	148	0	13.72551356	1.137528603	SL	1,2,6
UW	V-76026; 13769	cc. Prodesmatochoerus sp.	Eocene	150	0	14.28471223	1.154871496	SL	1,2,3,4,5
UW	V-76029; 13075	Merycoidodontidae	Eocene	155	0	15.74841323	1.197236802	SL	1,2,3,4,5
Sundell	DF 2534	oreodont	Eocene	160	0	17.308401	1.238256948	SL	1,2,3,4,5
Boulder	UCM 46221	Dinictis	Eocene	0	34	18.55803478	1.268531984	OC	1,2,6
UW	42578	Oreodontidae	Eocene	168	0	20.01221284	1.301295113	SL	1,2,3,4,5
UW	V-76025; 11185	Hoplophoneus cf. charri	Eocene	171	0	21.09421793	1.324163428	SL	1,2,6
UW	V-76024; 12859	Merycoidodontidae	Eocene	173	0	21.8367075	1.339187157	SL	1,2,3,4,5
UW	V-76025; 12875	Merycoidodontidae	Eocene	175	0	22.59634489	1.354038195	SL	1,2,3,4,5
Boulder	UCM 52150	Hoplophoneus	Eocene	159	36	22.92869008	1.360379244	OC	1,2,6
UW	V-76025; 12876	Merycoidodontidae	Eocene	176	0	22.98265442	1.361400187	SL	1,2,3,4,5
UW	V-76029; 12860	Merycoidodontidae	Eocene	181	0	24.98007628	1.39759376	SL	1,2,3,4,5
UW	V-76025; 11335	Hyaenodon crucians	Eocene	243	37	25.37501867	1.40440637	OC	1,2,6
UW	V-76027; 11336	Hyaenodon crucians	Eocene	249	41	37.09883409	1.569360261	OC	1,2,6
Boulder	UCM 46260	Hyaenodon crucians	Eocene	215	0	41.68736245	1.620004418	SL	1,2,6

Sundell	DF 3715	Subhyracodon	Eocene	410	0	284.4670531	2.454031974	SL	1,2,3,4
Boulder	UCM 20463	Archaeotherium	Eocene	0	92	738.031592	2.868074953	OC	1,2,3,4,6
Boulder	UCM 20462	Archaeotherium	Eocene	0	104	1161.671532	3.065083347	OC	1,2,3,4,6
Boulder	UCM 20501	Brontotheriidae	Eocene	669	0	1220.794883	3.0866427	SL	1,3
Boulder	UCM 20457	cf. Archaeotherium	Eocene	687	119	1321.132246	3.120946293	SL	1,2,3,4,6
Tate	v007-19	Brontotherium leidyi	Eocene	690	200	1338.369543	3.126576045	SL	1,3
Boulder	UCM 43750	Brontotheriidae	Eocene	731	201	1589.110863	3.201154196	SL	1,3
Sundell	DF 3177	rabbit	Oligocene	0	7	0.053570135	-1.271077261	OC	1,2
Sundell	DF 2072	rabbit	Oligocene	48	8	0.087799682	-1.056507057	OC	1,2
Sundell	DF 0838	rabbit	Oligocene	0	8	0.087799682	-1.056507057	OC	1,2
UW	V-75004; 11112	Paleolagus	Oligocene	49	8	0.087799682	-1.056507057	OC	1,2
Sundell	DF 2259	rabbit	Oligocene	0	9	0.135755451	-0.867242724	OC	1,2
Sundell	DF 2764	rabbit	Oligocene	55	9	0.135755451	-0.867242724	OC	1,2
UW	V-48003; 672	Paleolagus c.f. haydeni	Oligocene	0	9	0.135755451	-0.867242724	OC	1,2
UW	V-75004; 11126	Paleolagus	Oligocene	57	9	0.135755451	-0.867242724	OC	1,2
Sundell	DF 3512	rabbit	Oligocene	52	10	0.200474893	-0.697940009	OC	1,2
Sundell	DF 3669	rabbit	Oligocene	52	10	0.200474893	-0.697940009	OC	1,2
Sundell	DF 0674	Paleolagus	Oligocene	54	10	0.200474893	-0.697940009	OC	1,2
Sundell	DF 3472	rabbit	Oligocene	0	10	0.200474893	-0.697940009	OC	1,2
Sundell	DF 3914	rabbit	Oligocene	48	10	0.200474893	-0.697940009	OC	1,2
Sundell	DF 0831	rabbit	Oligocene	0	10	0.200474893	-0.697940009	OC	1,2
Sundell	DF 2336	rabbit	Oligocene	52	10	0.200474893	-0.697940009	OC	1,2
UW	V-75004; 10908	Paleolagus	Oligocene	52	10	0.200474893	-0.697940009	OC	1,2
UW	V-75004; 10911	Paleolagus	Oligocene	0	10	0.200474893	-0.697940009	OC	1,2
UW	V-75003; 10907	Paleolagus	Oligocene	54	10	0.200474893	-0.697940009	OC	1,2
UW	V-76033; 11236	Paleolagus	Oligocene	49	10	0.200474893	-0.697940009	OC	1,2
UW	V-75004; 11113	Paleolagus	Oligocene	36	0	0.204644435	-0.68900006	SL	1,2
Sundell	DF 2704	rabbit	Oligocene	37	0	0.222024106	-0.653599871	SL	1,2
UW	V-75004; 11126	Paleolagus	Oligocene	37	0	0.222024106	-0.653599871	SL	1,2
Sundell	DF 3144	rabbit	Oligocene	38	0	0.240356682	-0.6191438	SL	1,2

Sundell	DF 2494	rabbit	Oligocene	39	0	0.259667266	-0.585582794	SL	1,2
Sundell	DF 3612	rabbit	Oligocene	40	0	0.279980944	-0.552871526	SL	1,2
Sundell	DF 3621	rabbit	Oligocene	50	11	0.285241641	-0.544787074	OC	1,2
Sundell	DF 3315	rabbit	Oligocene	46	11	0.285241641	-0.544787074	OC	1,2
Sundell	DF 0917	rabbit	Oligocene	0	11	0.285241641	-0.544787074	OC	1,2
Sundell	DF 2885	rabbit	Oligocene	0	11	0.285241641	-0.544787074	OC	1,2
UW	V-48003; 708	Paleolagus	Oligocene	53	11	0.285241641	-0.544787074	OC	1,2
Sundell	DF 0646	rabbit	Oligocene	42	0	0.323717844	-0.489833361	SL	1,2
Sundell	DF 0882	rabbit	Oligocene	42	0	0.323717844	-0.489833361	SL	1,2
Tate	v1145	Paleolgaus	Oligocene	42	0	0.323717844	-0.489833361	SL	1,2
Sundell	DF 3508	rabbit	Oligocene	43	0	0.347191157	-0.459431345	SL	1,2
Sundell	DF 3530	rabbit	Oligocene	43	0	0.347191157	-0.459431345	SL	1,2
Sundell	DF 3426	rabbit	Oligocene	54	12	0.393577807	-0.404969398	OC	1,2
Sundell	DF 2937	rabbit	Oligocene	57	12	0.393577807	-0.404969398	OC	1,2
Boulder	UCM 99793	Paleolagus sp.	Oligocene	55	12	0.393577807	-0.404969398	OC	1,2
Boulder	UCM 17758	Paleolagus haydeni	Oligocene	53	12	0.393577807	-0.404969398	OC	1,2
Sundell	DF 3146	rabbit	Oligocene	45	0	0.39747263	-0.400692772	SL	1,2
Sundell	DF 2986	rabbit	Oligocene	46	0	0.424330793	-0.372295451	SL	1,2
Sundell	DF 3118	rabbit	Oligocene	46	0	0.424330793	-0.372295451	SL	1,2
Sundell	DF 3294	rabbit	Oligocene	46	0	0.424330793	-0.372295451	SL	1,2
Sundell	DF 3533	rabbit	Oligocene	47	0	0.45236722	-0.344508873	SL	1,2
Sundell	DF 3441	rabbit	Oligocene	47	0	0.45236722	-0.344508873	SL	1,2
Sundell	DF 3132	rabbit	Oligocene	47	0	0.45236722	-0.344508873	SL	1,2
Sundell	DF 3095	rabbit	Oligocene	47	0	0.45236722	-0.344508873	SL	1,2
Sundell	DF 2316	rabbit	Oligocene	48	0	0.481606879	-0.317307319	SL	1,2
UW	V-76034; 11344	Paleogale cf. lagophaga	Oligocene	53	13	0.529237239	-0.276349605	OC	1,2,6
Sundell	DF 3103	rabbit	Oligocene	50	0	0.543795692	-0.264564237	SL	1,2
Sundell	DF 3172	rabbit	Oligocene	50	0	0.543795692	-0.264564237	SL	1,2
Sundell	DF 3342	rabbit	Oligocene	50	0	0.543795692	-0.264564237	SL	1,2
Sundell	DF 2393	rabbit	Oligocene	50	0	0.543795692	-0.264564237	SL	1,2

Sundell	DF 3099	rabbit	Oligocene	51	0	0.576794717	-0.238978726	SL	1,2
Sundell	DF 3504	rabbit	Oligocene	51	0	0.576794717	-0.238978726	SL	1,2
Sundell	DF 0977	rabbit	Oligocene	51	0	0.576794717	-0.238978726	SL	1,2
UW	V-75004; 11087	Paleolagus	Oligocene	51	0	0.576794717	-0.238978726	SL	1,2
Sundell	DF 3037	rabbit	Oligocene	52	0	0.611096712	-0.213890053	SL	1,2
Sundell	DF 1993	rabbit	Oligocene	52	0	0.611096712	-0.213890053	SL	1,2
Sundell	DF 1426	rabbit	Oligocene	52	0	0.611096712	-0.213890053	SL	1,2
Sundell	DF 1359	rabbit	Oligocene	52	0	0.611096712	-0.213890053	SL	1,2
Sundell	DF 3273	rabbit	Oligocene	52	0	0.611096712	-0.213890053	SL	1,2
Sundell	DF 3143	rabbit	Oligocene	53	0	0.646726582	-0.189279288	SL	1,2
Sundell	DF 0926	rabbit	Oligocene	53	0	0.646726582	-0.189279288	SL	1,2
Tate	851v	Paleolagus	Oligocene	53	0	0.646726582	-0.189279288	SL	1,2
Sundell	DF 3660	rabbit	Oligocene	54	0	0.683709218	-0.165128565	SL	1,2
Sundell	DF 2839	rabbit	Oligocene	54	0	0.683709218	-0.165128565	SL	1,2
UW	V-73138; 6347	Paleolagus	Oligocene	55	0	0.722069501	-0.141420999	SL	1,2
UW	V-48003; 690	Paleolgaus	Oligocene	56	0	0.761832297	-0.11814062	SL	1,2
Sundell	DF 3564	rabbit	Oligocene	58	15	0.898664632	-0.04640235	OC	1,2
Boulder	UCM 22747	Hesperocyon gregarius	Oligocene	80	17	1.427976303	0.154721	OC	1,2,6
Boulder	UCM 99456	Hesperocyon sp.	Oligocene	84	18	1.764283044	0.24656826	OC	1,2,6
Boulder	UCM 99455	Hesperocyon sp.	Oligocene	85	19	2.155005162	0.333448315	OC	1,2,6
Sundell	DF 2966	oreodont (Miniocoris gracilis)	Oligocene	133	21	3.120839124	0.494271382	OC	1,2,3,4,5
UW	42580	Oreodontidae	Oligocene	91	0	3.229595581	0.509148142	SL	1,2,3,4,5
Sundell	DF 3417	oreodont	Oligocene	94	0	3.556766578	0.551055364	SL	1,2,3,4,5
Sundell	DF 3328	oreodont	Oligocene	124	22	3.707011304	0.56902391	OC	1,2,3,4,5
Boulder	UCM 87224	Merycoidodon culbertsoni	Oligocene	156	22	3.707011304	0.56902391	OC	1,2,3,4,5
KU	66205	Paleolagus	Oligocene	41	23	4.369713713	0.640452985	OC	1,2
Sundell	DF 3287e	oreodont	Oligocene	126	23	4.369713713	0.640452985	OC	1,2,3,4,5
Sundell	DF 3676	oreodont	Oligocene	151	24	5.114952272	0.708841586	OC	1,2,3,4,5
Sundell	DF 3524	oreodont	Oligocene	125	25	5.948918558	0.774438023	OC	1,2,3,4,5
Sundell	DF 3287a	oreodont	Oligocene	139	26	6.877987446	0.837461379	OC	1,2,3,4,5

Sundell	DF 3672	oreodont	Oligocene	145	26	6.877987446	0.837461379	OC	1,2,3,4,5
Tate	Unnumbered loan	Merycoidodon culbertsoni	Oligocene	153	26	6.877987446	0.837461379	OC	1,2,3,4,5
UW	V-48004; 554	Merycoidodontidae	Oligocene	145	26	6.877987446	0.837461379	OC	1,2,3,4,5
UW	V-52002; 1195	Merycoidodontidae	Oligocene	154	26	6.877987446	0.837461379	OC	1,2,3,4,5
UW	V-54003; 3337	Merycoidodontidae	Oligocene	167	26	6.877987446	0.837461379	OC	1,2,3,4,5
UW	V-52002; 4770	Merycoidodontidae	Oligocene	159	26	6.877987446	0.837461379	OC	1,2,3,4,5
Boulder	UCM 19123	Poebrotherium sp.	Oligocene	181	26	6.877987446	0.837461379	OC	1,2,3,4
Boulder	UCM 48604	Mesohippus	Oligocene	151	26	6.877987446	0.837461379	OC	1,2,3,4
KU	80105	Poebrotherium	Oligocene	118	0	6.995986645	0.844848972	SL	1,2,3,4
Sundell	DF 3606	camel	Oligocene	137	27	7.908714876	0.898105919	OC	1,2,3,4
Sundell	DF 3527	camel	Oligocene	145	27	7.908714876	0.898105919	OC	1,2,3,4
Sundell	DF 3147	Hyaenodon	Oligocene	171	27	7.908714876	0.898105919	OC	1,2,6
UW	V-48003; 678	Merycoidodontidae	Oligocene	125	27	7.908714876	0.898105919	OC	1,2,3,4,5
UW	V-75004; 11142	Merycoidodontidae	Oligocene	0	27	7.908714876	0.898105919	OC	1,2,3,4,5
UW	V-75002; 11053	Camelidae	Oligocene	163	27	7.908714876	0.898105919	OC	1,2,3,4
Boulder	UCM 40193	Merycoidodon culbertsoni	Oligocene	154	27	7.908714876	0.898105919	OC	1,2,3,4,5
Boulder	UCM 67273	Poebrotherium	Oligocene	153	27	7.908714876	0.898105919	OC	1,2,3,4
Boulder	UCM 55463	Poebrotherium oximium	Oligocene	130	27	7.908714876	0.898105919	OC	1,2,3,4
UW	V-48003; 686	Merycoidodontidae	Oligocene	127	0	8.705948021	0.93981607	SL	1,2,3,4,5
Sundell	DF 3667b	oreodont	Oligocene	128	0	8.911476367	0.94994966	SL	1,2,3,4,5
KU	2584	Hyaenodon mustelinus	Oligocene	121	28	9.047835735	0.956544707	OC	1,2,6
Sundell	DF 3089	camel	Oligocene	169	28	9.047835735	0.956544707	OC	1,2,3,4
Sundell	DF 3261	oreodont	Oligocene	163	28	9.047835735	0.956544707	OC	1,2,3,4,5
UW	V-75004; 10897	Merycoidodon	Oligocene	152	28	9.047835735	0.956544707	OC	1,2,3,4,5
Boulder	UCM 47354	Merycoidodontidae	Oligocene	172	28	9.047835735	0.956544707	OC	1,2,3,4,5
Sundell	DF 3650	oreodont	Oligocene	129	0	9.120200544	0.960004388	SL	1,2,3,4,5
Sundell	DF 3667a	oreodont	Oligocene	129	0	9.120200544	0.960004388	SL	1,2,3,4,5
Sundell	DF 3694	oreodont	Oligocene	133	0	9.987542304	0.999458632	SL	1,2,3,4,5
Sundell	DF 3659	oreodont	Oligocene	133	0	9.987542304	0.999458632	SL	1,2,3,4,5
Sundell	DF 3624	camel	Oligocene	153	29	10.30226184	1.012932584	OC	1,2,3,4

UW	V-52002; 1300	Poebrotherium c.f. wilsoni	Oligocene	177	29	10.30226184	1.012932584	OC	1,2,3,4
UW	V-52002; 1187	Merycoidodontidae	Oligocene	133	29	10.30226184	1.012932584	OC	1,2,3,4,5
UW	V-54004; 759	Merycoidodontidae	Oligocene	132	29	10.30226184	1.012932584	OC	1,2,3,4,5
UW	V-52002; 1185	Merycoidodontidae	Oligocene	200	29	10.30226184	1.012932584	OC	1,2,3,4,5
Boulder	UCM 20521	Mesohippus bairdi	Oligocene	0	29	10.30226184	1.012932584	OC	1,2,3,4
Sundell	DF 3435	camel	Oligocene	135	0	10.44102081	1.018742961	SL	1,2,3,4
Sundell	DF 3287b	oreodont	Oligocene	137	0	10.90796378	1.037743687	SL	1,2,3,4,5
UW	V-76034; 6472	Merycoidodontidae	Oligocene	138	0	11.14654522	1.047140282	SL	1,2,3,4,5
UW	V-75004; 11145	Camelidae	Oligocene	145	30	11.67908001	1.067408634	OC	1,2,3,4
UW	V-54004; 3327	Merycoidodontidae	Oligocene	199	30	11.67908001	1.067408634	OC	1,2,3,4,5
Boulder	UCM 52511	Poebrotherium	Oligocene	162	30	11.67908001	1.067408634	OC	1,2,3,4
Boulder	UCM 19830	Mesohippus	Oligocene	136	30	11.67908001	1.067408634	OC	1,2,3,4
Sundell	DF 3649	oreodont	Oligocene	144	0	12.65110365	1.102128414	SL	1,2,3,4,5
Sundell	DF 3561	oreodont	Oligocene	145	0	12.91426835	1.111069807	SL	1,2,3,4,5
KU	70518	Oreodon	Oligocene	145	31	13.18555026	1.120098259	OC	1,2,3,4,5
Sundell	DF 3571	oreodont	Oligocene	154	31	13.18555026	1.120098259	OC	1,2,3,4,5
UW	V-54003; 3342	Merycoidodontidae	Oligocene	199	31	13.18555026	1.120098259	OC	1,2,3,4,5
Boulder	UCM 53566	Merycoidodon	Oligocene	177	31	13.18555026	1.120098259	OC	1,2,3,4,5
Sundell	DF 3278	horse	Oligocene	202	32	14.829104	1.171114911	OC	1,2,3,4
Sundell	DF 3665	horse	Oligocene	0	32	14.829104	1.171114911	OC	1,2,3,4
UW	V-48003; 642	Merycoidodontidae	Oligocene	156	32	14.829104	1.171114911	OC	1,2,3,4,5
UW	V-54003; 3336	Merycoidodontidae	Oligocene	216	32	14.829104	1.171114911	OC	1,2,3,4,5
UW	4993	Hyaenodon sp.	Oligocene	169	32	14.829104	1.171114911	OC	1,2,6
Boulder	UCM 87225	Merycoidodon	Oligocene	220	32	14.829104	1.171114911	OC	1,2,3,4,5
Boulder	UCM 53567	Merycoidodon	Oligocene	193	32	14.829104	1.171114911	OC	1,2,3,4,5
Boulder	UCM 20998	Mesohippus	Oligocene	0	32	14.829104	1.171114911	OC	1,2,3,4
UW	V-75001; 10896	Merycoidodon	Oligocene	152	0	14.85883206	1.171984674	SL	1,2,3,4,5
UW	4690	Hoplophoneus primaevus	Oligocene	154	0	15.448067	1.188874144	SL	1,2,6
Sundell	DF 3691	oreodont	Oligocene	156	0	16.05261094	1.20554568	SL	1,2,3,4,5
Tate	v1849	oreodont	Oligocene	0	33	16.61734241	1.220561569	OC	1,2,3,4,5

UW	V-79002; 1308	Poebrotherium c.f. wilsoni	Oligocene	160	33	16.61734241	1.220561569	OC	1,2,3,4
UW	V-54003; 3341	Merycoidodontidae	Oligocene	204	33	16.61734241	1.220561569	OC	1,2,3,4,5
UW	V-75004; 11143	Merycoidodontidae	Oligocene	167	33	16.61734241	1.220561569	OC	1,2,3,4,5
Boulder	UCM 90696	Oreodont	Oligocene	186	33	16.61734241	1.220561569	OC	1,2,3,4,5
Boulder	UCM 53422	Merycoidodon	Oligocene	0	33	16.61734241	1.220561569	OC	1,2,3,4,5
Boulder	UCM 17756	Mesohippus bairdi Leidy	Oligocene	187	33	16.61734241	1.220561569	OC	1,2,3,4
UW	42611	Merycoidodontidae	Oligocene	158	0	16.67265769	1.222004834	SL	1,2,3,4,5
UW	V-54004; 4739	Merycoidodontidae	Oligocene	213	34	18.55803478	1.268531984	OC	1,2,3,4,5
UW	V-52002; 1204	Merycoidodontidae	Oligocene	208	34	18.55803478	1.268531984	OC	1,2,3,4,5
Boulder	UCM 53562	Agriochoerus	Oligocene	0	34	18.55803478	1.268531984	OC	1,2,3,4,5
Boulder	UCM 53421	Merycoidodontidae	Oligocene	0	34	18.55803478	1.268531984	OC	1,2,3,4,5
Sundell	DF 2182	oreodont	Oligocene	203	35	20.65911701	1.315111755	OC	1,2,3,4,5
UW	V-54003; 2243	Merycoidodontidae	Oligocene	202	35	20.65911701	1.315111755	OC	1,2,3,4,5
Boulder	UCM 41752	cf. Hoplophoneus	Oligocene	177	35	20.65911701	1.315111755	OC	1,2,6
KU	10572	Oreodon culbertsoni	Oligocene	218	36	22.92869008	1.360379244	OC	1,2,3,4,5
UW	V-54003; 3338	Merycoidodontidae	Oligocene	199	36	22.92869008	1.360379244	OC	1,2,3,4,5
UW	V-54004; 3333	Merycoidodontidae	Oligocene	202	36	22.92869008	1.360379244	OC	1,2,3,4,5
Boulder	UCM 19160	Hoplophoneus	Oligocene	154	36	22.92869008	1.360379244	OC	1,2,6
Boulder	UCM 47481	Dinictis	Oligocene	177	0	23.37332336	1.368720467	SL	1,2,6
Sundell	DF 3522	oreodont	Oligocene	179	0	24.16783611	1.383237767	SL	1,2,3,4,5
UW	V-52002; 1197	Merycoidodontidae	Oligocene	197	37	25.37501867	1.40440637	OC	1,2,3,4,5
Boulder	UCM 99454	Felidae	Oligocene	194	0	30.70507387	1.487210147	SL	1,2,6
Sundell	DF 1760	Hyaenodon	Oligocene	196	0	31.65642095	1.500461812	SL	1,2,6
Sundell	DF 3198	oreodont	Oligocene	197	0	32.13934509	1.507037023	SL	1,2,3,4,5
Tate	DF 2550	Hoplophoneus	Oligocene	141	40	33.8596106	1.529681959	OC	1,2,6
Sundell	DF 1562	Hyaenodon	Oligocene	205	0	36.1799312	1.558467737	SL	1,2,6
Sundell	DF 0937	oreodont	Oligocene	207	0	37.24018054	1.571011778	SL	1,2,3,4,5
Boulder	UCM 21451	Hoplophoneus	Oligocene	208	0	37.77795296	1.577238422	SL	1,2,6
Tate	DF 1363	Daphoenus	Oligocene	209	0	38.32085596	1.583435201	SL	1,2,6
Sundell	DF 2141	Merycoidon culbertsoni	Oligocene	219	0	44.03735657	1.643821242	SL	1,2,3,4,5

Boulder	UCM 46889	Agriochoerus	Oligocene	207	43	44.24796246	1.645893277	OC	1,2,3,4,5
Sundell	DF 1573	Hyaenodon	Oligocene	269	47	61.49248809	1.788822066	OC	1,2,6
Tate	Unnumbered loan	Hyracodon	Oligocene	261	0	74.21736127	1.870505509	SL	1,2,3,4
Tate	DF-0509	Subhyracodon	Oligocene	380	65	204.0983111	2.309839411	OC	1,2,3,4
Sundell	DF 3660	Archaeotherium	Oligocene	480	78	400.6914	2.602810021	OC	1,2,3,4,6
Tate	DF 1341	Archaeotherium	Oligocene	464	84	527.1004048	2.72189335	OC	1,2,3,4,6

TABLE 1— Table of analyzed taxa. OC = occipital condyle, SL = skull length. An entry of 0 indicates a parameter was not preserved on the specimen. Test number corresponds to the order described in the text.

CHAPTER III. BODY MASS INCREASE OF SMALL MAMMALS ACROSS THE EOCENE-OLIGOCENE BOUNDARY: POSSIBLE EFFECT OF CLIMATE CHANGE

Currently in review as:

Body mass increase of small mammals across the Eocene-Oligocene Boundary: Possible effect of climate change. Journal of Paleontology.

ABSTRACT

The link between the body mass of small mammals (< 1 kg) and global climate cooling at the Eocene-Oligocene Boundary was investigated. Body mass estimates were constructed using measurements collected from the first lower molar (m1) of multituberculates, insectivores, dermopterans, and rodents collected from Raben Ranch and Toadstool Park, Nebraska. The body mass estimates from the Eocene fauna were compared using one-way ANOVA to the Oligocene fauna to evaluate body mass change and to the modern tropical rodent fauna from Costa Rica to test the validity of Costa Rica as a modern analog. Estimated body masses were incredibly small, some approaching the smallest recorded masses for extant mammals: body mass of the Eocene fauna ranged from ~4.5 g to ~1,150 g, and body mass of the Oligocene fauna ranged from ~160 g to ~1,350 g. The body mass distribution of the Costa Rican rodents more closely matched the distribution of the Eocene than Oligocene. Body mass decrease is attributed to the decrease in forest canopy cover that occurred as global climate cooled. The loss of dense forest canopy for predation refuge and food source affected the small mammals adversely, driving them to increase body mass or extinction. Mammals during the Eocene achieved body masses much smaller than modern mammals living analogous lifestyles. These results confirm the hypothesis that

mammalian body mass is controlled by changes in the environment rather than metabolic requirements and contradict previous reports indicating that climate change had no effect on the Eocene mammal fauna.

INTRODUCTION

The purpose of this study is to test the following hypotheses concerning the relationship between body mass of small mammals (<1 kg) and the global cooling event at the Eocene-Oligocene Boundary (EOB): body mass (1) decreased, (2) increased (3) did not change. Mammal teeth of two local faunas collected from the Eocene and Oligocene of the White River Group in northwestern Nebraska (Fig. 9) were measured and used to create body mass estimates. The role of climate change in determining mammalian body mass is widely disputed. Mammalian body mass has been hypothesized to decrease as a consequence of catastrophic climate change during the Eocene-Oligocene Transition (EOT) as mammals adapted smaller body masses in response to diminished food resources. Schmerge et al. (in review) found that large-bodied fauna (> 1 kg) from the White River Formation of Wyoming decreased 28–41% in body mass during the EOT. Body mass has also been hypothesized to have an inverse relationship with climate change; Clyde and Gingerich (1998) and Gingerich (2003) demonstrated that the mammalian fauna of the Paleocene-Eocene Transition became smaller in response to dramatic global warming. Preliminary investigation of body mass change across the EOB by Prothero and Heaton (1996) concluded there was no body mass change attributed to climate change, based primarily on oreodonts. The results of the study presented herein will attempt to reconcile these controversial hypotheses.

Global climate changed dramatically during the EOT, becoming more similar to modern climatic conditions (Prothero, 1994), most notably the first formation of polar ice sheets in Antarctica (Zachos et al., 2001). Mean annual temperature in continental environments of North America dropped from ~21°C in the Eocene to ~13°C in the Oligocene (Zanazzi et al., 2007). North America was covered in dense tropical to subtropical rainforest during the Eocene (Retallack, 1983), and arboreal mammals at that time would have been able to occupy a wide variety of habitats within the forest canopy as occurs in modern rain forests (e.g., Malcom, 2004). Forest cover thinned at the beginning of the Oligocene as the climate cooled and dried dramatically (Evanoff et al., 1992; Wolfe, 1992). By the late Oligocene, savannah-like environments were prevalent in North America (Retallack, 1983). Rodents at this time began to diversify into burrowing niches (Janis et al., 2008).

The body mass of the mammals considered here are so small that they are referred to as microvertebrates (Ostrander, 1983, 1984). All but one taxon examined in this study have a body mass < 1 kg, and some have a body mass < 50 g. Multituberculates, insectivores, dermopterans (flying lemurs), and rodents comprise this incredibly diminutive mammal fauna. The body mass of small rodents has been understudied. Researchers have been interested in the upper body mass limit of rodents (e.g., Reynolds, 2002; Millien and Bovy, 2010), but the lower mass limit of extinct mammals has been of less interest (e.g., Bloch et al., 1998). Prothero and Heaton's (1996) study was based primarily on study of the large-bodied mammal fauna.

Body mass of extinct mammals is a quantity that is impossible to know directly but can be accurately estimated based on allometric scaling of skeletal elements (Damuth and MacFadden, 1990). Total body length and skull length (Van Valkenburgh, 1990), width of the occipital condyles (Martin, 1980), and femur head width (Martin, 1980) are elements that generally are associated with the greatest accuracy for body mass estimation (BME). These elements do not occur as abundantly as other skeletal elements in the fossil record, whereas teeth occur most abundantly. The reliability of teeth for BME is often disputed, but the first lower molar (m1) has been demonstrated to be a reliable tooth for the BME of rodents (r^2 = 0.89, Millien and Bovy, 2010) and insectivores (r^2 = 0.94, Gingerich and Smith, 1985). Individual teeth (Fig. 10) are incredibly abundant in the study area, which makes the production of body mass data sets reliably accurate using these fossils.

GEOLOGIC SETTINGS

The mammal teeth used in this study were collected from Raben Ranch and Toadstool Park, both located in northwestern Nebraska. Raben Ranch is located ~3.2 km (2 mi) southwest of Orella, Nebraska. Rocks of the Chadron Formation crop out in this area (Ostrander, 1983). The Chadron Formation of northwestern Nebraska was previously considered Oligocene and was subdivided into three members—A, B, and C (*sensu* Schultz and Stout, 1955) or lower, middle, and upper (*sensu* Vondra, 1960)—based primarily on event beds and paleosols. The Chadron Formation has since been determined to be Eocene and was revised to be compliant with international stratigraphic conventions (Terry Jr., 1998; Terry Jr. and LaGarry, 1998). The Chadron Formation now consists of a lower member and an upper member. The lower member, known as the Peanut Peak Member, is a smectite-rich mudstone, predominantly bluish green and gray colored with sparse pockets of red, green, or yellow mudstone. The Peanut Peak Member is also marked by a popcorn-weathered surface, weathers into hills, and in this area intertongues with the overlying member. The upper member is referred to as the Big Cottonwood Member and is composed of interbedded variegated siltstones and silty claystones and isolated channel sandstones. Badland erosion, abundant pedogenic modification, and five purplish white layers—bands of volcanic ash, gypsum, and limestone that are laterally extensive across the White River Group—characterize the Big Cottonwood Member. The fossils of the Raben Ranch area are found in the interbedded silty clays of this member (Ostrander, 1983). Raben Ranch is notable for being the site with the latest known occurrence of multituberculate mammals (Ostrander, 1984).

Mammal fossils described in this paper from Toadstool Park come from the Brule Formation. The Brule Formation is divided into three members (LaGarry, 1998). The Orella Member, the lowest member, is composed of interbedded beige, tan, and brown silty mudstones, siltstones, and sandstones. The contact between the base of the Orella Member and Chadron Formation is ~10 m above the youngest purplish white layer in the Chadron Formation. The Whitney Member, the middle member, contains pale brown volcaniclastic siltstone characterized by carbonate concretions and white to green fluvial siltstones, channel siltstones, and channel sandstones. The uppermost member is known as the Brown Siltstone Member and is characterized by weakly bedded and cross-bedded rocks of such nature. Both the Orella and Whitney Members are fossiliferous (Grandstaff and Terry Jr., 2009). The Brule Formation and the Chadron Formation form the White River Group, which crops out across much of the Midwest of North America.

Fossils from these localities are recovered primarily through the use of screen washing techniques. Specimens collected from the Raben Ranch locality (KU-NE-80) were bulk screened from larger samples that often contained larger vertebrate fossils (*sensu* Ostrander, 1983). The Toadstool Park locality (KU-Nebr-22) is an anthill locality; fossils are stratigraphically restricted and concentrated at the mound surfaces of ant nests, facilitating easy collection for fossil collectors. Ants collect the fossils from the surface, and then they shingle the top of the nest as a means to protect the nest from erosion. The Toadstool Park locality was collected from a single anthill collected consecutively over several years. The anthill is located in a restricted catchment, so that the fossils could only have come from a single level within the Orella Member. Ants are known not to exclude small particle sizes when excavating material (Halfen and Hasiotis, 2010), so there is no size bias introduced by using anthill sampling. Fossil material from these sites includes individual teeth and skull fragments containing one or more teeth. Teeth collected in this manner from Raben Ranch comprise a wide range of mammalian orders, including Multituberculata, Erinaceomorpha, Soricomorpha, Dermoptera, Chiroptera, Rodentia, and Artiodactyla. Toadstool Park yields rodent teeth.

METHODS AND MATERIALS

Data from previously measured mammals reported in Ostrander (1980, 1983, 1984, 1987) were used to construct the data set for the Eocene fauna. The Eocene fauna included 4 orders, 21 families, and 33 genera and consists primarily of arboreal taxa. The Oligocene data set was constructed with new measurements collected on fossil teeth housed in the collections of the University of Kansas Natural History Museum, Vertebrate Paleontology Section. The Oligocene fauna was composed entirely of rodents and included 4 families and 6 genera. The maximum transverse width and anterior to posterior to length of m1 was measured (Fig. 10). In some cases m1 and the second molar (m2) were difficult to distinguish. This occurred in cases where m1 and m2 are so close in morphology and size that they both yield approximately the same measurement. Substituting m2 in these cases, therefore, contributes no appreciable error to the BME. Teeth were measured to the nearest 0.1 mm under a Collins binocular microscope using a stage micrometer. Teeth were photographed using a Canon DS126181camera body mounted on a Seiler microscope. Data (Tables 2-4, Fig. 11) were graphically inspected to confirm the assumption of normality for the statistical methods.

The mean from each genus was calculated for both the Eocene and Oligocene faunas, and then body mass was calculated for each genus from the mean. Teeth data from rodents were converted to body mass estimates according to the regression equation of m1 length from Millien and Bovy (2010):

$$Y_1 = 10^{1.434+2.902*\log X_1}$$

where Y_1 is body mass in grams and X_1 is length of m1 in millimeters. Teeth data from insectivores were converted to body mass estimates according to the regression equation of m1 crown area (length x width) from Bloch et al. (1998):

$$Y_2 = e^{1.726+1.628*lnX_2}$$

where Y_2 is body mass in grams and X_2 is length x width of m1 in square millimeters. Body mass estimates where then log transformed (using base 10 logs for both estimation models) for statistical analysis. Log-transformed estimates were statistically compared, rather than the teeth measurements, as in Clyde and Gingerich (1998). This comparison is necessary because insectivorous mammals have lower body mass relative to their tooth size compared to other mammals (Gingerich and Smith, 1985). Log transformation further satisfies the normality assumption of the statistical tests (Sokal and Rohlf, 1995). One-way ANOVA was performed using Minitab 14 software. Type I error of $\alpha = 0.05$ was chosen as the determinant for statistical significance, as it is standard convention (Sokal and Rohlf, 1995) and has been established in this area of investigation (e.g., Clyde and Gingerich, 1998). Four ANOVA tests were performed to compare the Eocene and Oligocene faunas, the first on all mammals (ANOVA I) and the second on just the rodents (ANOVA II). Tests were also performed on the rodent families Eomyidae (ANOVA III) and Ischyromyidae (ANOVA IV), as representatives from each family spanning the EOB. Sample sizes, teeth measurements, and estimated body masses for each taxon are summarized in Table 4.

Some of the small mammals investigated do not have BME curves developed for their order. Multituberculates are extinct, so the reconstruction of a BME curve is impossible as we lack body mass data. Dermopterans are represented by two extant species (Feldhamer et al., 2007), and thus pose a similar problem. Grouping multituberculates and dermopterans with the insectivores should yield a reasonable BME because of their interpreted similar lifestyles (R. Timm, personal communication, 2010). ANOVA I was performed twice, however, using both estimation methods on the multituberculates and dermopterans; if the more conservative rodent estimation method (Millien and Bovy, 2010) yields significant results, then the accuracy of the other test would be irrelevant. Ostrander's (1980, 1983, 1984, 1987) data set included other small mammals, such as a single primate and several Chiropterans (i.e., bats). These were excluded from this study because of a lack of analogous organisms in the Oligocene and because of their overall differences in locomotion and dietary habits from rodents and insectivores.

Body mass estimates were further compared to modern rodent analogues from Costa Rica. Costa Rica serves as an excellent model for the Eocene environments represented by the White River Group because of overall climatic and ecologic similarity. Habitat preserves in Costa Rica have limited human activity and have enabled natural populations and conditions to persist (Timm et al., 2009). Costa Rica, therefore, is ideal for the study of body mass distributions, where anthropogenic influence on body mass, community structure, and natural habitat of the mammal populations are limited. Body mass ranges for the rodent fauna of the

Reserva Natural Absoluta Cabo Blanco (Timm et al., 2009) were collected from the literature (Table 5). Two additional ANOVA tests were performed on the Costa Rican fauna, comparing it to the Eocene Fauna (ANVOA V) and to the Oligocene Fauna (Oligocene VI).

RESULTS

The teeth measured from Toadstool Park are very small. The largest tooth belonged to the genus *Ischyromys*, measuring on average 3.84 mm long and 3.41 mm wide. The *Ischromys* tooth was the only tooth measured that exceeded 2.5 mm in length. Most teeth were < 2.5 mm long and 2 mm wide. The smallest teeth belonged to the genus *Adjidaumo*, which averaged ~1.3 mm along its length and width. The variation of the measurements was also small; in two cases the standard deviation was less than the precision of the measurements (0.1 mm) and the standard deviation was never more than three times the precision. Summary statistics for the teeth are presented in Table 3; raw data is included with the supplemental data.

Minimum BME from the Eocene was 4.47 g in the shrew-like genus *Oligoryctes*. Maximum BME from the Eocene was 1,152.17 g in the squirrel-like genus *Ischyromys*. Mean BME from the Eocene was 150.72 g. Minimum BME from the Oligocene was 56.73 g in the mouse-like genus *Adjidaumo*. Maximum BME from the Oligocene was 1,348.12 g in *Ischyromys*. Mean BME from the Oligocene was 456.69 g. Mean body mass, therefore, increased ~200% from the Eocene to Oligocene (Table 4). Body mass data from both faunas is plotted in Figure 11.

ANOVA shows that estimated body mass overall increased from the Eocene to the Oligocene. The test on the entirety of both faunas (ANOVA I) showed significant change, regardless of how the body mass of the multituberculates and dermopterans were calculated (p =

0.013 according to Gingerich and Smith, 1985; p = 0.021 according to Millien and Bovy, 2010). The test on the rodents (ANOVA II) showed no significant change (p = 0.064), but this result approaches statistical significance. The test on the Eomyidae (ANOVA III) showed no significant change (p = 0.694). The test on the Ischyromyidae (ANOVA IV) also showed no significant change (p = 0.549).

The body mass data of extant rodents from Costa Rica (Table 5) appears similar to the late Eocene rodent fauna. Cricetid (mouse-like) rodents are the smallest, and show a similar range of body masses that were found in the Eocene sample but not the Oligocene sample. Sciurid (squirrel-like) rodents demonstrate much larger body masses, similar to what was observed in the Eocene and smaller than what was observed in the early Oligocene. ANOVA demonstrates that there is no statistical difference between the body mass distributions of the Eocene fauna and Costa Rican fauna (ANOVA V; p = 0.604). Comparison to the Oligocene rodent fauna (ANOVA VI) also demonstrated no significant differences (p = 0.091), but the difference approaches statistical significance. The Costa Rica body mass distribution, therefore, more closely resembles the mass distribution found in the Eocene.

DISCUSSION

There was a clear overall body mass increase observed across the EOB. ANOVA I demonstrates a clear overall change in the entire fauna and supports the hypothesis that body mass increases as climate cools. ANOVA II–IV, on the other hand, showed no significant change and lend support to the hypothesis that body mass is independent of climate. The lack of statistical significance observed in ANOVA II may be due to the presence of rodent groups that did not undergo significant mass change (as was observed for the Eomyidae and Ischyromyidae) masking body mass change for other groups. Body mass for small mammals in the Eocene had a greater range than for small mammals in the Oligocene. The Eocene body mass range overlapped most of the Oligocene range, but also included much smaller body masses (Fig. 12). The smallest estimate of 4.5 g is two orders of magnitude smaller than most of the estimates produced for the Oligocene. The difference between the maximum observed body mass of the Eocene and Oligocene was not statistically significant (ANOVA IV), but the lower body mass limit of mammals was clearly much lower in the Eocene than in the Oligocene. The local extinction of the insectivores, which all had body mass less than that of the entire Oligocene fauna except *Adjidaumo*, clearly indicate that their particular lifestyle was not adaptive in the Oligocene environment. Though some rodent taxa do not change much across the EOB, the overall change in the microfauna supports the hypothesis that body mass increases in response to global cooling.

Climate change and the resulting environmental change during the EOT clearly had a dramatic effect on the observed body mass range of the small mammal fauna. The similarity of the rodent fauna of the Eocene to the Costa Rican fauna (ANOVA V) suggests that small body mass is related to the presence of forest canopy, which correlates with warm and wet climate. Small forest mammals depend on dense tree cover as a means of predation defense; small individuals are able to escape from predators by climbing out onto smaller branches, and they can leap to closer trees (Malcom, 2004). Arboreal mammals rely on the forest canopy as a food source for more than fruit; arboreal rodents consume fruits, nuts, seeds, and other plant material (Nowak, 1991). Insect abundance and diversity around the globe declined sharply during the EOT from a tropical fauna consisting of numerous plant feeders and pollinators in the Eocene to a fauna more similar to the modern, with tropical insects restricted to equatorial regions (Grimaldi and Engel, 2005). Insectivorous mammals would have been devastated by a reduction and change in composition of the insect fauna. The decline of insect diversity as a consequence of climate change, therefore, may account for the loss of insectivoran families across the EOB.

Rodent body mass in the Oligocene is consistent with the body mass of extant fossorial rodents of open, dry environments. For example, African ground squirrels (genus *Xerus*) range in body mass from 300–945 g (Nowak, 1991), a range slightly smaller than observed in the non-Eomyid portion of the Oligocene sample. Eomyids are considered arboreal to ground dwelling based on their squirrel-like skeletons (Flynn, 2008), therefore, the Oligocene rodents were likely not obligatorily arboreal and spent significant portions of their time on the ground and in burrows despite the somewhat smaller estimated body mass of Eomyids. Comparison to modern rodents of similar sizes suggests that Eomyids foraged for seeds, nuts, and occasionally fruit, like modern ground squirrels and mice. The presence of Cricetid rodents in the Oligocene, which are primarily granivorous and whose modern examples include rats and mice, underscores this observation.

Environmental changes that occurred during the EOT can be considered responsible for the loss of the Eocene small mammal fauna. A decrease of forest canopy resulted in a loss of usable habitat for the arboreal mammals of the Eocene. The loss of fine branches in dense forest canopy would have limited the ability of small mammals to escape from predators, and the increased distance between trees would have restricted their habitat to the point of extinction. The presence of *Thylacaelurus* (Order Dermoptera) and the Family Eomyidae (Order Rodentia) indicate that some members of the fauna relied upon dense forest cover entirely for their lifestyle. Any Dermopteran would require substantial forest canopy in order to successfully glide from one tree to another, and modern members of the order are completely helpless on the ground (Nowak, 1991). Some Eomyids from Europe have been described as gliders (Storch et al., 1996). Although there is no reason to suspect that any of the Eomyids in the present study were gliders, the Eomyids described here were likely leaping from branch to branch as means of locomotion (obligatory arboreality). The body mass of some of the largest rodents from the Eocene sample is consistent with the body mass of modern squirrels, which is no coincidence as these taxa (*Leptotomus* and *Centimanomys*) are squirrel-like. The largest members of the Eocene rodent fauna, therefore, may have had a lifestyle similar to that of modern arboreal squirrels. One hypothesis for the extinction of Multituberculates, including the genus *Ectypodus*, at the end of the Eocene is the vegetation change from forest to savannah ecosystems (Ostrander, 1984). The loss of other incredibly small, obligatorily arboreal mammals from the study area at the end of the Eocene reinforces that conclusion.

Climatic cooling itself would have caused another fatal change to the Eocene fauna. Fruit likely would no longer have been available year round as the climate cooled and became more seasonal. Fruit productivity and fleshiness, as well as overall tree biomass in tropical dry forests depends on high environmental moisture (Lieberman, 1982). The loss of this food supply would surely have been an irrecoverable blow; limited availability of fruit as a consequence of seasonal variability is reported to cause diet shifting and emigration in extant mammalian taxa (Leighton and Leighton, 1983). The Eocene mammalian fauna is reported to have persisted for the most part without change into the Oligocene, and those taxa that did go extinct did so before the environment transitioned (Prothero and Heaton, 1996). If this tiny fauna was dependent on fruit, however, they would have gone extinct or been forced out of the region well before the forest canopy thinned and a steppe environment set in. The loss of the seed-consuming fauna would have further caused environmental turnover by limiting seed dispersal (Howe and Miriti, 2004), thereby slowly thinning the forest canopy through time.

The body mass change of the mammals across the EOB is similar to the Island Effect (Van Valen, 1973), where large mammals dwarf (Raia and Meiri, 2006) and small mammals become larger (Adler and Levins, 1994) in response to diminished resources. Schmerge et al. (in review) demonstrated that large mammals (> 1 kg) overall decreased in size across the EOB. Large herbivores tended to undergo the most body mass change. The mass change in small mammals considered alone might appear consistent with temperature-related controls (i.e., metabolic effects), but when considered in relation to the simultaneous body mass decrease of larger mammalian fauna, loss of food and habitat resources are the greater limiting factor for determining mammalian body mass.

The smallest mammals reported here from the Eocene number among the smallest known mammal taxa. The smallest extant mammal is the bumblebee bat (*Craseonycteris thonglongyai*), massing ~2 g (Nowak, 1991). Bloch et al. (1998) described what is currently known as the smallest extinct mammal, a geolabid insectivore (*Batodonoides vanhoutei*) from the Eocene that masses ~1.3 g. The geolabids from the Eocene described here were also small, ~20.3 g, and the smallest mammal in this study is another insectivore genus (*Oligoryctes*) that massed ~4.5 g. The smallest modern insectivores are pygmy shrews (*Suncus etruscus*), which mass ~2.5 g (Nowak 1991), but they are fossorial rather than arboreal.

There are several contributing factors to these incredibly small body masses. Small-bodied fossorial and semifossorial mammals (<60 g) have high metabolic rates relative to their body mass, which is linked both to their dietary requirements and thermal requirements imposed by their burrowing lifestyle (e.g., prevention of overheating; McNab, 1979). Semifossorial insectivores, namely shrews, rely on subsurface digging and foraging (Dickman, 1988) to uncover the large amount of invertebrates required to sustain their incredibly high metabolisms

(McNab, 1980). Shrews also require high levels of moisture to survive (Chew, 1951; McCay and Storm, 1997), a factor best exploited in below ground or rain forest environments. A fossorial lifestyle also protects them from most predators.

Ischyromys, one of the few generic taxa present in both the Eocene and Oligocene faunas, happens to be the largest taxa from both samples. There is no statistical difference between the body mass distributions of *Ischyromys* from the Eocene and Oligocene (ANOVA TEST IV). Members of the family Ischyromyidae are variously hypothesized to be semifossorial or burrowing animals (Anderson, 2008). The fact that they were large and that their body masses did not change from the Eocene to the Oligocene comes as no surprise, as they likely relied very little on the forest canopy for their lifestyle. The lack of body mass change in the Ischyromyidae from the Eocene to the Oligocene could, therefore, be accurately described as preadaptation for the more open environments of the Oligocene.

CONCLUSIONS

Body mass of small mammals increased from the Eocene to the Oligocene. These results contradict previous studies that concluded mammalian body mass did not respond positively to global cooling (Prothero and Heaton, 1996; Schmerge et al., in review), and suggests that the body mass of small mammals is more closely controlled by the extent of forest canopy than larger mammals. This conclusion makes intuitive sense, as small mammals, especially those in densely forested areas, spend the majority or all of their lives in trees, whereas most large mammals (> 1 kg) spend little or no time in the canopy itself. Loss of forest canopy, therefore, means not only a loss of food source but is also a loss of habitat.

Temperature changes do affect the survivability of mammals by affecting their metabolism; ultimately the overriding control on mammalian body size is their environment. The lack of statistically significant change in the largest rodents considered here, which were almost certainly nonarboreal, indicates temperature change alone does not dramatically affect the body mass of mammals. The loss of forest habitat for arboreal mammals, on the other hand, had a much stronger effect on body mass, eliminating an entire size range from the observed body mass distribution. While a metabolic effect on body mass is impossible to rule out from this study, we conclude that mammalian body mass responds more strongly to environmental change influenced by climate than simply to temperature change alone.

Schmerge et al. (in review) concluded that body mass in large mammals (> 1 kg) decreased across the EOB, because they evolved more conservative body mass in response to diminishing food resources. Body mass increased for small mammals, but they likely did so in response to similar controls, similar to the Island Effect phenomenon. Insectivorous mammals thrive in tropical environments with dense insect populations; the advent of more open and more arid environments would have severely impacted such a lifestyle, resulting in local extinction for those lineages. Rodents were also affected by the change of food resources; forms that might have fed on fruits and flowers gave way to granivirous rodents as climate became more seasonal and fruit became less common.

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FIGURES

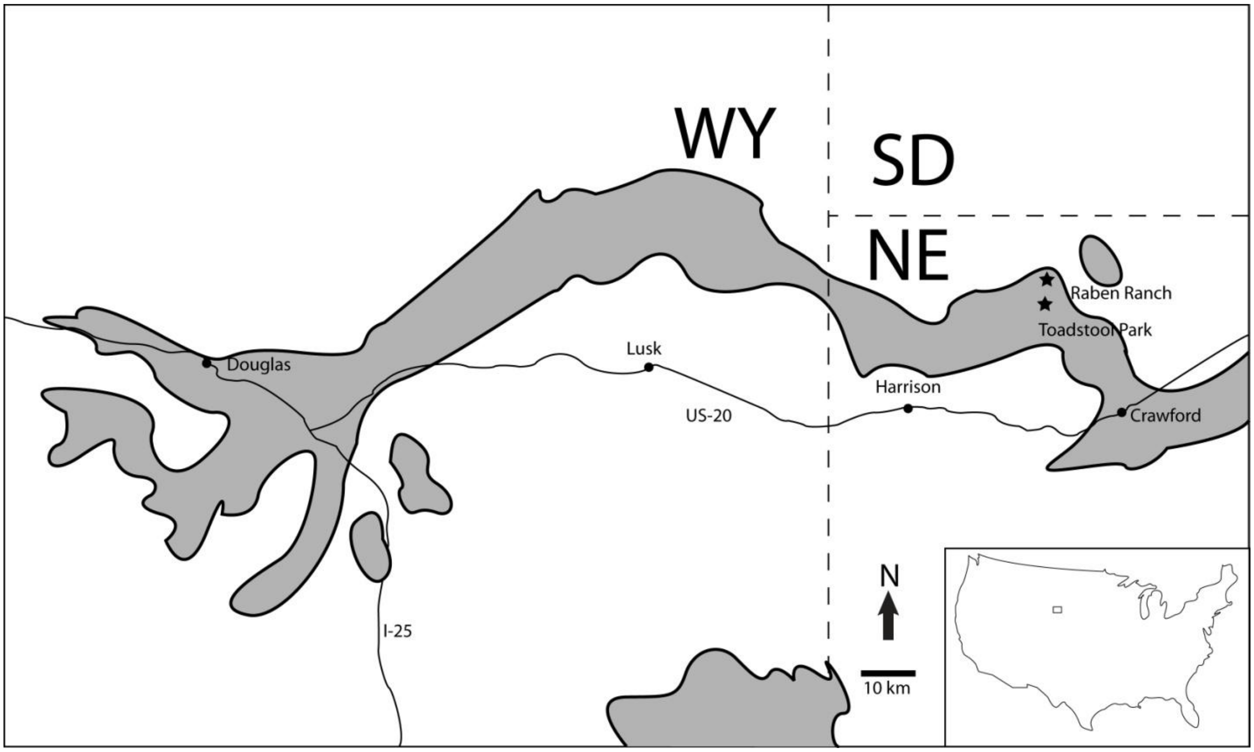

FIGURE 9—White River Group map showing the extent of outcrops in Wyoming and Northeastern Nebraska. Locations of Raben Ranch and Toadstool Park are also shown. Modified from Evanoff et al. (1992).

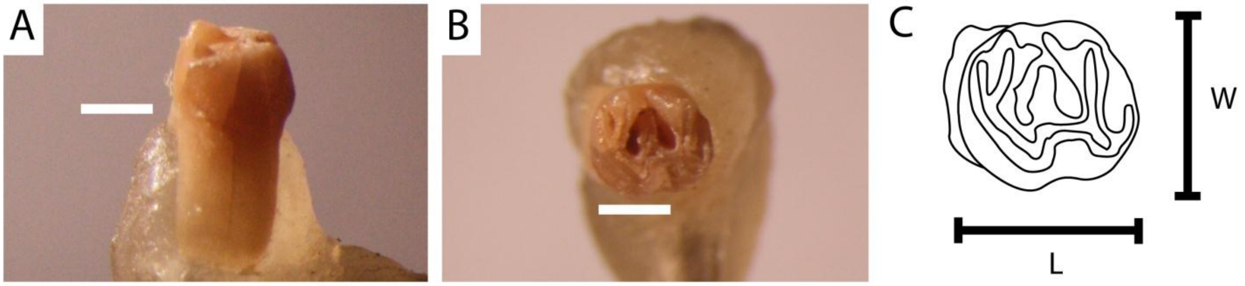

FIGURE 10—Side (A) and occlusal (B) views of KUVP 92778. Tooth is an m1 from the genus *Protadjidaumo*. Scale bar is 1 mm. (C) is a schematic of the occlusal view showing the measured elements of m1 in this study. Length is the greatest anterior to posterior length across the occlusal surface. Width is the greatest transverse width across the occlusal surface.

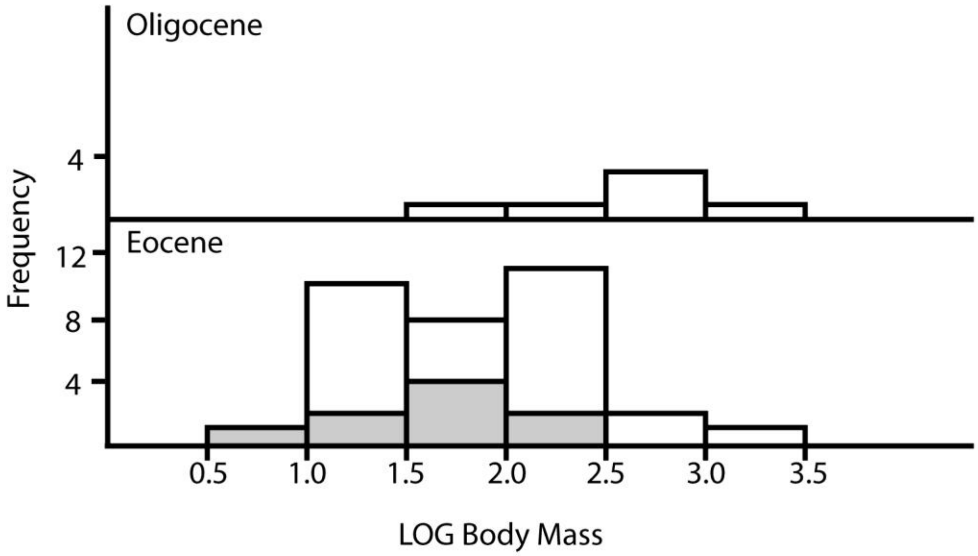

FIGURE 11—Frequency plot of body mass estimates for the Eocene and Oligocene faunas. Shaded bars indicate mass estimates produced using the insectivore estimation equation.

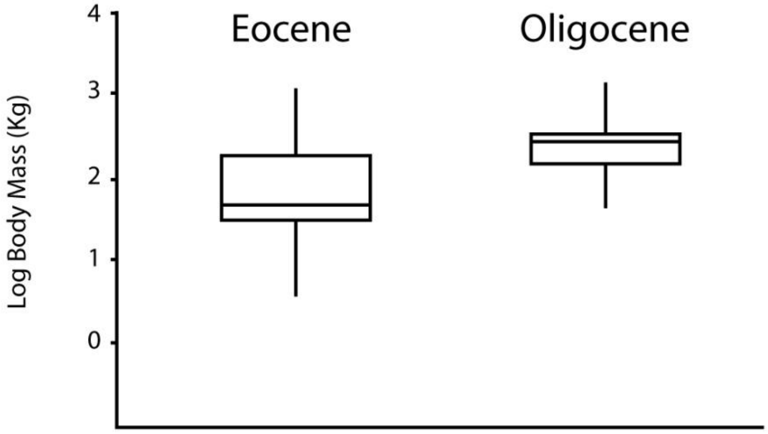

FIGURE 12—Box and whisker plot comparing log-transformed body mass of the Eocene fauna to the Oligocene fauna. Maximum body mass changes very little, but minimum body increases dramatically in the Oligocene.

TABLES

Name	ID	Length	Width	Body Mass
Adjidaumo	92777	1.4	1.3	72.12130219
Adjidaumo	92779	1.4	1.8	72.12130219
Adjidaumo	92783	1.3	1.2	58.16525125
Adjidaumo	92784	1.2	1.2	46.1088166
Adjidaumo	92785	1.2	1.3	46.1088166
Adjidaumo	92787	1.3	1.4	58.16525125
Adjidaumo	92788	1.3	1.2	58.16525125
Adjidaumo	92790	1.3	1.3	58.16525125
Adjidaumo	92791	1.2	1.3	46.1088166
Eumys	93238	2.7	1.5	485.0847746
Eumys	93239	2.7	1.8	485.0847746
Eumys	93240	2.3	1.6	304.6030027
Eumys	93241	2.2	1.6	267.7383729
Eumys	93242	2.3	1.4	304.6030027
Eumys	93243	2.8	1.8	539.0792394
Eumys	93244	2.7	1.9	485.0847746
Eumys	93246	2.8	2	539.0792394
Eumys	93247	2.3	1.5	304.6030027
Eumys	93248	2.3	1.5	304.6030027
Eumys	93211	3	2.1	658.5759715
Eumys	93212	2.9	1.9	596.8689542
Eumys	93213	3	2.2	658.5759715
Eumys	93214	2.9	2.1	596.8689542
Eumys	93215	2.9	1.9	596.8689542
Eumys	93216	2.9	2.1	596.8689542
Eumys	93217	2.8	1.9	539.0792394
Eumys	93218	3	2.2	658.5759715
Eumys	93219	2.8	2	539.0792394
Eumys	93220	2.9	2	596.8689542
Ischyromys	92342	3.4	3	947.0040084
Ischyromys	92343	3.7	3.4	1210.379065
Ischyromys	92345	3.7	3.2	1210.379065
Ischyromys	92346	3.8	3.3	1307.771888
Ischyromys	92348	4.2	3.6	1748.515316
Ischyromys	92349	4.1	3.5	1630.417215
Ischyromys	92350	4.2	3.7	1748.515316
Ischyromys	92351	4.1	3.8	1630.417215

Ischyromys	92353	3.6	3.3	1117.866283
Ischyromys	92354	3.6	3.3	1117.866283
Prosciurinae	68357	2.6	2.1	434.763079
Prosciurinae	68358	2.3	2	304.6030027
Prosciurinae	68356	2.5	1.9	387.9912265
Prosciurinae	68368	2.7	2.3	485.0847746
Prosciurinae	68347	2	1.7	203.0434796
Prosciurinae	68360	2.1	1.7	233.9270227
Prosciurinae	68318	2	1.8	203.0434796
Prosciurinae	68339	2	1.8	203.0434796
Prosciurinae	68319	2.4	1.8	344.6458263
Prosciurinae	68354	2.7	2.1	485.0847746
Protadjidaumo	92778	1.7	1.8	126.6959609
Protadjidaumo	92780	1.7	1.6	126.6959609
Protadjidaumo	92781	1.7	1.6	126.6959609
Protadjidaumo	92782	1.9	1.7	174.9616839
Protadjidaumo	92786	1.6	1.6	106.2566671
Protadjidaumo	92789	1.7	1.7	126.6959609
Protadjidaumo	92792	1.9	1.6	174.9616839
Wilsoneumys	93286	2.4	1.3	344.6458263
Wilsoneumys	93287	2.4	1.7	344.6458263
Wilsoneumys	93288	2.3	1.5	304.6030027
Wilsoneumys	93289	2.4	1.6	344.6458263
Wilsoneumys	93290	2.3	1.7	304.6030027
Wilsoneumys	93291	2.7	1.9	485.0847746
Wilsoneumys	93292	2.4	1.8	344.6458263
Wilsoneumys	93293	2.7	1.9	485.0847746
Wilsoneumys	93294	2.6	1.9	434.763079
Wilsoneumys	93295	2.9	1.5	596.8689542

TABLE 2—Estimated body masses of individual rodents from the Oligocene fauna. Length and width dimensions measured in millimeters. Masses are measured in grams.

Length Summary Statistics	N	$\bar{x}$	s	Minimum	Q1	Median	Q3	Maximum
Wilsoneumys	10	2.51	0.20248457	2.3	2.4	2.4	2.675	2.9
Eumys	20	2.71	0.2712544	2.2	2.6	2.8	2.9	3
Ischyromys	10	3.84	0.28751812	3.4	3.625	3.75	4.1	4.2
Adjidaumo	9	1.288889	0.0781736	1.2	1.2	1.3	1.3	1.4
Protadjidaumo	7	1.742857	0.11338934	1.6	1.7	1.7	1.8	1.9
Sciurinae gen. et. Spec. indet.	10	2.33	0.29078438	2	2.025	2.35	2.575	2.7

Width Summary Statistics	N	$\bar{x}$	s	Minimum	Q1	Median	Q3	Maximum
Wilsoneumys	10	1.68	0.20439613	1.3	1.525	1.7	1.875	1.9
Eumys	20	1.85	0.25235731	1.4	1.6	1.9	2.025	2.2
Ischyromys	10	3.41	0.24244129	3	3.3	3.35	3.575	3.8
Adjidaumo	9	1.333333	0.18708287	1.2	1.2	1.3	1.3	1.8
Protadjidaumo	7	1.657143	0.07867958	1.6	1.6	1.6	1.7	1.8
Sciurinae gen. et. Spec. indet.	10	1.92	0.19888579	1.7	1.8	1.85	2.075	2.3

TABLE 3—Summary statistics of the length and width measurements collected from the teeth from Toadstool Park. Tooth dimensions are in millimeters.

Epoch	Order	Family	Genus	N	Length x̄	Width x̄	Body Mass	Log Body Mass
Eocene	Multituberculata	Neoplagiaulacidae	Ectypodus	4	1.79	1.025	15.09021624	1.178695463
							147.1565156	2.167779496
Eocene	Insectivora	Lepticitidae	Leptictis	3	3.01	2.33	133.8917969	2.12675397
Eocene	Insectivora	Geolabidae	Centetodon	30	1.82	1.21	20.31248597	1.307763078
Eocene	Insectivora	Adapisoricidae	Ankylodon	1	1.94	1.67	38.08166314	1.580715907
Eocene	Insectivora	Soricidae	Domnina	1	2.03	1.48	33.6807612	1.527381898
Eocene	Insectivora	Talpidae	Oligoscalops	1	1.66	1.69	30.12505151	1.478927798
Eocene	Insectivora	Apternodontidae	Apternodus	4	2.055	1.96	54.28037171	1.734642813
Eocene	Insectivora	Apternodontidae	Oligoryctes	2	1.005	0.865	4.472814089	0.650580847
Eocene	Insectivora	Micropternodontidae	Micropternodus	22	2.194545455	1.947272727	59.77066022	1.776488053
Eocene	Insectivora	Apatemyidae	Sinclairella	3	3.256666667	2.16	134.5482116	2.12887793
Eocene	Dermoptera	Plagiomenidae	Thylacaelurus	1	2.08	1.72	44.75480783	1.650839697
							227.5201147	2.357019798
Eocene	Rodentia	Ischyromyidae	Leptotomus	3	2.91	2.94	602.8613671	2.780217454
Eocene	Rodentia	Ischyromyidae	Ischyromys	13	3.637692308	3.498461538	1152.171003	3.061516941
Eocene	Rodentia	Aplodontidae	Prosciuris	31	1.99	2.01	200.1113066	2.301271628
Eocene	Rodentia	Prosciurinae	Gen. et sp. indet.	1	2.3	2.03	304.6030027	2.48373418
Eocene	Rodentia	Cylindrodontidae	Cylindrodon	7	2.137142857	2.265714286	246.1370393	2.391176972
Eocene	Rodentia	Cylindrodontidae	Pseudocylindrodon	29	2.057241379	2.187586207	220.3706734	2.343153799
Eocene	Rodentia	Cylindrodontidae	Jaywilsonomys	2	2.065	2.205	222.7911845	2.347898002
Eocene	Rodentia	Eomyidae	Aulolithomys	63	1.75	1.71	137.8149771	2.139296417
Eocene	Rodentia	Eomyidae	Centimanomys	7	2.73	2.61	500.8918919	2.699744002
Eocene	Rodentia	Eomyidae	Namatomys	26	1.06	1.04	32.16900447	1.507437621
Eocene	Rodentia	Eomyidae	Yoderimys	25	2.07	1.88	224.3602641	2.350945943
Eocene	Rodentia	Eomyidae	Adjidaumo	250	1.04484	1.01272	30.85194099	1.489282492
Eocene	Rodentia	Eomyidae	Cupressimus	32	0.980625	0.9415625	25.66501915	1.409341593
Eocene	Rodentia	Eomyidae	Paradjidaumo	330	1.361757576	1.385545455	66.55146494	1.82315762
Eocene	Rodentia	Eomyidae	Protadjidaumo	34	1	1.02	27.16439269	1.434
Eocene	Rodentia	Eomyidae	Gen. et sp. indet.	2	0.885	0.92	19.0558959	1.280029372

Eocene	Rodentia	Heteromyidae	Heliscomys	78	0.83	0.85	15.81847542	1.199164624
Eocene	Rodentia	Meliakrouniomys	Meliakrouniomys	1	0.92	0.79	21.32614094	1.328912275
Eocene	Rodentia	Castoridae	Pipestoneomys	56	1.709642857	1.566785714	128.7927628	2.10989146
Eocene	Rodentia	Eutypomyidae	Eutypomys	1	1.78	1.91	144.7834252	2.160718847
Eocene	Rodentia	Zapodidae	Simimys	4	1.245	0.9725	51.30757136	1.710181458
Eocene	Rodentia	Incertae sedis	Idiogenomys	2	1.025	0.905	29.18237657	1.465120657
Oligocene	Rodentia	Cricetidae	Wilsoneumys	10	2.51	1.68	392.5121817	2.59385314
Oligocene	Rodentia	Cricetidae	Eumys	20	2.71	1.85	490.3169221	2.690476882
Oligocene	Rodentia	Ischyromyidae	Ischyromys	10	3.84	3.41	1348.122053	3.129729213
Oligocene	Rodentia	Eomyidae	Adjidaumo	9	1.288888889	1.333333333	56.73425056	1.753845322
Oligocene	Rodentia	Eomyidae	Protadjidaumo	7	1.742857143	1.657142857	136.1889014	2.134141716
Oligocene	Rodentia	Prosciurinae	Gen. et sp. indet.	10	2.33	1.92	316.2764699	2.500066883

TABLE 4—Estimated body masses of the small-bodied mammal fauna from the Eocene and Oligocene. Estimates of body mass for *Ectypodus* and *Thylacaelurus* were made using both the insectivore (upper) and rodent (lower) body mass estimation methods. Length and width dimensions measured in millimeters. Masses are measured in grams. Taxonomy of insectivorous mammals from Ostrander (1980, 1987) updated according to Janis et al. 2008.

Family	**Genus & Species**	**Minimum**	**Median**	**Maximum**	**LOG Median**
Cricetidae	Oligoryzomys fulvescens	11	13.5	16	1.130333768
Heteromyidae	Liomys salvini	30	47.5	65	1.67669361
Cricetidae	Oryzomys couesi	43	62.5	82	1.795880017
Cricetidae	Sigmodon hirsutus	38	62.5	87	1.795880017
Sciuridae	Sciuris variogatoides	447	678	909	2.831229694

TABLE 5—Summary of body masses of small-bodied rodents (<1 kg) from the Reserva Natural Absoluta Cabo Blanco, Costa Rica. Masses are measured in grams. Body masses according to Reid (1997). Faunal list according to Timm et al. (2009).

CHAPTER IV. CONCLUSIONS

This study was designed to test three hypotheses for the relationship of mammalian body mass to the climate change that occurred across the Eocene-Oligocene Boundary (EOB), that in response to global cooling body mass either (1) increased, (2) decreased, or (3) did not change. While oreodonts and carnivores showed no body mass change that occurred across the EOB (chapter II), seemingly in support of hypothesis 3 (i.e., Prothero and Heaton, 1996), ungulates (chapter II) showed a decrease in body mass and arboreal rodents (chapter III) showed an increase in mass. Rather than wholesale support of one of the three hypotheses, this thesis demonstrated that the range of mammalian body mass contracted across the EOB. The maximum limit of mammalian body mass decreased from the Eocene into the Oligocene, accommodated by extinction of the largest fauna and evolution of smaller body mass by surviving taxa, and the minimum limit of body mass increased, as the smallest taxa went extinct.

How can these results be reconciled in terms of existing hypotheses? Allen’s Rule and Bergmann’s Rule both posit a monodirectional change in body mass as a result of climate change. If these rules are strictly valid, we must reject one study in favor of the other. Allen’s rule likewise cannot explain a decrease in body mass, as lineages should continue to increase in size through time. Smith et al. (2010) found that maximum body size of mammals increased rapidly early in the Cenozoic, after which maximum potential mass stabilized ~40 Ma ago. This conclusion appears consistent with Allen’s Rule, but only when considering the maximum body size attainable by each taxonomic order. Some caution should be further taken when invoking Allen’s rule as an explanation for body mass increase during a mass extinction event. None of these rules can satisfactorily explain the body mass change across the EOB, and rather than seeking an explanation for body mass changes that depends on temperature, mammalian body mass, instead, appears to be a function of environmental parameters.

Isolation on islands has been recognized as a factor responsible for a wide variety of body mass change in mammals, as was observed in this study. Large mammals on islands tend to dwarf, sometimes dramatically as has been observed in elephants and hippopotamuses (e.g., Raia and Meiri, 2006), whereas small mammals tend towards giant forms (e.g., Heaney, 1978; Adler and Levins, 1994). This phenomenon is referred to as the Island Effect Hypothesis (Van Valen, 1973), and has been recognized for island faunas across the globe (e.g., van der Geer et al., 2010). The Island Effect Hypothesis postulates that mammalian body mass depends more strongly on such environmental parameters as habitat area and vegetation quality rather than on temperature itself, which certainly is a prediction demonstrated by the data presented in this study. This hypothesis is more appealing than any of the previously mentioned rules because it can accommodate the bidirectionality of body mass change; if Bergmann’s Rule, for example, were true, we would expect only to see increase in body mass, not the decrease observed in many ungulate groups in chapter II. The Island Effect hypothesis is also intuitively satisfying, as it explains the wide variability of body mammalian body mass within a single environment more satisfactorily than a rule like Bergmann’s rule.

The Island Effect hypothesis further explains the lack of observed body mass change in the carnivores demonstrated in chapter II. Just as there was no body mass change observed across the EOB, island carnivores demonstrate little if any body mass difference from their mainland relatives. Of the very few carnivores able to disperse to islands successfully, few undergo body mass reduction, and those that do only undergo moderate mass reduction (van der Geer et al., 2010). The pressures of carnivory are so high, that body size is too difficult to modify to accommodate the smaller size of prey available on islands. This finding is consistent with the conclusion of the study in chapter II: prey-switching was more adaptive for carnivorous mammals of the Oligocene than to decrease in body mass along with their prey from the Eocene, because the body mass of carnivores is optimized to the size of its prey and not the environment itself.

Heaney (1978) established that body mass of island mammals is a function of five factors: island area, food availability, predation, interspecific competition, and physiological efficiency. The findings of this study parallel this conclusion. As climate cooling during the Eocene-Oligocene Transition, habitat and food resources that were heavily exploited by mammals were decimated as climate became seasonal and the environment opened up. This environmental turnover is comparable to the limitation of island area (i.e., habitat) and limitation of food resources in islands. While Heaney (1978) also concluded that body mass does not change strictly in a linear fashion as island area increases, there is still significant linkage between food availability, habitat area, and predation avoidance in environments with large area. The application of the Island Effect Hypothesis can be very well applied to the study of continental mammals, and it may be more appropriately referred to as the Environmental Effect Hypothesis.

Continued study of mammalian body mass change is warranted. This study was concerned with change across the EOB only. Further investigation of the development of the size of the Oligocene fauna into the late Oligocene will demonstrate the validity of the Island Effect Hypothesis over long time scales (>10 million years), or if such a rule as Allen’s rule is preferable for explaining long-term changes in mass (i.e., Alroy, 1998; Smith et al., 2010). Time series analysis should be considered a useful method for studying the change in mass within the

Oligocene. The study of the Island Effect Hypothesis to explain body mass change should be investigated for the Paleocene Eocene Thermal Maximum, which is to date the best studied time with respect to changing mammalian body mass (i.e., Clyde and Gingerich, 1998; Gingerich, 2003). The megafauna of the Pleistocene and the fauna of the Miocene, during which tremendous environmental and vegetation change occurred, should also be evaluated in terms of the Island Effect Hypothesis.

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