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Ecometric Estimation of Present and Past Climate of North America Using Crown Heights of Rodents and Lagomorphs: With Application to the Middle Miocene Climatic Optimum

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Ecometric Estimation of Present and Past Climate of North America Using Crown Heights of Rodents and Lagomorphs: With Application to the Middle Miocene Climatic Optimum

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by

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ABSTRACT

Ecometric Estimation of Present and Past Climate of North America Using Crown Heights of Rodents and Lagomorphs: With Application to the Middle Miocene Climatic Optimum

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Continental scale studies on ungulate crown heights in relation to climate and habitat changes have revealed a correlation between increasing hypsodonty and a shift to more arid environments. Small mammals have been shown to adapt to changing habitats millions of years earlier than larger mammals. In this study I examined fossil localities throughout the last 37 Ma across North America. Diversity of rodents and lagomorphs were analyzed through this time period, with examination of community structure characterized by relative percentages of taxa with different crown heights. Overall, a decrease in precipitation and temperature was found across North America from 37 Ma to the present. The Mid Miocene Climatic Optimum (around 15 Ma) was an pronounced period of warming, comparable to the warming we see today. Nebraska and California showed increases in crown height before Oregon. Overall, these findings help demonstrate how communities react at different time scales to climate change.

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CHAPTER 1

INTRODUCTION

Climate Through Paleontology

Due to ongoing changes in climate, entire ecosystems may be altered beyond repair with a loss of biological diversity. Geological, paleontological, and evolutionary perspectives need to be incorporated into climate and biological studies (Eronen et al. 2010a), allowing for a more complete understanding of the past. Paleontology can play a unique role in studies of climate change, by tracing deep time climate fluctuations and directly examining the response of organisms to those changes (Janis 1988; Damuth et al. 2002; Badgley 2010; Eronen et al. 2010c; Badgley and Finarelli 2013, Eronen et al. 2015; Ceradini and Chalfoun 2017; Samuels and Hopkins 2017). Throughout history, there have been many fluctuations and natural variations in climate observed (Zachos et al. 2001, 2008; Lyle et al. 2008). However, climate data alone does not provide complete picture of past environments or localized changes in climate and habitat; the flora and fauna that interacted with the abiotic environment must also be studied (Bailey and Sinnott 1915; Wolfe 1979; Box 1996; Weiher et al. 1996; Uhl and Mosbrugger 1999; Damuth et al. 2002; Fortelius et al. 2002; Janis et al. 2004; Stromberg 2004, 2005; Greenwood 2005; Royer 2005; Eronen et al. 2010a,b,c; Polly et al. 2011; Fortelius et al. 2014). Climate impacts entire biomes, and by examining climate over thousands and millions of years community changes and individual species' changes can be better observed.

Ecometrics

Ecometrics is a method of studying traits that are functionally related to an organism's biological or physical environment that allows for taxon-free trait analysis, which can be applied to multiple species in a community and studied across time and space (Eronen et al. 2010a; Polly et al. 2011; Andrews and Hixon 2014; Vermillion et al. 2018). Organisms directly interact with their environment and show measurable anatomical adaptations that allow them to best function in their ecosystem, such as leaf shape, locomotor changes, body mass, and dental adaptations (Box 1996; Royer et al. 2005; McGill et al. 2006; Eronen et al. 2010a; Polly et al. 2011; Fortelius et al. 2014). Cross-scale measurements from individual level up to community level are possible, as well as comparisons between sites with varying taxa that possess similar traits, allowing observation of how traits change throughout an entire community through time (Eronen et al. 2010a; Polly et al. 2011).

An ecometric approach to studying climate change is relatively new, but many studies have already appeared using this approach (Eronen et al. 2010a,b; Polly et al. 2011; Fortelius et al. 2014; Maguire 2015). However, most of these studies focus on larger mammals, such as ungulates, examining ungulate crown heights in relation to climate. These studies found a correlation between an increase in hypsodonty and a shift to arid environments over time (Damuth et al. 2002; Fortelius et al. 2002; Eronen et al. 2010b, c; Eronen et al. 2012; Jardine et al. 2012; Fortelius et al. 2014; Maguire 2015; Semprebon et al. 2019). Fewer studies have analyzed small mammals' anatomical response to changing environments through time (Legendre et al. 2005; Montuire et al. 2006; Van Dam 2006; Samuels and Hopkins 2017). Small mammals have been shown to adapt to a changing environment, such as a shift to open habitats, millions of years earlier than larger mammals, likely due to shorter generation times and smaller dispersal distances and home ranges (Smith et al. 1998; Bowman et al. 2002; Barnosky et al. 2004; Yom-Tov 2004; Renaud et al. 2005; Bofarull et al. 2008; Wolf et al. 2009; Finarelli and Badgley 2010; Evans et al. 2012; Jardine et al. 2012; Badgley and Finarelli 2013; Badgley et al.

2014; Fortelius et al. 2014; Samuels and Hopkins 2017). It is generally agreed that an increase in crown heights corresponds to an increase in arid environments that are rich in grit and dust near an animal's food source (William and Kay 2001; Polly et al. 2011; Damuth and Janis 2014; Semprebon et al. 2019).

Ecometric studies have come to the same general conclusion that many observed traits of an organism are directly correlated to the environment it inhabits and therefore can be a useful proxy to gain information about the surrounding environment and potential community shifts through time (Polly et al. 2011). Mammal based ecometrics first proved useful in a study conducted by Fortelius et al. (2002) who examined rising tooth crown height, from brachydont to mesodont to hypsodont, in relation to arid environments and paleoprecipitation throughout Eurasia, resulting in a positive correlation. That study provided sufficient background for future papers to give a more definitive name to this method of study.

Ecometrics later became the term associated with studying anatomical traits of an organism in relation to their response to local environment. Eronen et al. (2010b,c) and Polly et al. (2011) published findings on the interrelatedness of character traits and environment. Traits' ability to work across species, to help define regional differences in climate, and to view these aspects not only spatially, but through time, were highlighted in these papers. Therefore, these studies represent an important theoretical framework for any ecometric study. Ecometric traits range from leaf shape to limb proportions to tooth crown complexity (Polly et al. 2011); however, tooth crown height is the method used in research that will be the main focus here.

Small Mammal Importance

By studying small mammals, researchers can examine anatomical changes caused by changing habits with reduced lag time. It has been found that small mammal distribution is closely correlated to climate and with smaller dispersal potential there is evidence of in situ environmental response by small mammals, rather than shifting ranges typical of larger mammals (Hokr 1951; Kowalski 1971; Horacek 1985, 1990; Bowman et al. 2002; Eronen and Rook, 2004; Montuire et al. 2006; Heikinheimo et al. 2007; Raia et al. 2011, Fortelius et al. 2014). Given these factors, study of small mammals may provide a more accurate and timely regional response to shifting habitats and climate. Rodents first show higher-crowned teeth in the middle Eocene with an overall increase in crown height, including the first hypsodont rodents, through the middle and late Eocene (Samuels and Hopkins 2017). Lagomorphs have always had relatively high-crowned teeth, possibly because they have always eaten close to ground level and therefore have consistently ingested grit (Jardine et al. 2012). By the late Eocene, lagomorphs show hypselodonty, ever-growing teeth (Samuels and Hopkins 2017). Within the Great Basin, Badgley et al. (2014) found the number of rodents grew substantially around 16 million years ago and there was high diversity during the middle Miocene, with eight rodent families represented. Rodents and lagomorphs were the only mammal groups to sustain their level of diversity after the middle Miocene until the present (Badgley et al. 2014). Great Plains rodent diversity showed fluctuations between 25 and 12 million years, with a peak during the cooling period following the Mid-Miocene Climatic Optimum (MMCO), followed by a decline from 12 to 9 million years (Badgley and Finarelli 2013; Badgley et al. 2014). These studies focused on changes in rodent morphology and diversity in relation to localized climatic changes, which can be important when examining which environmental conditions become too extreme for oganism survival.

Dietary Proxies

Multiple dietary proxies exist and each tells a different story when examining the life history of an animal. Depending on the question at hand and the temporal scale of interest, from seconds to millions of years, one method would be more beneficial than another (Fortelius and Solounias 2000; Dalerum and Angerbjörn 2005; Kaiser et al. 2013; Münzel et al. 2014; Davis and Pineda-Munoz 2016; Green and Croft 2018). Diet can help reconstruct various ecological facets including lifestyle changes through time, changes in climate, and ecological niches (Pineda-Munoz and Alroy 2014; Davis and Pineda-Munoz 2016).

Microwear evalutates microscopic wear features on the surface of the tooth to help determine the abrasiveness of the food being consumed the last few days or weeks of an animal's life (Teaford and Oyen 1989; Münzel et al. 2014; Davis and Pineda-Munoz 2016). Therefore, microwear is most useful when only examining life at the temporal scale of a few weeks and might not be indicative of usual preferences (Daegling et al. 2013). Mesowear examines the overall wear and general flattening of teeth to determine attrition-abrasion wear rate at the temporal scale of multiple years to help inform about the overall diet of that individual during its lifetime (Fortelius and Solounias 2000; Mihlbachler et al. 2011; Damuth and Janis 2014; Maguire 2015; Mihlbachler et al. 2018). Hypsodonty (tooth crown height) is widely used in ecometric studies, as it is easily measured and compared across taxonomic groups of herbivorous mammals (Janis 1988; Jernvall 1995; Jernvall et al. 1996; Jernvall and Fortelius 2002). Discrete groups of crown heights (brachydont, mesodont, hypsodont, and hypselodont) provide potential precipitation proxies (Damuth 2002; Fortelius et al. 2002; Jernvall and Fortelius 2002; Eronen et al. 2010b, c; Polly et al. 2011; Damuth and Janis 2014). Hypsodonty helps infer ecology at an evolutionary time scale to help determine generation scale changes in diet and by extension, how environments and climate changed over hundreds of thousands, or even millions of years (Janis 1988; Damuth and Janis 2011).

Each of these proxies answer slightly different questions related to how an animal lived and how they changed over time. Caution must be taken when making inferences at each of these different time scales as diet can drastically change or be misrepresented when compared between weeks and generations for individuals, even of the same species, in various geographic locations (Hobson et al. 1999; Kurle and Worthy 2002; Munro et al. 2006; Rivals and Semprebon 2011; Rivals et al. 2012; Cerling et al. 2015; Davis and Pineda-Munoz 2016).

A shift in understanding about which environmental pressures give rise to increasing crown height has occurred over the last several decades. High-crowned hypsodont teeth were formerly interpreted as primarily indicating increased ingestion of fibrous, silica rich grasses (Stirton 1947; White 1959; Webb 1977, 1978; Stebbins 1981; MacFadden 1997; Janis et al. 2000; Damuth 2002; Strömberg 2001; Eronen et al. 2010a; Damuth and Janis 2011; Polly et al. 2011; Jardine et al. 2012). Recent studies suggested hypsdonty is more indicative of open, arid environments which possess high levels of airborne grit and dust being consumed (Williams and Kay 2001; Fortelius et al. 2002; Eronen et al. 2010b, c; Damuth and Janis 2011; Jardine et al. 2012; Damuth and Janis 2014; Semprebon et al. 2019), which had been hypothesized earlier (Stirton 1947; Janis 1988). Strong evidence supporting this comes from hypsodonty in larger herbivores not closely following the emergence of grasslands in many places (MacFadden and Hulbert 1988; Strömberg 2004; Damuth and Janis 2011; Semprebon et al, 2019). However, processes which led to increased dominance of grasses and grasslands often coincide with aridity and an increase in airborne grit (Fortelius et al, 2002; Eronen et al, 2010b, 2010c; Damuth and Jani, 2011; Jardine et al, 2012). Additionally, many small mammals with high-crowned teeth do not even eat grasses. As small mammals have shorter generation times and a broader range of diets and life-styles than larger mammals (French et al. 1976; Schmidt-Kittler 2002; Hopkins 2005; Evans et al. 2007; Samuels 2009; Calede et al. 2011; Jardine et al. 2012; Samuels and Hopkins 2017), further analysis of these groups could provide some unique discoveries and a clearer understanding of the temporal disparity between regional hypsodonty and arid environments (Damuth 2001; Fortelius et al. 2002; Eronen et al. 2010b, c; Polly et al. 2011).

Notable research conducted by Eronen et al. (2010b,c) compared modern ungulates to modern climate using the WorldClim data set (Fick and Hijmans 2017) and species accounts from the World Wildlife Fund's species distribution (Eronen et al. 2010b). Precipitation variables were measured and linear regressions, as well as regression trees, were used to predict precipitation. Their findings showed a correlation between low precipitation and increased hypsodonty, and therefore provide a useful method to estimate precipitation from ecometric characteristics of these large mammals. Eronen et al. (2010c) then applied this same method to investigate paleoclimate and once again found a similar correlation between increased hypsodonty and aridity over time. The dispersal of ungulates was studied by examining the changing climate of Eurasia and tracking open habitats where ungulates were found (Eronen et al. 2010b). A very similar study was conducted by Fortelius et al. (2014) on Neogene mammal community interactions in Eurasia through observing hypsodonty in response to changing environment versus changing diet. The main conclusion from that study is that there is a need to evaluate how traits are all related to diet and environment, and how they work together to study this information as an interdisciplinary synthesis (Fortelius et al. 2014). While these studies use the same methods of mapping climate records against species accounts, it is worth noting that most of the research was conducted across Eurasia, not North America, and focused on large mammals instead of small mammals.

Cenozoic Climate

Cenozoic climate changes over the last 65 million years have been more easily observed in part from deep-sea carbon and oxygen isotopes from foaminifera (Zachos et al. 2001). A combination of climatic events, tectonic events, and biotic events shaped ecosystems and led to the diversity seen today. Throughout the last 50 million years of the Cenozoic, there was an overall trend towards cooler and more arid climates in North America with levels of CO_2 much higher than in present day (Zachos et al. 2001, 2008). Several glacial events and warming spikes are also found during this time, disrupting the steady trend with sudden drops or increases in temperature and precipitation (Zachos et al. 2001, 2008). Notable climate events include the Mid-Miocene Climatic Optimum, early Miocene (Mi-1) Glaciation, Late Oligocene Warming, earlu Oligocene (Oi-1) Glaciation, and the Paleocene/Eocene Thermal Maximum (Zachos et al. 2001). These climate events were impacted by tectonic activity ranging from volcanism, uplift, see floor spreading, and sea rifts (Miller et al. 1992; Miller 1993). In response to changing in climate, environments shifted from forested habitats to more open habitats (Leopold et al. 1992; Graham et al. 1999; Jacobs et al. 1999; Retallack 2001, 2007, 2013; Dillhoff et al. 2009; Zachos et al. 2001, 2008; Strömberg 2011).

Mid-Miocene Climatic Optimum

Paleontology is a window into past climates and the natural variability which functions over long periods of time (Eronen et al. 2010a; Polly et al. 2011). The Mid Miocene Climatic Optimum (around 15 Ma) represents an extreme change in climate, (Zachos et al. 2001, Retallack 2007; Kürschner et al. 2008; Zachos 2008; Eronen et al. 2012; Goldner et al. 2014;

Maguire 2015; Smiley and Terry 2017), with global mean temperatures rising to 18ºC, which is approximately 3ºC warmer than it is today (You et al. 2009; Maguire 2015). The early Miocene in North America was relatively humid, with precipitation levels greater than 800mm/yr in many western localities with a drop to between 500-700 mm/yr in the late middle Miocene (Eronen et al. 2012). Increased aridity not found in the milder late Oligocene warming (Barnosky and Carrasco 2002) may have appeared across the mid-continental range of North America, beginning in the Southwest and Great Plains in the early middle Miocene (Eronen et al. 2012; Maguire 2015). Changes brought on by uplift patterns in western North America and Pacific Ocean upwelling and cooling led to non-uniform regional and temporal differences in climate (Lyle et al. 2008; Eronen et al. 2010b, c; Eronen et al. 2012; Eronen et al. 2015).

The Mid-Miocene was a transitional period in Earth's history when observing geography, oceanic currents, and the atmosphere (Shevenell et al. 2004; Kohn and Fremd 2008; Kurschner et al. 2008; Lyle 2008; Mulch et al. 2008; Goldner et al. 2014; Smiley and Terry 2017). It is through these transitions across a global scale that we see change in climate brought on during the MMCO. Many aspects of the Mid-Miocene make it a desirable time period for climate researchers to study.

A range of explanations for the rise in temperature during the middle Miocene have been presented. From the Rocky Mountains, Himalayas, the Alps, and the Andes, most of Earth's mountain ranges experienced high rates of uplifting during the Miocene (Pound et al. 2012). Some associate these uplifts with rain-shadow effects that led to an increase in aridity in western North America at different latitudes (Retallack et al. 2007), while others think western North American topography has not changed much since the Paleogene (Mulch et al. 2008). For instance, it is thought that elevation in the modern high Cascade Mountains only occurred around

7 Ma, suggesting changes in climate in the area before 7 Ma is due to global influences and not regional tectonic activity (Kohn and Cerling 2002; Kohn and Fremd 2007; Drewicz and Kohn 2018). An increase in atmospheric CO_2 levels during the MMCO may have been caused by the Columbian River flood basalt eruptions or released from the Earth's surface as part of a positive feedback loop from the start of the warming period (Zachos 2001, 2008; Kürschner et al. 2008; Kasbohm and Schoene 2018).

Changes in oceanic currents have also been attributed to the Mid-Miocene climate increase. A combination of atmospheric circulation changes and tectonic shifts may have led to these altered oceanic currents (Shevenell et al. 2004) which would lower coastal waters and give rise to a shift in summer-dry Western North American weather (Eronen et al. 2012). However, the factor most often studied while examining Miocene climate is the level of CO_2 present in the atmosphere.

CO_2 concentrations have a wide range of effects on the environment not limited to an increase in temperature and precipitation (Zachos et al. 2008), and past changes can be useful to understand current CO_2 levels and an ecosystem's response to the increase. This period has the highest $p\mathrm{CO_2}$ levels of the last 20 Ma followed by a decrease around 14-10 Ma (Tripati et al. 2011). Debates over the major cause of temperature increase still exist, but some combination of factors across Earth's Environmental systems, including oceanic currents and orogenic events, caused this cycle and gave rise to a cooling period during the late Miocene (Shevenell et al. 2004; Pound et al. 2012). These factors and debates are important to keep in mind when making a hypothesis for how a community might react based on their proximity to any of these environmental factors, especially volcanism, and the accompanying reaction of their environment.

Globally, temperatures during the MMCO were approximately 3-4° C higher than presently observed (You et al. 2009; Goldner at el. 2014; Maguire 2015). As stated before, climate shifts during the Miocene did not happen uniformly across North America at the same time, rather there was a gradient of change. Paleosols have been examined across many studies in an effort to better understand past climates (Retallack 1997, 2007; Sheldon 2006; Smiley and Terry 2017). Many important findings on regional climatic changes during the MMCO were discussed with general conclusions on paleoclimate in the United States (Retallack 2007; Badgley et al. 2014, 2017; Maguire 2015, Smiley et al. 2017). Warm periods were tied to periods of high precipitation (Retallack 2007), as evidenced through paleosols, indicating sharp increases in temperature correlate with sharp precipitation increases. The Mid-Miocene showed an increase in temperature and humidity in the Pacific Northwest (Maguire 2015; Drewicz and Kohn 2017) and warm-wet and cold-dry periods within the span of a few million years (Retallack 2007), which was well observed within southern Nebraska.

The transition of vegetation during the Miocene has also been examined using paleosols and phytolith assemblages (Strömberg 2002, 2004, 2005, 2011). For example, paleosols indicate short sod grasses dominating plant assemblages in the Great Plains during the early Miocene (Retallack 2007), giving rise to savanna woodlands in the Great Plains from the early Miocene to the Mid-Miocene (Samuels and Hopkins 2017). Drying climate through regions of North America resulted from many orogenic events. By the Miocene, the central Rocky Mountains confined the rain shadow, which changes in coverage on million-year timescales, to a much narrower range than was seen in the Oligocene (Retallack 2007) producing a sub-humid climate (Maguire 2015). Elevation of the Nevada Basin and Range was around 1000m higher than today (Wolfe et al. 1997; Retallack 2007). The MMCO corresponded with block-faulting extension in the southern Great Basin, which was followed by an increase in the size of the east Antarctic ice sheet and an abrupt cooling trend around 14 million years ago (Badgley et al. 2014). Shifts in elevation and relief throughout the many landscape changes in the Great Basin led to habitat fragmentation allowing a diversity of mammalian habitats to arise and accommodate a wider variety of lifestyles (Badgley et al. 2014).

Artiodactyls, perissodactyls, carnivores, and rodents have been present in the Great Basin over the past 30 million years, with lagomorphs being present from the Mid-Miocene until today (Badgley et al. 2014). There was a peak in mammalian diversity in the Great Basin during the Mid-Miocene, followed by fluctuations in diversity leading to the current diversity seen today. Contrasting the Great Basin, the Great Plains have been tectonically stable since the late Mesozoic (Badgley et al. 2014). Paleoclimate in the Pacific Northwest (Oregon, Washington, and Idaho) was heavily affected by a series of regional volcanic eruptions coinciding with the eruption of the Columbia River flood basalts between 17-5 Ma in the Steen Mountain (OR), Columbia River (OR and WA), Snake River basin (ID), and Yellowstone Hotspot (ID and WY), in sequential order, which was the largest volcanic event of the Cenozoic and potentially aided in the Mid-Miocene climate spike (Maguire 2015; Kasbohm and Schoene 2018). These findings prove to be significant in noting that not all climate changes happened uniformly and therefore one would expect a gradient of anatomical responses throughout multiple western localities through time.

Anthropogenic Climate Change

Anthropogenic-driven climate change, a commonly supported conclusion, has led to an increase in global mean surface temperature with regional fluctuations (Abatzoglou 2014) that have been examined to gain a more complete and accurate account of modern climate trends and the effects on the future. Reinemann et al. (2014), Abatzoglou (2014), and Mote and Salathé (2010) studied climate trends throughout North America and examined the fluctuations and potential influence on the flora and fauna of regions. They have also noted the importance of the local environment on an organism's distribution and the factors that may affect this. The mountainous western United States has been experiencing detrimental droughts, leading to many regional environmental issues related to precipitation levels, as well as a reduction in forest coverage. The Pacific Northwest is presently associated with wet winters and dry summers (Mote and Salathé 2010) and has experienced an increase in seasonal warming resulting in longer freeze-free seasons (Abatzoglou 2014), and it is predicted a general warming trend can be expected through the year 2100 with an associated increase of precipitation to a lesser degree (Mote and Salathé 2010).

While seasonal fluctuations play a role in the overall time scale of climate change (Abatzoglou 2014), annual temperature trends are increasing across all seasons and are primarily driven by increases in greenhouse gases. Within the century, the Pacific Northwest has warmed nearly 2ºF since 1900 compared to more inland locations, like Nebraska, that have experienced 1ºF of warming (Frankson et al. 2017a,b,c; May et al. 2018). Increasing temperatures lead to a decrease in snowpack on the mountain, which in turn leads to an increase in precipitation falling as rain instead of snow causing droughts and wild fires (Mote et al. 2016; Frankson et al. 2017a,b; May et al. 2018). Many of these impacts, like an increase in wildfires, changes in snowmelt, and an increase in temperature are also found throughout California, Oregon, and much of the Northwest and Southwest (California Environmental Protection Agency 2013; Gonzalez et al. 2018; Frankson et al. 2017a,b; May et al. 2018). The decrease in snowpack also leads to an increase in beetle infestations which can play a huge role in damaging mountain environments in places like central Idaho, eastern Oregon, and Washington (Hicke et al. 2013; Frankson et al. 2017a, b; May et al. 2018). All locations along the coast, especially California, are in danger of rising sea levels associated with rising temperatures which are projected to increase by 1 to 4 feet by the end of the century (Frankson et al. 2017b).

Due to the decrease in snowpack, in Oregon it is projected that winter precipitation will increase while summer precipitation will decrease causing problems for water management (Frankson et al. 2017a). Rising temperatures will also affect the level at which snow falls, increasing about 300 feet per degree disrupting the ranges of plants and animals which rely on snowy habitats (Frankson et al. 2017a,b).

The Great Basin spans many western North American states, is comprised of horst and graben topography, over 120 mountain ranges, 8 floral belts (Badgley et al. 2017), and low valleys (Reinemann et al. 2014), and is highly susceptible to changes in climate (McEvoy et al. 2014). Currently, 172 mammal species are native to the Great Basin, showing great diversity which is suggested to be influenced by past geographic events such as volcanism, changes in climate, and tectonic shifts; however, recent human influence on the landscape has altered the distribution and abundance of these mammals (Badgley et al. 2014, 2017). Precipitation levels and temperature vary across these different landscapes, but produce an overall arid regional climate (Reinemann et al. 2014). Snowmelt built up from October to March provides almost all the annual runoff and groundwater recharge needed in the Great Basin, which is why changes in climate, particularly precipitation, can play a major role in the function of the Great Basin and why land development of the surrounding area, which alters groundwater systems, is so problematic (McEvoy et al. 2014). These studies all find that modern climatic changes are already showing major effects on topographically diverse environments across the western US, with direct effects on the plants and animals that have lived there for years. Shifts in precipitation and an increase in temperature are interesting aspects within these ranges to observe due to their varied landscapes and complex diversity.

Using what is known about past climate trends and small mammals' ability to respond quickly and locally to these climatic changes, the goal of this study is to examine if small mammal crown height is significantly correlated with regional temperature and precipitation variables throughout North America, specifically more western localities due to a lack of fossil records from the east. A correlation between these variables would allow regional comparisons to the onset of multiple temperature and precipitation variables across time and space. Using past studies analyses of crown heights, an increase in overall community crown height would be expected in colder, drier environments and a decrease in community wide crown height would be expected in warmer, wetter environments. With the Mid-Miocene Climatic Optimum acting as a proxy for modern warming, the trends examined across western North America at this time have the potential to inform about trends expected within the next 100 years.

CHAPTER 2

METHODS

Modern data

This study uses an ecometric approach study similar to methods used in Eronen et al. (2010 b, c). Crown height and climate relationships were examined in rodents and lagomorphs to test if accurate temperature and precipitation estimates could be determined in the present and applied to paleoenvironments. All precipitation variables were tested similarly to methods used in Eronen et al. (2010b). Temperature variables were added to the analysis to determine if small mammal crown height could accurately estimate temperature in addition to precipitation (Table 1). As temperature also plays a role in determining landscape ecology, it was important to test whether these additional climate factors could be estimated from studies of hypsodonty. Modern climate data were downloaded from the WorldClim website (Fick and Hijmans 2017) using version 2.0 (1970-2000) for the Bioclimatic variables at the 10 arc minute resolution (~340 km^2).

Table 1. Each of the 13 temperature and precipitation bioclimatic variables used in the study and what they represent

Bioclimatic Variable	**Description**
BIO1	Mean Annual Temperature
BIO4	Temperature Seasonality
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range
BIO12	Annual Precipitation

BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Variables were projected onto a map of North America created in ArcMap 10.5.1. Distributions of North American rodent and lagomorph species were collected from the NatureServe website, based on the Digital Distribution Maps of Mammals of the Western Hemisphere dataset (Patterson et al. 2007). One hundred random points were created in ArcMap and added to the map as sample points to test the relationship of crown height to the various bioclimatic variables at these locations. Within this dataset, one species of castorid, one species of cuniculid, one species of dasyproctid, 3 species of dipodid, 3 species of erethizontid, 2 species of ochotonid, 14 species of leporids, 11 species of geomyids, 29 species of heteromyids, 51 species of sciurids, and 102 species of cricetids were present at one or more of the random points. A full list of all species is located in the appendix (See Appendix A). A spreadsheet was created for each point listing: the latitude, longitude, species found at that given point, number of taxa within each crown height category, total number of species, percent of the total number of species found in each crown height category, mean crown height, and the value of each bioclimatic variable in millimeters or Celsius. Three points did not contain any climate data for the variables tested, as those points were on the edge of the ocean, so those points were excluded from the subsequent analyses. Crown height variables included number brachydont (bra), number mesodont (mes), number hypsodont (hyp), number hypselodont (hys), total number of taxa (total), percent brachydont (PerBra), percent mesodont (PerMes), percent hypsodont (PerHyp), percent hypselodont (PerHys), and the mean crown height (MeanCH).

To assess the relationships between crown heights and climate variables, regression analyses were run. Each crown height variable was regressed against climate variables using ordinary least squares (OLS) regression to determine the strength of correlation between the variables and to see which variables are the best predictors of climate. Stepwise multiple OLS regression performs better in estimation; however, the variables here are not truly independent of each other. To account for autcorrelation of the predictor variables, a bivariate correlation was performed for crown height variables against one another to examine which variables were significantly correlated ($r > 0.5$) (Table 2) (Menendez et al. 2017). Crown height data were also regressed against the climate variables to see which crown height variables were more strongly correlated with the climate variable (Table 3). Methods to determine autocorrelation were based on Menéndez et al. (2017).

Table 2. Bivariate correlations among crown height variables. Brachydont (Bra), mesodont, (Mes), hypsodont (Hyp), hypselodont (Hys), total taxa (total), percent brachydont (PerBra), percent mesodont (PerMes), percent hypsodont (PerHyp), percent hypselodont (PerHys), mean crown height (MeanCH). Correlations with $r < 0.5$ are in bold

		Bra	Mes	Hyp	Hys	Total	PerBra	PerMes	PerHyp	PerHys	MeanCH
Bra	*r*	1	0.749	0.587	**0.310**	0.822	0.930	0.505	**0.080**	-0.761	-0.862
	p		<0.001	<0.001	**0.002**	<0.001	<0.001	<0.001	**0.430**	<0.001	<0.001
Mes	*r*	0.749	1	0.794	0.579	0.926	0.612	0.794	**0.215**	-0.747	-0.755
	p	<0.001		<0.001	<0.001	<0.001	<0.001	<0.001	**0.033**	<0.001	<0.001
Hyp	*r*	0.587	0.794	1	0.625	0.847	0.507	0.636	0.565	-0.737	-0.673
	p	<0.001	<0.001		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Hys	*r*	**0.310**	0.579	0.625	1	0.748	**0.187**	**0.353**	**0.130**	**-0.294**	**-0.278**
	p	**0.002**	<0.001	<0.001		<0.001	**0.064**	**<0.001**	**0.200**	**0.003**	**0.005**
Total	*r*	0.822	0.926	0.847	0.748	1	0.701	0.666	0.229	-0.748	-0.776
	p	<0.001	<0.001	<0.001	<0.001		<0.001	<0.001	0.022	<0.001	<0.001
PerBra	*r*	0.930	0.612	0.507	**0.187**	0.701	1	0.518	**0.141**	-0.827	-0.925
	p	<0.001	<0.001	<0.001	**0.064**	<0.001		<0.001	**0.163**	<0.001	<0.001
PerMes	*r*	0.505	0.794	0.636	**0.353**	0.666	0.518	1	**0.376**	-0.833	-0.784
	p	<0.001	<0.001	<0.001	**<0.001**	<0.001	<0.001		**<0.001**	<0.001	<0.001
PerHyp	*r*	**0.080**	**0.215**	0.565	**0.130**	**0.229**	**0.141**	**0.376**	1	-0.565	**-0.377**
	p	**0.430**	**0.033**	<0.001	**0.200**	**0.022**	**0.163**	**<0.001**		<0.001	**<0.001**
PerHys	*r*	-0.761	-0.747	-0.737	**-0.294**	-0.748	-0.827	-0.833	-0.565	1	0.973
	p	<0.001	<0.001	<0.001	**0.003**	<0.001	<0.001	<0.001	<0.001		<0.001
MeanCH	*r*	-0.862	-0.755	-0.673	**-0.278**	-0.776	-0.925	-0.784	**-0.377**	0.973	1
	p	<0.001	<0.001	<0.001	**0.005**	<0.001	<0.001	<0.001	**<0.001**	<0.001	

Table 3. Bivariate correlations for climate values against crown height variables. Significant correlations with $p < 0.05$ are indicated in bold

		Bra	Mes	Hyp	Hys	total	PerBra	PerMes	PerHyp	PerHys	MeanCH
Annual Precip	*r*	**0.389**	0.157	0.148	**-0.226**	0.146	**0.538**	**0.332**	**0.207**	**-0.518**	**-0.540**
	p	**0.000**	0.126	0.147	**0.026**	0.155	**0.000**	**0.001**	**0.042**	**0.000**	**0.000**
Max Temp of Warmest Month	*r*	**0.775**	**0.720**	**0.636**	**0.290**	**0.732**	**0.765**	**0.600**	**0.207**	**-0.761**	**-0.803**
	p	**0.000**	**0.000**	**0.000**	**0.004**	**0.000**	**0.000**	**0.000**	**0.042**	**0.000**	**0.000**
Mean Annual Temp	*r*	**0.801**	**0.700**	**0.625**	**0.194**	**0.701**	**0.813**	**0.632**	**0.255**	**-0.819**	**-0.856**
	p	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Min Temp of Coldest Month	*r*	**0.732**	**0.593**	**0.513**	**0.045**	**0.569**	**0.729**	**0.550**	**0.216**	**-0.723**	**-0.760**
	p	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
Precip of Coldest Quarter	*r*	**0.315**	0.121	0.137	0.043	**0.199**	**0.389**	0.182	0.079	**-0.326**	**-0.360**
	p	**0.002**	0.239	0.181	0.678	**0.050**	**0.000**	0.074	0.443	**0.001**	**0.000**
Precip of Driest Month	*r*	0.147	-0.017	-0.039	-0.109	0.009	**0.305**	0.092	0.030	**-0.222**	**-0.258**
	p	0.150	0.870	0.701	0.286	0.933	**0.002**	0.370	0.768	**0.029**	**0.011**
Precip of Driest Quarter	*r*	0.184	0.019	-0.009	-0.090	0.046	**0.342**	0.129	0.041	**-0.262**	**-0.300**
	p	0.071	0.857	0.927	0.381	0.654	**0.001**	0.209	0.692	**0.009**	**0.003**
Precip of Warmest Quarter	*r*	**0.308**	0.165	0.131	**-0.239**	0.108	**0.500**	**0.367**	**0.246**	**-0.524**	**-0.531**
	p	**0.002**	0.107	0.201	**0.018**	0.291	**0.000**	**0.000**	**0.015**	**0.000**	**0.000**
Precip of Wettest Month	*r*	**0.453**	**0.224**	0.193	**-0.245**	0.192	**0.558**	**0.383**	**0.240**	**-0.563**	**-0.578**
	p	**0.000**	**0.028**	0.058	**0.016**	0.059	**0.000**	**0.000**	**0.018**	**0.000**	**0.000**
Precip of Wettest Quarter	*r*	**0.434**	**0.206**	0.181	**-0.242**	0.178	**0.553**	**0.379**	**0.240**	**-0.558**	**-0.573**
	p	**0.000**	**0.043**	0.077	**0.017**	0.081	**0.000**	**0.000**	**0.018**	**0.000**	**0.000**
Precip Seasonality	*r*	0.057	0.034	-0.049	-0.185	-0.040	-0.039	0.011	-0.041	0.030	0.030
	p	0.576	0.742	0.632	0.070	0.697	0.706	0.914	0.687	0.774	0.774
Temp Annual Range	*r*	**-0.460**	**-0.294**	**-0.243**	0.177	**-0.248**	**-0.465**	**-0.331**	-0.153	**0.459**	**0.479**
	p	**0.000**	**0.003**	**0.016**	0.082	**0.014**	**0.000**	**0.001**	0.134	**0.000**	**0.000**
Temp Seasonality	*r*	**-0.661**	**-0.536**	**-0.461**	-0.029	**-0.510**	**-0.631**	**-0.482**	-0.187	**0.629**	**0.659**
	p	**0.000**	**0.000**	**0.000**	0.781	**0.000**	**0.000**	**0.000**	0.066	**0.000**	**0.000**

If two crown height variables were autocorrelated with each other and both significantly correlated with the same climate variable, the crown height variable with a stronger correlation was retained in the multiple stepwise OLS regression analysis while the other variable was left out. Stepwise regressions were performed with crown height data as the independent variables and climate data as the dependent variables.

Reported results for each regression included: r^2, p-value, regression equation, and standard error of the estimate (Table 4). These variables are used to determine the relative utility of the crown height data in predicting variance in the climate data and how much the predictions vary from the actual values in the training dataset. Which variables were not excluded during the stepwise analysis is also important when considering localities where the prediction equation can be applied. For example, if a locality does not have any high crowned taxa, but hypsodont and hypselodont are the only significant variables, then the equation will not work at this site.

Once these regressions were completed, predicted climate for each of the points was calculated in SPSS as well as the residuals. Using ArcMap, the predicted climatic variables were imported for all points. Ordinary Kriging was then used to interpolate climate data between the points to get a predicted climate range for all of North America, which was then used as a comparison to known climate data allowing examination of areas where predictions were similar and where they varied. Anisotropic variograms were used for temperature variables, since there is a known, easily understood north to south temperature gradient, but not for precipitation variables. Semivariograms with standard neighbors was used and all default settings were kept. Overall climate trends were also compared between predicted and actual climate maps as well to determine whether these predictions were reliable enough to apply to the fossil record.

Table 4. Stepwise regression models for estimation of bioclimate variables, including the corresponding r^2 value, p-value, regression equation, standard error of the estimate

Climate Variable	r^2	p	**Regression equation**	**SEE**
Annual Precipitation	0.434	0.000	2421.912 - 491.597(MeanCH) - 63.447(Hys)	366.804
Max Temp of Warmest Month	0.644	0.000	51.913 - 10.659(MeanCH)	5.003
Mean Annual Temp	0.732	0.000	47.774 - 15.987(MeanCH)	6.106
Min Temp of Coldest Month	0.602	0.000	41.339 - 19.150(MeanCH) - .817(Hys)	9.583
Precip of Coldest Quarter	0.152	0.000	56.449 + 314.186(PerBra)	114.067
Precip of Driest Month	0.093	0.002	14.591 + 45.893(PerBra)	22.033
Precip of Driest Quarter	0.117	0.001	48.694 + 165.606(PerBra)	69.900
Precip of Warmest Quarter	0.433	0.000	619.570 - 115.192(MeanCH) - 15.467(Hys)	86.851
Precip of Wettest Month	0.500	0.000	380.442 - 78.339(MeanCH) - 10.168(Hys)	51.271
Precip of Wettest Quarter	0.491	0.000	1003.371 - 205.621(MeanCH) - 26.683(Hys)	136.976
Temp Annual Range	0.326	0.000	8.295 + 8.795(MeanCH) + 1.066(Hys)	8.162
Temp Seasonality	0.493	0.000	1355.323 - 84.845(Bra) + 25.447(Hys) - 774.006(PerHyp)	290.036

Fossil Data

Given the relatively high correlations between crown height and climatic variables from modern climate mapping, the crown heights show promise for estimation of past precipitation and temperature levels at fossil sites across North America, allowing for examination of climate trends through time with estimates based directly on terrestrial communities. Mean Annual Temperature and Annual Precipitation predictions were made using the regression equations from the training dataset for a wide range of Cenozoic fossil sites in North America. A reference map has been provided with the names of the states within the United States of America (Figure 1).

Figure 1. Names of states within the United States of America with latitude and longitude graticules

Localities were chosen with ≥ 10 taxa present and were listed oldest to youngest geologically. Localities were organized according to their geographic regions including: the Central Great Plains (CP), Southern Great Basin (SB), Pacific Northwest (PN), Northern Great Plains (NP), Northern Great Basin (NB), California Central Region and Coastal Ranges (CC), Southern Great Plains (SP), and Gulf Coast (GC) according to Janis (2008) (Figure 2, Appendix B). Fossil rodent and lagomorph crown height data were compiled from the Samuels and Hopkins (2017) database with locality information for these species from the NOW database (Fortelius 2017: http://www.helsinki.fi/science/now). Unfortunately, published fossil records are lacking in most of eastern North America, therefore the regions focused on in this study are from western and central North America with the Gulf Coast localities being the only eastern data available.

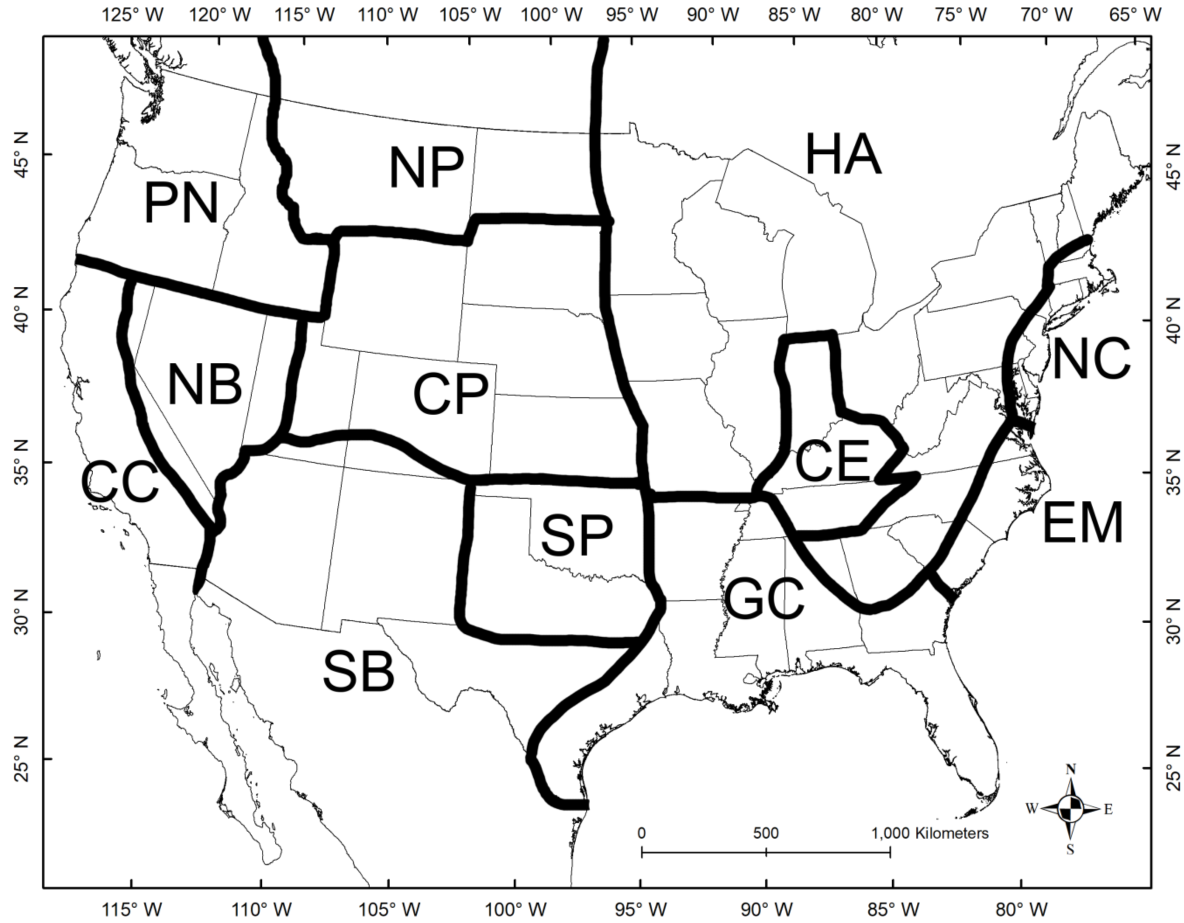

Figure 2. Regions studied for comparison across fossil localities. Region designations follow Janis 2008

Sites from the MMCO were examined in detail in several regions of Western North America. Further, to examine local changes through time, Nebraska, California, and Oregon (Figure 3) were chosen for analysis because localities had high numbers of taxa from the early to Mid-Miocene. The MMCO is being used as a way to examine past warming events to inform about modern warming trends. The number of taxa within each crown height category was determined, allowing for the relative hypsodonty for each site to be compared the same way as the modern sites. Stepwise multiple linear regression equations derived from the modern dataset (Table 4) were used to apply these predictions to the Nebraska, California, and Oregon Miocene fossil data. Samples were compiled into bins based on North American Land Mammal Ages (NALMA). When there was more than one locality at a given NALMA, each locality's taxa lists were compared, duplicate species were only counted once, and a new total was created for crown heights. A list of the formations can be found in Table 5.

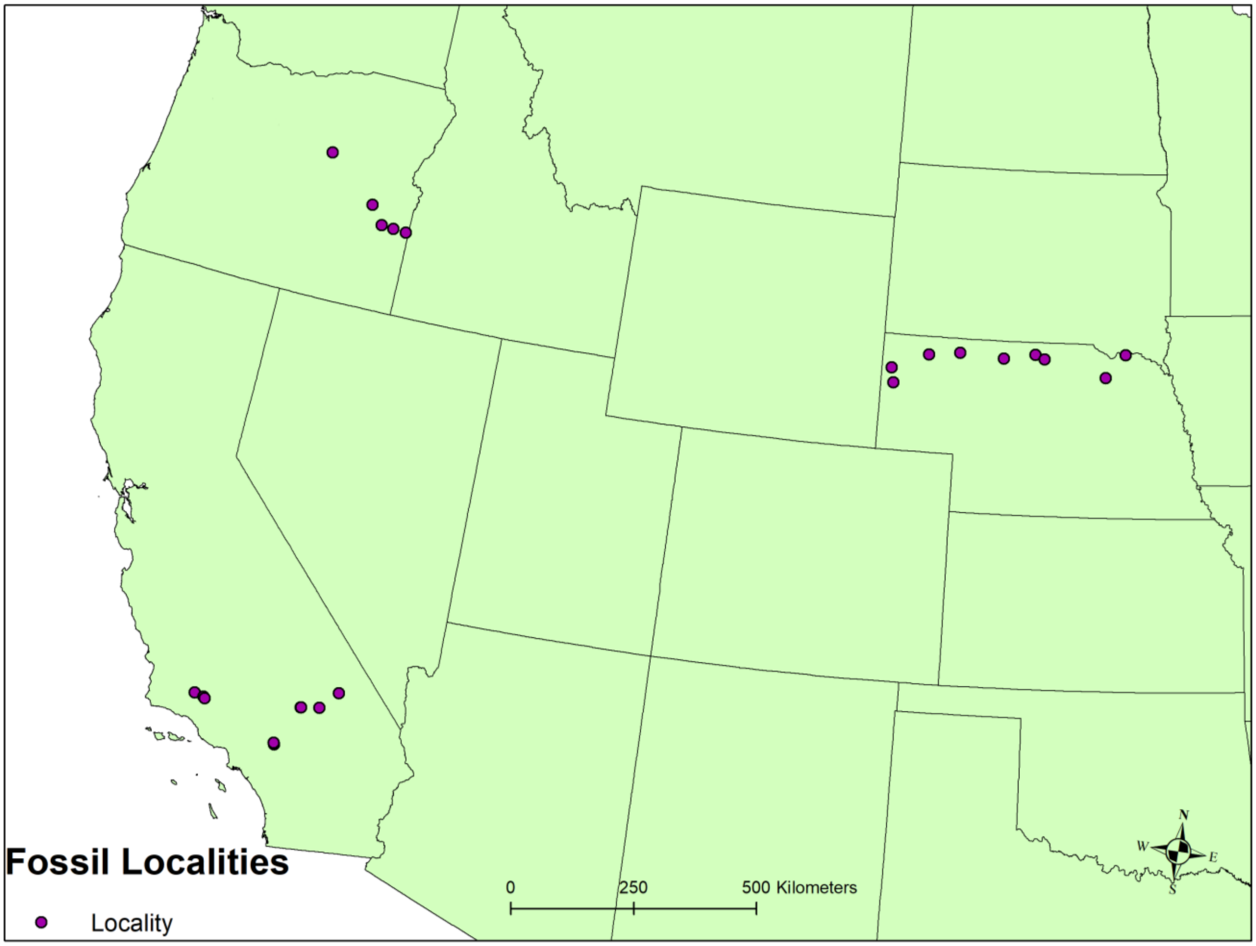

Figure 3. Map of selected Early and Middle Miocene fossil localities in Oregon, California, and Nebraska listed in table 7

Table 5. List of corresponding geologic age, locality ID, formation name, North American Land Mammal Age (NALMA), and number of taxa in each crown height category for Miocene fossil sites in Nebraska, California, and Orgeon

Nebraska	**Locality**	**Formation**	**NALMA**	**Bra**	**Mes**	**Hyp**	**Hys**
23-19.5	CP103A	Harrison Formation	Ar3	6	3	9	0
18.8-17.5	CP105	Runningwater Formation	He1	2	9	5	1
16-14.8	CP110	Olcott Formation	Ba1	0	4	4	0
16-14.8	CP111	Sand Canyon Beds	Ba1	0	2	3	0
14.8-12.5	CP114A	Valentine Formation	Ba2	8	9	5	2
14.8-12.5	CP114B	Valentine Formation	Ba2	6	8	9	4
14.8-12.5	CP114C	Valentine Formation	Ba2	1	2	5	0
14.8-12.5	CP114D	Valentine Formation	Cl1	1	1	5	1
12.1-10.1	CP116A	Ash Hollow Formation	Cl2	2	4	8	2
12.1-9	CP116B	Ash Hollow Formation	Cl3	7	5	10	4
California	**Locality**	**Formation**	**NALMA**	**Bra**	**Mes**	**Hyp**	**Hys**
17.5-16	CC19	Branch Canyon Sandstone	He2	2	2	3	2
17.5-16	CC22A	Crowder Formation	He2	8	4	0	0
16-14.8	CC22A	Crowder Formation	Ba1	8	1	3	1
16-14.8	CC22A	Cajon Formation	Ba1	2	0	1	1
16-14.8	NB6C	Barstow Formation	Ba1	3	5	2	1
16-14.8	NB6D	Barstow Formation	Ba1	5	2	0	1
14.8-12.6	CC22B	Cajon Formation	Ba2	8	4	4	1
14.8-12.5	NB6E	Barstow Formation	Ba2	11	3	3	1
12.1-10.1	NB8	Avawatz Formation	Cl2	1	0	2	2
12.1-10.1	CC17G	Caliente Formation	Cl2	6	2	0	2
10.1-9	CC17H	Caliente Formation	Cl3	4	2	0	0
Oregon	**Locality**	**Formation**	**NALMA**	**Bra**	**Mes**	**Hyp**	**Hys**
23-19.5	PN6G	John Day Formation	Ar2	4	4	5	2
23-19.5	PN6H	John Day Formation	He1	3	2	1	0
16-14.8	PN7	Mascall Formation	Ba1	4	2	2	3
16-14.8	PN8B	Butte Creek Volcanic Sandstone	Ba1	2	3	2	0
15.5-14.9	PN9A	Sucker Creek Formation	Ba1	4	0	1	0
14.8-12.5	PN9B	Sucker Creek Formation	Ba2	3	5	1	0
10.1-9	PN10	Juntura Formation	Cl3	4	0	3	0

CHAPTER 3

RESULTS

Modern Predictions

Results for the bivariate analysis of crown height variables run against one another found that brachydont was not strongly correlated ($r < 0.5$) to hypselodont or percent hypsodont (Table 2). Mesodont was not strongly correlated to only percent hypsodont. Hypsodont was strongly correlated with every crown height variable. Hypselodont was not strongly correlated with brachydont, percent brachydont, percent mesodont, percent hypsodont, percent hypselodont, and mean crown height. The total taxa at each point were strongly correlated with every crown height variable which would be expected since this value comes from the other values. Mean crown height was not strongly correlated to hypselodont and percent hypsodont. (Table 2)

When comparing crown height variables to climate variables, Annual Precipitation was the only variable not significantly correlated ($p > 0.05$) with mesodont, hypsodont, and the total taxa (Table 3). Maximum Temperature of the Warmest Month, Mean Annual Temperature, and Minimum Temperature of the Coldest Month were significantly correlated with every crown height variable. Precipitation of the Coldest Quarter was not significantly correlated with mesodont, hypsodont, hypselodont, percent mesodont, and percent hypsodont. Precipitation of the Driest Month and Precipitation of the Driest Quarter were both only significantly correlated with percent brachydont, percent hypselodont, and mean crown height. Precipitation of the Warmest Quarter was significantly correlated with every variable except mesodont, hypsodont, and total taxa. Precipitation of the Wettest Month and Precipitation of the Wettest Quarter were both significantly correlated with all variables except hypsodont and total taxa. Precipitation Seasonality was not significantly correlated with any crown height variable as previously stated.

Temperature Annual Range and Temperature Seasonality were significantly correlated with all crown height variables excluding hypselodont and percent hypsodont. (Table 3)

When running stepwise multiple regressions, mean crown height, percent hypsodont, and hypselodont were the three variables most important (Table 4), after excluding autocorrelated variables, for Annual Precipitation, Mean Annual Temperature, Maximum Temperature of the Warmest Month, Minimum Temperature of the Coldest Month, Precipitation of the Warmest Quarter, Precipitation of the Wettest Month, Precipitation of the Wettest Quarter, and Temperature Annual Range. Percent brachydont, number hypsodont, and percent hypselodont were used in regressions for Precipitation of the Coldest Quarter, Precipitation of the Driest Month, and Precipitation of the Driest Quarter. Temperature Seasonality had number brachydont, number hypsodont, and percent hypselodont used in the regression.

After running the stepwise multiple linear regressions and accounting for autocorrelation of the crown height variables, mean crown height, number hypselodont, and percent brachydont were most often found to the be variables with the strongest correlation to climate. For Annual Precipitation, the mean crown height and number hypselodont were included in the regression equation (Table 4). For Mean Annual Temperature only mean crown height was included in the regression. The remaining linear regressions produced some variable results for each of the climate variables (Table 4). Mean Annual Temperature and Annual Precipitation will be the focus of further analysis, as they are the main variables of interest with annual precipitation being compared to similar ecometric studies of hypsodonty. Precipitation Seasonality did not have any significant correlation to crown height variables, therefore regressions were not performed for this climate variable. Mean Annual Temperature had the highest r^2 value (0.732) while Precipitation of the Coldest Quarter had the lowest r^2 value (0.152) (Table 4).

The stepwise multiple OLS regression equations produced the highest r^2 values for Mean Annual Temperature, Maximum Temperature of the Warmest Month, Minimum Temperature of the Coldest Month, and Temperature Seasonality suggesting the rodent and lagomorph crown height data would be a better predictor of temperature rather than precipitation. Overall, the r^2 values were comparable to the values for ungulates from the Eronen et al. (2010b) studies when estimating modern precipitation. When examining tooth crown height alone, Eronen et al. (2010b) reported r^2 values of 0.658 for annual precipitation and 0.663 for precipitation of wettest quarter which are roughly 0.200 higher than the values reported in this study (Table 4).
The rest of the climate variables are as follows:

Maximum Temperature of the Warmest Month only included mean crown height. Minimum Temperature of the Coldest Month, Precipitation of the Warmest Quarter, Precipitation of the Wettest Month, and Precipitation of the Wettest Quarter did not exclude mean crown height and number hypselodont in the regression. Precipitation of the Coldest Quarter, Precipitation of the Driest Month, and Precipitation of the Driest Quarter only included precent brachydont in the regression. Temperature Annual Range did not exclude mean crown height or number hypselodont. Temperature Seasonality did not exclude number brachydont, number hypselodont, or percent hypsodont.

Fossil Predictions

Examination of broad scale patterns in regional climate revealed patterns of change in both temperature and precipitation consistent with prior studies (Appendix B), showing an overall decrease in mean annual temperature and annual precipitation estimates. It should be noted, many regions studied do include gaps in the fossil records which make observing a consistent trend difficult, however, overall patters can be observed and often compared to other regions from the same time period. The Central Great Plains (localities in Wyoming, Nebraska, Colorado, South Dakota, and Kansas) includes localities well-sampled through time with no large gaps in the record. Overall, Annual Precipitation slowly declined from 36.5 to 1.9 Ma. Estimates decreased fairly steadily through time, punctuated by increases in the middle Miocene and early Pliocene. Similar to Annual Precipitation, Mean Annual Temperature predictions decreased slowly through time as well, starting around 29ºC (37 Ma) and declining to 8.3ºC in the early Miocene and then punctuated by warm intervals in the middle Miocene and early Pliocene. After the Oligocene in South Dakota, temperature estimates do not rise above 20 degrees again. A spike in temperature and precipitation estimates occurs in Nebraska and Wyoming around 14.8-12.5 Ma, potentially reflecting MMCO warming.

In the Southern Great Basin (localities within Texas, Mexico, and Arizona) all localities but one in Texas are from the late Miocene to early Pleistocene. Annual Precipitation and Mean Annual Temperature estimates show cooler and drier climate in younger localities. Most of the localities from this region are younger in age (5.9-1.41 Ma). Mean Annual Temperatures range from 18.7 to 3.5 degrees Celsius from 4.9 to 1.41 Ma.

In the Pacific Northwest, localities are mostly from Oregon with one site in Washington and one in Idaho. A deeper record is found in this region compared to the Southern Great Plains, with estimates stretching from 31 to 3 Ma. Annual Precipitation estimates remain relatively constant through time fluctuating within 300 mm of each other in Oregon while estimates are lower in Washington and Idaho, but similar to each other (855 mm and 894 mm, respectively). Mean Annual Temperature estimates also remain relatively constant in Oregon with a slight decrease of 3 degrees from 26.57-23.79 Ma. Around 6.8 Ma, (late Miocene) temperatures begin to more drastically drop across all three states.

In the Northern Great Plains (localities from Canada and Montana) records span from 37 to 12.5 Ma, not representing ages as young as the other regions. Annual Precipitation estimates remain relatively high, between approximately 1750 mm to 1315 mm through time, with correspondingly high Mean Annual Temperature estimates from approximately 26 to 12 degrees Celsius until 14.8-12.5 Ma when both precipitation and temperature estimates drop to 1109 mm and 9.22 degrees.

The Northern Great Basin includes relatively younger sites ranging from 16 to 0.85 Ma in California and Nevada. A temperature and precipitation spike is seen in California from 14.8-12.5 Ma. Some of the lowest estimates for both precipitation and temperature are estimated in Nevada from 4.9-2.5 Ma (approximately 600 mm and -1.13 degrees) and California from 2.5-0.85 (approximately -56 mm and -12.18).

California Central Region and Coastal Ranges are represented by sites in California from 18 to 10 Ma. Precipitation and temperature estimates are higher than seen in other regions from the same time and do not fall below approximately 1356 mm and 17.25 degrees.

The Southern Great Plains and Gulf Coast are not well represented with only two sites from Texas and one from Florida, respectively. Precipitation estimates are comparable to other regions from 4.9 to 1.9 Ma ranging from 1066 mm to 800 mm. Temperature estimates in Texas are higher for the time period than is seen in other sites, reaching almost 8 degrees. Florida’s temperature estimate is also higher than other regions for 2.5 Ma, around 5.6 degrees.

A closer examination is taken for localities in Nebraska, California, and Oregon during the MMCO because, as stated previously, it represents a natural experiment on how small mammals adapted to rising tempertures and can offer insight into how communities will respond to modern warming. Based on the linear regression equations, past temperature and precipitation values for the Miocene sites are listed in Table 6.

Table 6. Precipitation (mm) and temperature (Celsius) estimates for corresponding North American Land Mammal Ages (NALMA) for Nebraska, California, and Oregon

		Nebraska		**California**		**Oregon**	
NALMA	Age(Ma)	Precip (mm)	Temp (ºC)	Precip (mm)	Temp (ºC)	Precip (mm)	Temp (ºC)
Ar2	23.8-19.5					1147.96	10.47
Ar3	19.5-18.8	1356.79	13.14				
He1	18.8-17.5	1230.68	11.10			1602.58	21.13
He2	17.5-15.9			1360.98	17.40		
Ba1	15.9-14.8	1508.95	18.08	1487.00	19.43	1201.56	14.28
Ba2	14.8-12.5	1054.80	11.57	1545.44	21.33	1547.96	19.35
Cl1	12.5-12.0	1006.57	3.81				
Cl2	12.0-10.0	1004.58	5.81	1086.61	12.60		
Cl3	10.0-9.0	976.95	9.04	1766.45	26.46	1508.95	18.08

When examining fossil localities in Oregon, Nebraska, and California, (Table 6) there are similar warming trends seen in the late Barstovian for California, reaching 21.33ºC, and Oregon, reaching 19.35ºC, while Nebraska shows warmer climates in the early Barstovian, 18.08ºC. However, each of the three locations show varying trends of precipitation with a maximum annual precipitation in the early Barstovian in Nebraska, the late Barstovian in California, and multiple peaks in early Hemingfordian and late Barstovian in Oregon.

CHAPTER 4

DISCUSSION

Modern Analysis

The stepwise OLS regression equations produced the highest r^2 values for Mean Annual Temperature, Maximum Temperature of the Warmest Month, Minimum Temperature of the Coldest Month, and Temperature Seasonality (Table 4), suggesting the data would be a better predictor of temperature rather than precipitation. Overall, the r^2 values were comparable to the values from the Eronen et al. (2010b) studies when estimating modern precipitation (Table 4). When examining tooth crown height alone, Eronen et al. (2010b) reported r^2 values of 0.658 for annual precipitation and 0.663 for precipitation of wettest quarter, which are roughly 0.200 higher than the values reported in this study. Multiple studies examined mean annual precipitation estimates using large herbivores with a standard error of ±412 mm from Eronen et al. (2015), standard deviation of 387.98 mm from Eronen et al. (2010), and 437 mm from Eronen et al. (2011). Results are relatively comparable when examing r^2 values between the methods used in this study to the multiple previous ecometric studies examing crown height and climate. While values for precipitation estimates were slightly higher in ungulates, small mammals were estimated to have stronger correlations to temperature, in some cases even stronger than the ungulates had to precipitation. These results suggest tooth crown heights are a useful indicator of climate and both of these groups of mammals are useful to consider when trying to reconstruct paleoclimates. It is worth noting that these studies examined different groups from different continents and previous studies did not test for temperature variables, so these caveats should be considered before comparisons between those results are made.

Small mammals are found in a wide range of environments from deserts to forests to polar regions and high altitudes to lowlands (Hayward and Phillipson 1979). A wide variety of diets and life style modes (Samuels and Hopkins 2017) are also found within these groups some of which are more closely tied to precipitation than others. Small mammals have also been able to withstand increases in temperature better than larger mammals which sometimes cannot withstand even acute increases (Peck et al. 2009). If groups with constraints on temperature are studied, a wider scale of temperatures would not be able to be predicted. Precipitation is also not as easily tracked as temperature, with a less clear gradient, due to oceanic and topographic influences causing increased precipitation in some regions and decreased in others in relation to these factors (Lyle et al. 2008; Chamberlain et al. 2012; Siepielski et al. 2017). This vast range of environmental conditions makes them useful for this type of study and may explain why they predict temperature better than precipitation.

Based on results of significant crown height variables, the stepwise regression models proposed for estimating temperature and precipitation would not prove to be as accurate or useful for sites with only mesodont, but would be beneficial for sites with brachydont, hypsodont, and hypseledont taxa. The stepwise regression models would also be less useful for many climate predictions at sites early in the Cenozoic before the appearance of hypselodont taxa around 37 million years ago. However, sites with a relatively complete taxa list would allow for more accurate results as mean crown height alone was a highly significant predictor of climate and does not have the same restrictions as the other stepwise model predictors (Appendix B). Mean crown height allows these methods to extend back prior to 37 Ma.

For each Ordinary Kriging ran, the root-mean-square standardize error vslue was noted (Table 7). Using Ordinary Kriging, standard error maps were created to highlight regions where predictions differed the most from known climate data (Figure 4), and therefore could be improved upon in these areas. By comparing the maps of known climate data to predicted climate data (Figures 5-8), trends in accuracy can be more clearly examined. Models were not mapped for Precipitation of the Coldest Quarter, Precipitation of Driest Month, Precipitation of Driest Quarter, and Temperature Annual Range, as the r^2 values were low (Table 4). Mean Annual Temperature (Figure 5) shows a north-south gradient in both the predicted and known maps with temperatures increasing to the south. Annual Precipitation (Figure 5) shows more of an east-west gradient with higher levels of precipitation to the east, specifically the Southeast. For Annual Precipitation (Figure 5), general trends were captured throughout North America.

Table 7. Root-mean-square standardize for each Ordinary Kriging ran to compute prediction models

Bioclimatic Variable	**Root-mean-square Standardized Error**
Mean Annual Temperature	0.969
Temperature Seasonality	1.140
Maximum Temperature of the Warmest Month	0.969
Minimum Temperature of the Coldest Month	0.989
Annual Precipitation	0.975
Precipitation of the Wettest Month	1.010
Precipitation of the Wettest Quarter	1.011
Precipitation of the Warmest Quarter	1.005

The locations with the lowest prediction accuracy was in mountainous areas where elevation, and by association climate, changes are most dramatic and especially along coastal regions where training data points were missing. The Great Lakes also show disparity due to no sample points being derived from non-terrestrial habitats. As climate data were interpolated across only 100 random points, prediction maps did not often reveal small localized changes in climate or detect “hotspots” where temperature or precipitation varied from surrounding areas well when compared to known climate data (Figures 5-8). In the future, utilizing a larger and more comprehensive training data-set with more than 100 points would likely improve the accuracy of predictions in the topographically complex western region of North America and the coast.

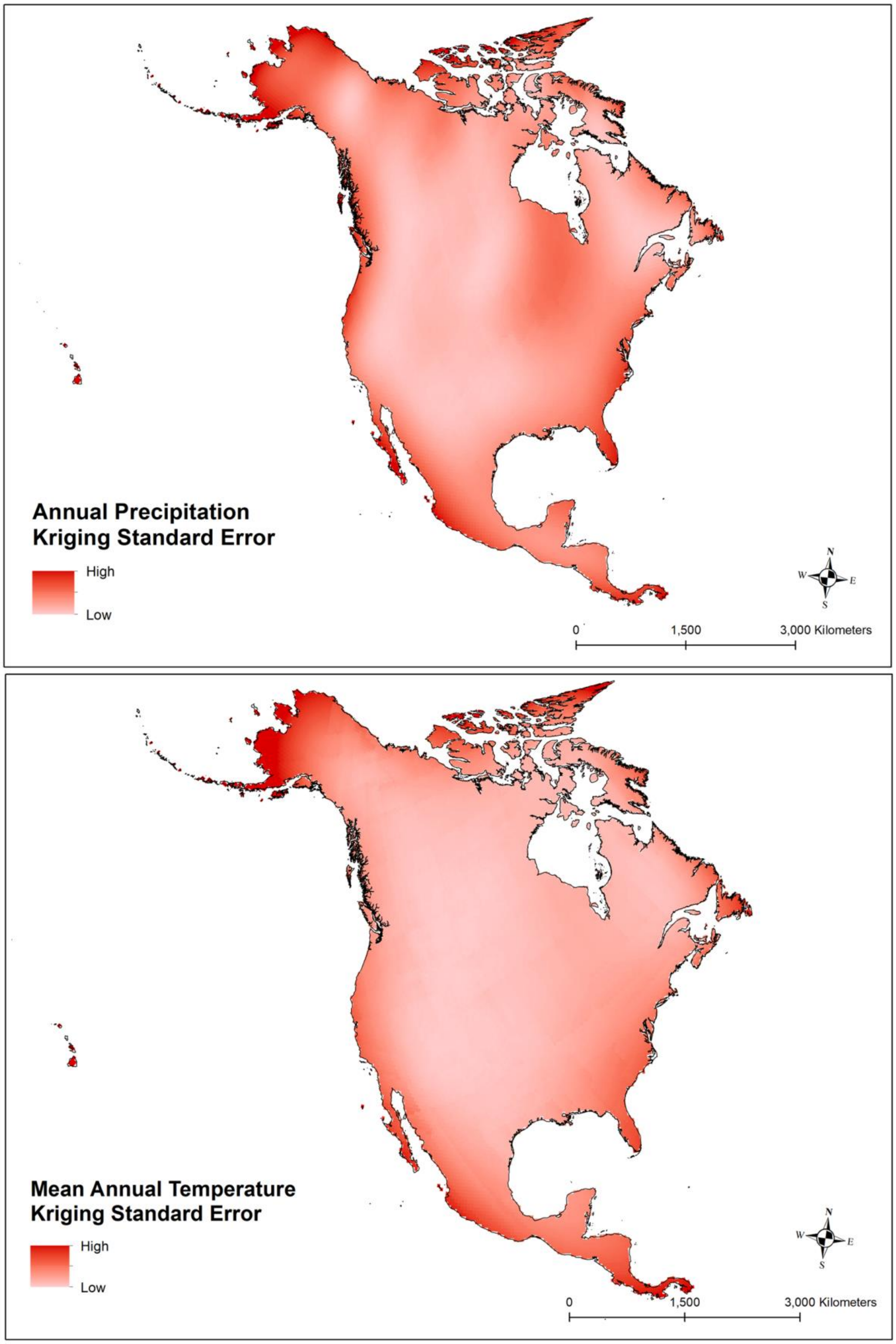

Figure 4. Standard error predictions from Kriging analysis on predicted annual precipitation and mean annual temperature displaying where predictions were most accurate (lighter red) and least accurate (darker red)

Annual Precipitation predictions (Figure 5) were still able to pick up on a ‘bullseye’ effect of lower precipitation in the western mountainous region with precipitation increasing in concentric rings, correctly representing the signal from known climate data. However, the known annual precipitation gradients in the west appear more longitudinal as they shift to the east. The western coast stretching from California to Alaska has higher precipitation estimates, as is expected from most coastal areas, than predicted due to a lack of training data set points along the coast, as previously mentioned. The eastern coast captures annual precipitation gradients fairly closely. The Southeast into the Northeast and Midwest has estimates falling within the same ranges as known precipitation data. Central America also has annual precipitation estimates closely matching known annual precipation values with some locations in Panama not reaching quite as high of values as the known data. The Arctic matched known data well, with very low annual precipitation values.

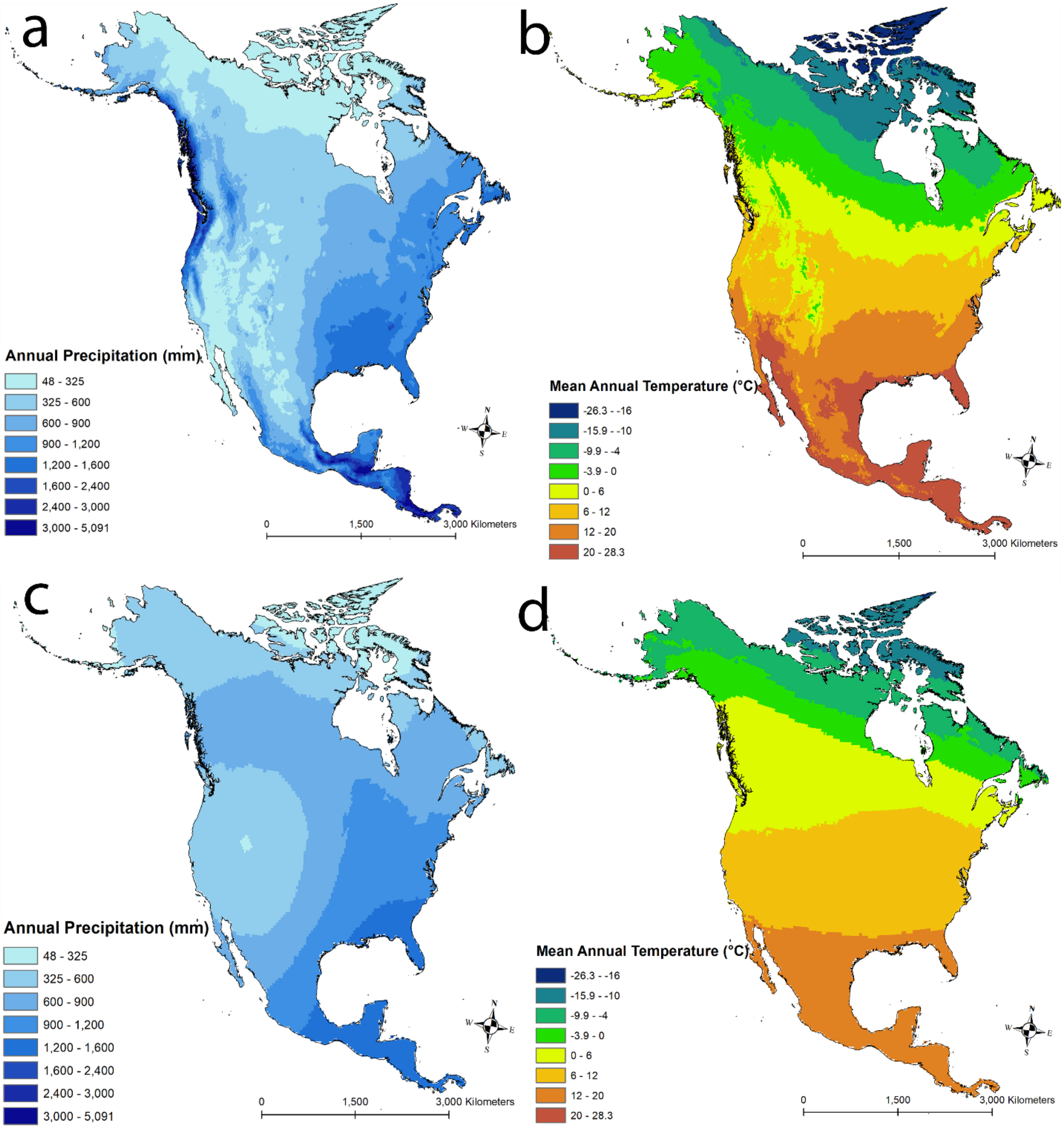

Figure 5. Current (1970-2000) North America annual precipitation (a) and mean annual temperature (b) based on WorldClim bioclimatic data and predicted annual precipitation (c) and mean annual temperature (d) using known crown height data as a proxy

Precipitation of the Warmest Quarter (Figure 6) represented the same prediction trends as Annual Precipitation but with a larger bullseye around the western mountains. Precipitation of the Wettest Month (Figure 6) predictions only predicted the lowest values in the Arctic and never identified the highest precipitation values along the coast or into Central America. However, overall patterns of increased precipitation towards the Southeast were predicted, as well as moderate to low levels predicted throughout most of North America. Some local increases in precipitation which match known climate data were predicted in western Canada in British Columbia and Alberta. Precipitation of the Wettest Quarter (Figure 7) followed along with the other precipitation prediction trends including underpredicting in areas across central and western North America.

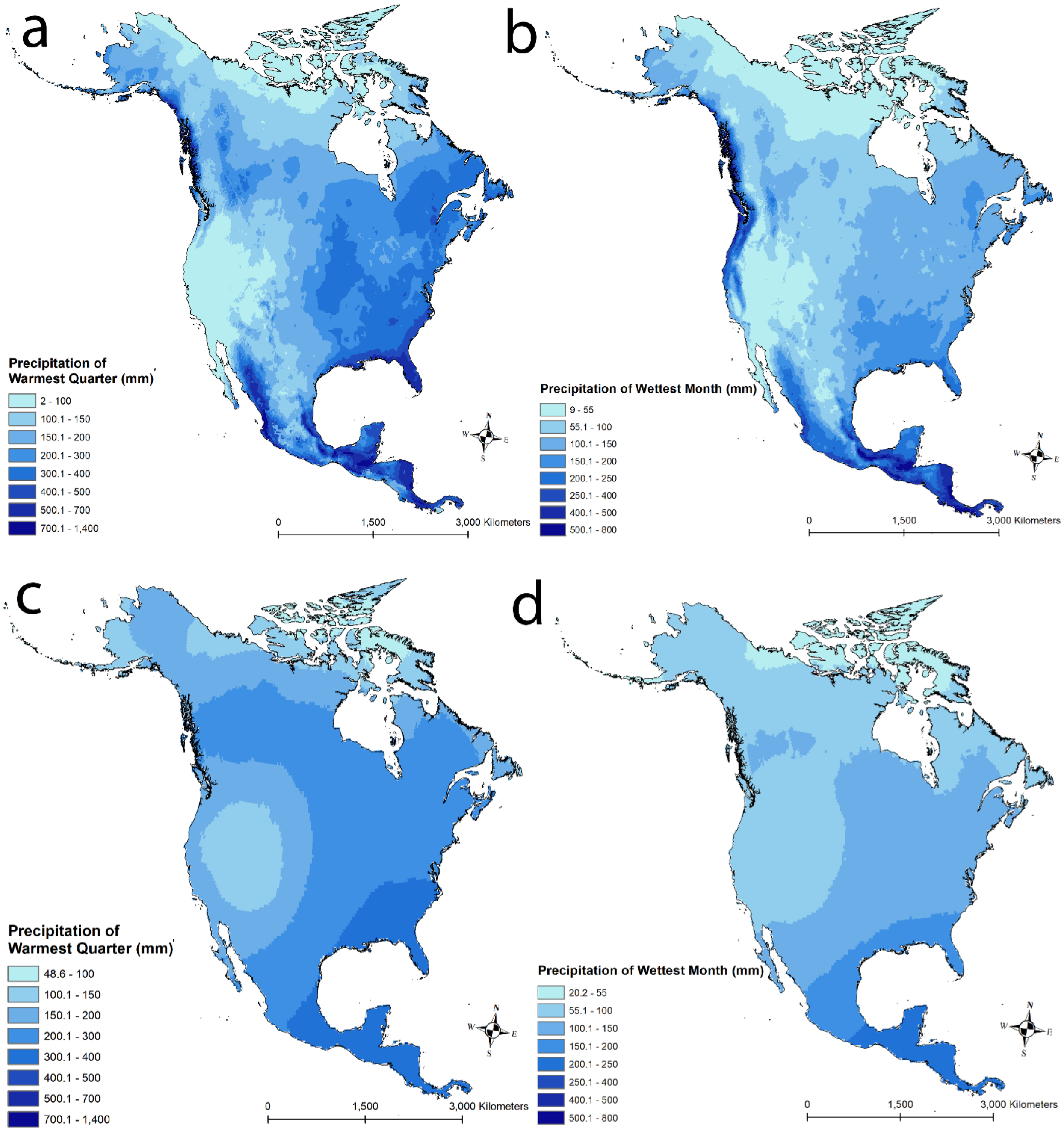

Figure 6. Current (1970-2000) North America precipitation of the warmest quarter (a) and precipitation of the wettest month (b) based on WorldClim bioclimatic data and predicted precipitation of the warmest quarter (c) and precipitation of the wettest month (d) using known crown height data as a proxy

Mean Annual Temperature predictions (Figure 5) captured the north-south trend of temperature increasing southward, but like the precipitation models the highest and lowest temperatures seen today were not predicted in the northern most parts of the Arctic and Florida into Mexico and Central America, respectively. Alaskan predictions for Mean Annual Temperature did not show temperatures as cold as they actually are found in the north and did not pick up on warmer temperatures in the Alaskan Peninsula. Fine-scale mountainous changes in Mean Annual Temperature were not detected, as was expected with limited training data points. Overall latitudinal banding temperature gradients matched fairly well with known data. Overestimates of Mean Annual Temperature were predicted in central and southeastern North America, excluding Florida where it was slightly underestimated.

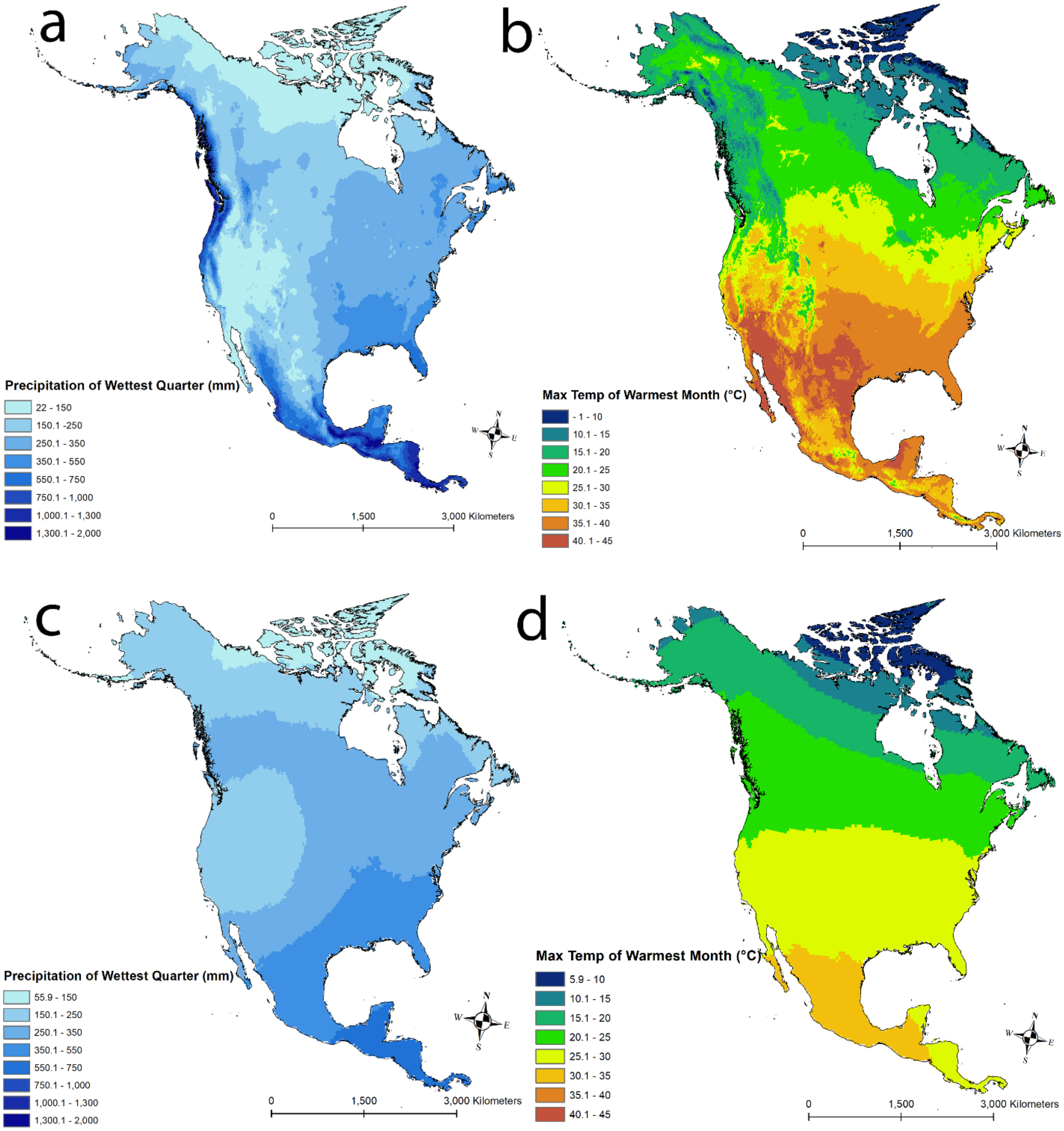

Figure 7. Current (1970-2000) North America precipitation of the wettest quarter (a) and maximum temperature of the warmest month (b) based on WorldClim bioclimatic data and predicted precipitation of the wettest quarter (c) and maximum temperature of the warmest month (d) using known crown height data as a proxy.

Maximum Temperature of the Warmest Month (Figure 7) followed the north-south gradient while picking up even less of an increase in temperature in the southwestern United

States and into Mexico. A slight decrease in Maximum Temperature of the Warmest Month was predicted in Panama matching known climate patterns. Due to quickly changing elevation in mountains, the western mountains produced a more complex trend of values which the predictions were unable to capture therefore much of that area is predicted to have a higher Maximum Temperature of the Warmest Month than is actually found today in certain parts. Some areas of British Columbia towards the west coast were predicted to have slightly higher temperatures and central Alaska was predicted to have a slightly colder value than is known. Predictions in the Arctic and the northeastern United States into Quebec have the closest fit to known climate data. Minimum Temperature of the Coldest Month (Figure 8) did not have as much disparity in the western mountains, where only one spot underpredicted temperature. Just like the Maximum Temperature of the Warmest Month, the highest and lowest predicted values in the north and south of the map were not captured. However, one area of Panama did predict a warmer climate, which was comparable to the known data. Overall, warmer values were predicted across Canada and slightly colder in Alaska. Temperature Seasonality (Figure 8) greatly overestimated values all throughout the Arctic, Alaska, and Canada. Temperature predictions along the Western Coast overestimated temperature seasonality as well. The model better predicted values along eastern North America and into Mexico and Central America.

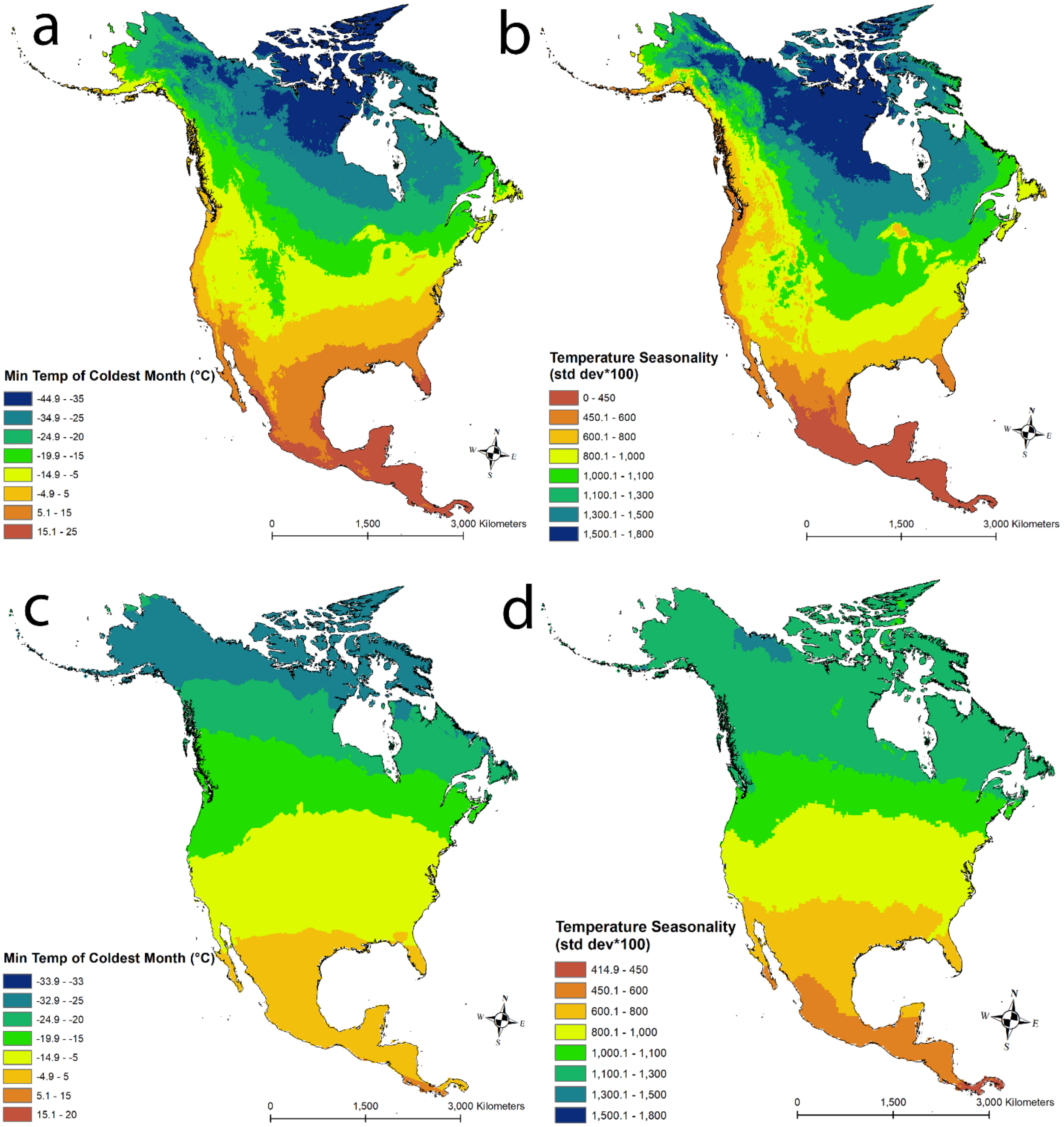

Figure 8. Current (1970-2000) North America minimum temperature of the coldest month (a) and temperature seasonality (b) based on WorldClim bioclimatic data and predicted minimum temperature of the coldest month (c) and temperature seasonality (d) using known crown height data as a proxy

For Mean Annual Temperature (Figure 5), trends across the map were predicted more accurately than they were for Annual Precipitation (Figure 5). The mountainous region of western North America had the most disparity in prediction values once again, due to high variance in elevation over short distances (Figures 5-8).

Fossil Sites

A region of interest is the Central Great Plains, which has the most complete record over the past 37 million years and many trends in climate can be observed. Mulitple warming and cooling events can be tracked within this region through time. The early Miocene (Mi-1) Glaciation event near the Oligocene/Miocene boundary coincides with a drop in Mean Annual Temperature estimates from approximately 20ºC to approximately 11-13ºC. Temperature then spikes back up to 15ºC during the MMCO before dropping back down in temperature reaching single digit temperature estimates at the onset of the Pliocene/Pleistocene boundary. One locality to address in detail would be the Sharps Formation, which ranges in age from 30-23 Ma. Compared to localities spanning the same time period, the estimated Mean Annual Temperature is approximately 10ºC warmer and several hundred millimeters wetter than other annual precipitation estimates. This could be due to the time interval for this formation being significantly longer than the other localities examined and also the fact many recorded species are from the early part of that interval. Caution should be taken when comparing localities with such long time spans, due to species adapting to a wide range of changing climatic conditions at the time and then estimates simply averaging these adaptations instead of detecting trends over time.

Localities across regions can be analyzed within time periods to compare climate changes and whether they occurred contemporaneously between regions in North America (Appendix B). In the Late Eocene, locations in the Central Great Plains show warmer temperatures, and by association wetter climate estimates than the Northern Great Plains, which were colder and drier.

During the Late Eocene, temperature estimates fell below 20ºC and precipitation estimates fell below 1500 mm only in the Northern Great Plains. Given the latitudinal gradient of temperature, these estimates fall in line with what would be expected.

In the Early Oligocene, the Central Great Plains and Northern Great Plains both had relatively high temperature and precipitation estimates, while the Pacific Northwest had lower estimates (Appendix B). The Central Great Plains estimates only fell by approximately 1ºC through the Late Oligocene, while the Northern Great Plains increased in temperature and precipitation. During the Oligocene, some Central Great Plain estimates dropped below 20ºC for the first time, around 30 Ma. Lower temperature estimates would be explained by the Early Oligocene glaciation. Once again, latitudinal trends in temperature and precipitation explain higher temperatures to the south.

Across regions, temperature and precipitation estimates continued to drop into the Late Oligocene with a high temperature of 15.8ºC in the Northern Great Plains and a fairly similar estimate of 14.6ºC in the Pacific Northwest (Appendix B). All lower temperatures at this time period are found in the Pacific Northwest. Relatively similar estimates are to be expected at this latitude. The Central Great Plains and Pacific Northwest were estimated with temperatures approximately 10ºC colder and precipitation several hundred millimeters less than their earliest estimates. Steady decreases in temperature and precipitation were estimated into the Early Miocene with highs in the California Coast around 17 Ma, just prior to the Middle Miocene. This time period is the first where the California Coast is represented.

An increase in both temperature and precipitation predictions was seen around the late Early Miocene and into the Middle Miocene, in accordance with the onset of the MMCO (Appendix B). The California Coast and Northern Great Basin had the highest estimates

(21ºC/1539 mm and 17ºC/1356 mm), and the Northern Great Plains and the Central Great Plains had estimates close to 10ºC and approximately 400 mm less. At this time it appears a more longitudinal gradient is evident in climate change. Similar to the Early Miocene, increased tectonic activity on the western coast during the Miocene played a role in warmer temperatures and increased precipitation (Liu & Stegman 2012; Kent-Corson et al. 2013). The Late Miocene experienced lower temperatures and precipitation amounts after the Mid-Miocene spike, with a high temperature of 13.5ºC and 1305 mm precipitation in the Pacific Northwest and a low of 5.63ºC and 1062 mm in the Northern Great Basin. Unforunately, this time period is not well represented with only four localities preserved; however all localities in the Pacific Northwest have higher estimates than the Northern Great Basin contrary to what would be expected latitudinally. Sites in the Pacific Northwest from Oregon may be showing increased temperature due to the volcanic activity at the time (Retallack 2007), and a selection for higher crowned species to account for the excess of ash in their diets, compared to more tectonically stable regions.

Early Pliocene Mean Annual Temperature estimates all dropped below 10ºC and precipitation only ever slightly rose above 1000 mm except in the Southern Great Basin and one locality in the Central Great Plains (Appendix B). Two Mean Annual Temperature estimates drop to approximately -1.00ºC with low precipitation estimates of approximately 600 mm in the Northern Great Basin and another locality in the Central Great Plains. The Pacific Northwest also had low prediction estimates for precipitation and temperature. Notably high estimates from Arizona and Kansas are coupled with an equally low estimate at the same time interval, suggesting perhaps the high estimates are artifacts of preservation bias. A site in Mexico in the

Southern Great Basin, has a moderately high estimate of approximately 13ºC and 1222 mm, which would be expected from such a southern location.

Late Pliocene and Early Pleistocene estimates continue the trend of colder climates with all predictions in the single digits for temperature, and two localities in the Central Great Plains and the Northern Great Basin not reaching above 1ºC (Appendix B). This time interval is represented by mostly southern regions with an overall trend in warmer climates to the east. Kansas in the Central Great Plains had estimates colder than any site in the south which is likely attributable to its latitude.

When examining comparisons across the Miocene of Nebraska, California, and Oregon, (Table 6) temperature and precipitation estimates were greater in Oregon than Nebraska during the early Hemingfordian. The early Barstovian estimated an increase in precipitation in Nebraska and California, with a decrease in precipitation in Oregon. Temperatures increased in California and Nebraska, but decreased in Oregon for the same time period. Into the late Barstovian, Oregon and California had increased temperature estimates and Nebraska had a lower estimate. Precipitation increased in Oregon and California, while in Nebraska it fell. The middle Clarendonian estimated fairly equal amounts of precipitation in California and Nebraska, which was a decrease in California and Nebraska from the late Barstovian. In both California and Nebraska, temperatures fell from the late Barstovian on. Temperatures were high in California and Oregon in the late Clarendonian, with very high precipitation estimates in California and Oregon as well. In contrast, Nebraska temperature estimates were approximately 9ºC cooler than Oregon with precipitation estimates slightly decreased from the middle Clarendonian.

Overall, precipitation slowly decreased in Nebraska through time after the early Barstovian, where the highest precipitation estimate was predicted (Table 6). Californian precipitation increased through the Hemingfordian into the late Barstovian and then decreased in the middle Clarendonian. Oregon precipitation estimates fluctuated through time with peaks in the early Hemingfordian and late Barstovian. Temperatures across the three states all showed an increase in the Barstovian, occurring in the early Barstovian in Nebraska and late Barstovian in California and Oregon, with California estimated with the highest temperatures. Oregon temperature estimates fluctuated within approximately 11ºC through time, while Nebraska and California fluctuated within approximately 14.5ºC. Higher precipitation and temperature estimates were found in California more frequently than either Nebraska or Oregon.

Mountainous environments are hotspots for ecological diversity due to the heterogenenous topography, which yields varied habitats that appeal to a wide variety of species (Barnosky and Carassco 2002; Badgley 2010; Finarelli and Badgley 2010; Badgley et al. 2014 2017; Antonelli et al. 2018). Areas such as these are fairly accurate representations of local climate, since much of the species diversification that occurs there is created in situ, rather than containing species which migrated to the area (Badgley 2010; Badgley et al. 2014, 2017; Antonelli et al. 2018).

The western United States was a very tectonically active region throughout the Miocene. Tectonic activity led to the creation of mountainous regions, like the Cascade and Sierra Nevada, expanded flatlands such as the Basin and Range, and volcanism in the Columbia Plateau all warping the landscape during the Miocene (Kent-Corson et al. 2013). Many climatic trends are linked to mountains, including precipitation, rain shadows, temperature gradients, and interference with global circulation patterns (Kent-Corson et al. 2013; Antonelli et al. 2018). When examining precipitation patterns, an increase is seen on the windward side and a rain shadow is found on the leeward side of the mountain (Antonelli et al. 2018). Studies of paleosols proxies have shown that past temperature and precipitation have a positive correlation, with warmer times having higher precipitation levels (Retallack 2007).

Flood basalts erupting in the Columbia River during the Middle Miocene played a role in Oregon's warm wet climate, as these eruptions did not create rain shadows (Retallack 2007; Zachos 2001, 2008; Kürschner et al. 2008; Kasbohm and Schoene, 2018). Rather, these basalt eruptions, as well as Eocene volcanism, did aid in warming temperatures at the time, as water vapor and carbon dioxide were released into the atmosphere (Courtillot 2002; Retallack 2007). As the tectonic plates have shifted, the Yellowstone hotspot caused volcanism and rapid tectonic uplift in Oregon around 16 Ma (Zachos 2001, 2008; Kürschner et al. 2008; Liu and Stegman 2012; Kent-Corson et al. 2013; Kasbohm and Schoene 2018).

Paleoclimate estimates of temperature and precipitation have primarily been conducted in the Central Great Plains with a few from the Pacific Northwest, Northern Great Basin, and the California Coast which are able to be compared with this study. Retallack (2007) has reported a large sample of sites from western North America through studying paleosols. Mean Annual Precipiation estimates from both the Retallack (2007) study and this study show a decline in precipitation through time from approximately 36 Ma to 4.9 Ma in Nebraska. However, precipitation estimates are consistently higher in this study, occasionally as much as over 1000 mm greater. Estimates become closer, only 34 mm different, when examining localities closer to the present (approximately 12 – 4.9 Ma). Temperature estimates from Nebraska are between 10 to 15ºC warmer in this study until 23 Ma when they become approximately 5ºC warmer, and eventually fell right in between estimates from 12.1 – 9 Ma. Paleoprecipitation estimates follow the same trend when compared to localities in South Dakota from 33.7 – 18.8 Ma with estimates from this study being greater than estimates found by Retallack (2007) study. Estimates are never as different as they were in Nebraska and begin to be fairly close around 28.1 Ma with a maximum difference of approximately 270 mm and a minimum difference of approximately 55 mm. Similarly, temperature estimates are approximately 13ºC warmer in this study than Retallack (2007) until 30 – 28.1 Ma when they become approximately 7ºC warmer and within 1ºC of the Retallack (2007) estimates 28.1 – 23 Ma. Unlike Nebraska and South Dakota, precipitation estimates from Kansas approximately 2.5 – 1.9 Ma were lower in this study than Retallack (2007) by approximately 232 mm. Mean Annual Temperature was estimated approximately 8ºC colder in this study.

In the Pacific Northwest, Washington and Oregon have localities with comparable paleoclimate estimates. The John Day Fossil Beds National Monument has many well documented localities available for paleosols comparisons (Retallack 2007). The early Oligocene localities, ranging from 31.42 – 29.09 Ma, have annual precipitation estimates between 683 - 853 mm, well under the 1244 mm estimate from this study. The mean annual temperature estimate from this study, 11.5ºC, falls within the range of 6.8 – 13.03ºC estimate from paleosols for the same time period. Mid-Oligocene estimates from John Day (29.07 – 26.58 Ma) for precipitation in this study were from approximately 1208 – 1285 mm, far higher than paleosols estimates of 654 – 683 mm. Mean annual temperature estimates were also slightly higher in this study, from 12.6 to 12.9ºC, compared to 8.5ºC from paleosols. From the late Oligocene, 26.57 – 23.79 Ma, Retallack (2007) estimated an annual precipitation of 617 – 686 mm, compared to 1170 – 1339 mm in this study. Temperature estimates from that time were closer ranging from 9 – 14.6ºC in this study compared to 6.5 – 8.5ºC from paleosols. Estimates from this study match most closely with the early Miocene (23.79 – 18. 467 Ma) of John Day with precipitation estimated at 1148 mm in this study and temperature estimates of 10.5ºC compared to 592 – 1062 mm and 4.7 – 14.7ºC from the Retallack (2007) study of paleosols.

Leaf physiognomic characters have estimated a Mean Annual Temperature of approximately 17ºC and annual precipitation of approximately 1270 mm from the middle Miocene age Mascall Formation (Early Barstovian NALMA) (Chaney and Axelrod 1959; Graham 1999; Retallack 2007, Dillhoff et al. 2009). While other studies using leaf morphology estimated an annual precipitation of approximately 620 mm/yr for the Mascall Formation (Yang et al. 2011). Another method of estimating paleoclimate from alfisols predicted a Mean Annual Precipitation of 1000 mm and a Mean Annual Temperature of 11ºC for the Mascall Formation (Bestland and Krull 1997; Sheldon et al. 2002; Bestland et al. 2008; Drewicz and Kohn 2017). These are closely comparable to estimates from this study, including an estimated Mean Annual Temperature of 15.27ºC and an annual precipitation of approximately 1061 mm from the early Barstovian of Oregon, and 9.99ºC and 1257 mm specifically from the Mascall Formation. The late Miocene age Shutler formation in Oregon was estimated at 1091.96 mm/yr which is approximately 342 mm greater than Retallack (2007) and 10.71ºC, only 1.69ºC warmer than Retallack (2007) showing closer estimates than most sites in the Central Great Plains. Annual Precipitation estimates from the Ringold Formation in Washington of 855 mm/yr fall within the range estimated from Retallack (2007) of 1036 – 845 mm. However, Mean Annual Temperature was estimated at 3ºC, whereas Retallack (2007) had a range of 9.4 – 11.8ºC.

Only one site from the Northern Great Plains, the Cook Ranch Formation, had been previously studied for paleoclimate estimates. Annual precipitation was estimated to be 1703 mm which is over 800 mm greater than Retallack (2007) estimated. Mean Annual Temperature estimates are over 10ºC warmer from this study. Two sites in the California Coast have annual precipitation estimates from paleosols (Smiley et al. 2017). The Cajon Formation was estimated at 1433 mm/yr in this study, with significantly less precipitation estimated from paleosols, between 740 - 800 mm ±182 mm, and similar estimates were found from the Crowder Formation of 1488 mm/yr in this study and 807 ±182 mm from the Smiley et al. (2017) study.

Many applications of this study are possible across various fields of paleontology and biology. For example, Minimum Temperature of the Coldest Month is a useful estimate for paleoherpetologists to determine which environments were too cold for some reptiles to survive in and which localities could have frozen. Species such as the beaded lizard (*Heloderma*) are not found in temperatures below 24ºC today due to metabolic requirements (Bogert and Martín del Campo 1956; Mead et al. 2012), whereas alligators are affected by temperatures below 16ºC and will stop eating if temperatures drop lower (Lance 2003). This is informative for studies of floral compositions of sites, as well as tropical broadleaf evergreen plants that do no tolerate freezing temperatures (Morin et al. 2007) and have root growth affected by low temperatures (Alvarez-Uria and Körner 2007). If it is to be assumed these species have always reacted similarly to temperature, estimates of the Minimum Temperature of the Coldest Month would impact which species are expected to be found at a past site.

One benefit of this method of analysis is the applicability to any site with a moderately well-defined taxa list. A local example of interest would be the Gray Fossil Site in northeastern Tennessee. This site is interpreted as a sinkhole which, over thousands of years, filled into a lake within a dense canopied forest approximately 4.9-4.5 Ma. A wide variety of flora and fauna are known from the site, including mammals, reptiles, and amphibians (Parmalee et al. 2002; Wallace and Wang 2004; Shunk et al. 2006, 2009; Zobaa et al. 2009, 2011; Boardman and Schubert 2011; Ochoa et al. 2012; 2016; Jasinski 2013; Worobiec et al. 2013; Bourque and

Schubert 2015; Crowe 2017; Samuels et al. 2018). Given the age and occurrences of frost intolerant plants and reptiles at the site, estimates would be expected to be relatively warm and wet in this area. Applying the equations for Mean Annual Temperature and Annual Precipitation yielded estimates of 16.8ºC and 1342.6 mm, which fall in line with a warm, wet forested environment. These estimates would be contemporaneous with the annual temperature of Knoxville, Tennessee and the annual precipitation of Tampa, Florida (NOAA, 2017). When looking at the Minimum Temperature of the Coldest Month, it was estimated to be 2.60ºC, which is above freezing and would be expected in order to accommodate reptiles and evergreen plants.

One take away of key importance of this study is that it provides a new proxy for precipitation and temperature complimenting methods like stable isotopes and leaf margin analysis, which can be used in areas where other proxies might not be manageable or possible. Results from this study can be useful in a broader context within the field providing a new proxy for past climate, which would facilitate comparison between mammal adaptations and changes in climate. These estimates can be compared to results fom other proxies including ungulate studies. Additionally, the equations can be applied to any fossil locality with a known taxa list of small mammals to provide insight to in situ climate patterns, particularly working well for localities after the appearance of hypselodonty and containing brachyodont and hypselodont taxa. To appropriately examine a complete ecosystem response to climate change, both small and large mammals need to be studied to assess community-wide transformation. By studying these past communities, we can shed light on what changes in ecosystems are to be expected if current temperatures continue to increase. Through the use of ecometrics, this study can help further the understanding of past environmental changes on more precise regional scales.

Future Research

While this research gives insights into novel methods for estimating regional and continental paleoclimate through time, many improvements can be made. For instance, increasing the sample points (random points) from 100 to 500 or even 1,000 would be beneficial in capturing more nuanced climate changes. Areas where points were lacking in this study, the coasts and throughout more fine-scale elevation changes within mountainous regions would help estimates in those areas, and prevent some parts of the continent being estimated by interpolation alone. With more points, a mesoenviromental scale analysis could be conducted, giving an even more regional climate approximation.

In addition to increasing the number of sample points, comparing crown heights across ecoregions would be another way to compare climate trends. One way to do this would be to map ecoregions and place an equal number of points within in each ecoregion and compare crown height regression data between regions. Mapping past climate for intervals of particular interest in terms of substantial climate change, such as the Pleistocene and the Paleocene/Eocene boundary, would allow for comparisons across more warming periods and also an examination of colder climates.

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APPENDICES

Appendix A. List of the 100 random training data set points with corresponding latitude, longitude, and all occurrences of species of small mammals (listed within the given families).

Point #	1	2	3	4	5	6
Lat	57.9956	64.7187	50.0905	38.9513	58.3632	56.3051
Long	-110.555	-124.832	-71.5972	-97.8233	-127.231	-96.9445
Castoridae	*Castor canadensis*	*Castor canadensis*	*Castor canadensis*	*Castor canadensis*	*Castor canadensis*	*Castor canadensis*
Cricetidae	*Microtus pennsylvanicus, Microtus xanthognathus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Microtus miurus, Microtus oeconomus, Microtus pennsylvanicus, Microtus xanthognathus, Myodes rutilus, Ondatra zibethicus, Synaptomys borealis*	*Microtus chrotorrhinus, Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis, Synaptomys cooperi*	*Microtus ochrogaster, Microtus pinetorum, Neotoma floridana, Ondatra zibethicus, Onychomys leucogaster, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys megalotis, Reithrodontomys montanus, Sigmodon hispidus, Synaptomys cooperi*	*Lemmus trimucronatus, Microtus longicaudus, Microtus pennsylvaticus, Neototoma cinerea, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*
Cuniculidae						
Dasyproctidae						
Dipodidae	*Zapus hudsonius*		*Napaeozapus insignis, Zapus hudsonius*	*Zapus hudsonius*	*Zapus hudsonius, Zapus princeps*	*Zapus hudsonius*
Erethizontidae	*Erethizon dorsatum*	*Erethizon dorsatum*	*Erethizon dorsatum*		*Erethizon dorsatum*	*Erethizon dorsatum*
Geomyidae				*Geomys bursarius*		
Heteromyidae				*Chaetodipis hispidus, Dipodomys ordii, Perognathus flavescens*		
Leporidae	*Lepus americanus*	*Lepus americanus*	*Lepus americanus*	*Lepus californicus, Sylvilagus floridanis*	*Lepus americanus*	*Lepus americanus*
Ochotonidae		*Ochotona collaris*				

Point #	7	8	9	10	11	12
Lat	25.0612	48.8181	59.8965	74.9645	79.8326	59.4831
Long	-102.24	-118.331	-108.099	-89.591	-84.1009	-117.149
Castoridae		*Castor canadensis*	*Castor canadensis*			*Castor canadensis*
Cricetidae	*Neotoma goldmani, Neotoma leucodon, Neotoma mexicana, Onychomys arenicola, Peromyscus eremicus, Peromyscus maniculatus, Peromyscus melanophrys, Peromyscus pectoralis, Reithrodontomys fulvescens, Reithrodontomys megalotis, Sigmodon hispidus*	*Microtus longicaudus, Microtus montanus, Microtus pennsylvanicus, Microtus richardsoni, Myodes gapperi, Neotoma cinerea, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys intermedius, Synaptomys borealis*	*Microtus pennsylvanicus, Microtus xanthognathus, Myodes gapperi, Ondatra zibethicus, Phenacomys ungava, Synaptomys borealis*			*Microtus pennsylvanicus, Microtus xanthognathus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*
Cuniculidae						
Dasyproctidae						
Dipodidae		*Zapus princeps*	*Zapus hudsonius*			*Zapus hudsonius*
Erethizontidae		*Erethizon dorsatum*	*Erethizon dorsatum*			*Erethizon dorsatum*
Geomyidae		*Thomomys talpoides*				
Heteromyidae	*Chaetodipus eremicus, Chaetodipus hispidus, Chaetodipus nelsoni, Dipodomys merriami, Dipodomys nelsoni, Dipodomys ordii, Perognathus flavus*	*Perognathus parvus*				
Leporidae	*Lepus californicus, Sylvilagus audubonii*	*Lepus amercanus, Sylvilagus nuttallii*	*Lepus americanus*	*Lepus arcticus*	*Lepus arcticus*	*Lepus americanus*
Ochotonidae		*Ochotona princeps*				

Point #	13	14	15	16	17	18
Lat	68.9046	48.1304	19.9091	8.4805	36.001	52.0824
Long	-159.676	-57.3896	-100.357	-77.7945	-109.73	-66.9829
Castoridae					*Castor canadensis*	*Castor canadensis*
Cricetidae	*Dicrostonyx groenlandicus, Lemmus trimucronatus, Microtus miurus, Microtus oeconomus, Myodes rutilus*	*Ondatra zibethicus*	*Baiomys taylori, Neotoma mexicana, Oryzomys couesi, Peromyscus difficilis, Peromyscus gratus, Peromyscus maniculatus, Peromyscus melanophrys, Peromyscus melanotis, Peromyscus truei, Reithrodontomys fulvescens, Reithrodontomys megalotis, Reithrodontomys microdon, Reithrodontomys sumichrasti, Sigmodon hispidus, Sigmodon leucotis*	*Oryzomys couesi, Oryzomys talamanca, Reithrodontomys darienensis, Sigmodontomys alfari, Tylomys watsoni, Zygodontomys brevicauda*	*Neotoma albigula, Neotoma cinerea, Neotoma mexicana, Ondatra zibethicus, Onychomys leucogaster, Peromyscus boylii, Peromyscus crinitus, Peromyscus maniculatus, Peromyscus nasutus, Peromyscus truei, Reithrodontomys megalotis*	*Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*
Cuniculidae				*Cuniculus paca*		
Dasyproctidae				*Dasyprocta punctata*		
Dipodidae						*Zapus hudsonius*
Erethizontidae				*Coendou rothschildi*		*Erethizon dorsatum*
Geomyidae			*Thomomys umbrinus*	*Orthogeomys dariensis*	*Thomomys bottae*	
Heteromyidae			*Liomys irroratus, Perognathus flavus*	*Heteromys desmarestianus*	*Dipodomys ordii, Dipodomys spectabilis, Perognathus flavus, Perognathus flavescens*	
Leporidae		*Lepus americanus, Lepus arcticus*	*Lepus callotis, Sylvilagus audubonii*		*Lepus californicus, Sylvilagus audubonii, Sylvilagus nuttallii*	*Lepus americanus*
Ochotonidae						

Point #	19	20	21	22	23	24
Lat	35.7787	48.7077	61.9291	39.9865	14.6652	69.8907
Long	-120.54	-103.302	-152.017	-81.8898	-87.8831	-143.989
Castoridae		*Castor canadensis*	*Castor canadensis*	*Castor canadensis*		
Cricetidae	*Microtus californicus, Neotoma fuscipes, Neotoma lepida, Peromyscus californicus, Peromyscus maniculatus, Peromyscus truei, Reithrodontomys megalotis*	*Microtus ochrogaster, Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Onychomys leucogaster, Peromyscus leucopus, Peromyscus maniculatus*	*Lemmus trimucronatus, Microtus miurus, Microtus oeconomus, Microtus pennsylvanicus, Myodes rutilus, Ondatra zibethicus, Synaptomys borealis*	*Microtus ochrogaster, Microtus pennsylvanicus, Microtus pinetorum, Ondatra zibethicus, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys humilis, Synaptomys cooperi*	*Baiomys musculus, Neotoma chrysomelas, Nyctomys sumichrasti, Oligoryzomys fulvescens, Oryzomys alfaroi, Oryzomys couesi, Handleyomys saturatior, Ototylomys phyllotis, Peromyscus beatae, Peromyscus mexicanus, Reithrodontomys fulvescens, Reithrodontomys mexicanus, Reithrodontomys sumichrasti, Scotinomys teguina, Sigmodon hispidus, Tylomys nudicaudus*	*Dicrostonyx groenlandicus, Lemmus trimucronatus, Microtus oeconomus*
Cuniculidae					*Cuniculus paca*	
Dasyproctidae					*Dasyprocta punctata*	
Dipodidae		*Zapus princeps*	*Zapus hudsonius*	*Zapus hudsonius*		
Erethizontidae		*Erethizon dorsatum*	*Erethizon dorsatum*		*Sphiggurus mexicanus*	*Erethizon dorsatum*
Geomyidae	*Thomomys bottae*	*Thomomys talpoides*				
Heteromyidae	*Chaetodipus californicus, Dipodomys heermanni, Perognathus inornatus, Perognathus longimembris*	*Perognathus fasciatus*			*Heteromys desmarestianus*	
Leporidae	*Lepus californicus, Sylvilagus audubonii, Sylvilagus bachmani*	*Lepus townsendii, Sylvilagus nuttallii*	*Lepus americanus*	*Sylvilagus flordanus*	*Sylvilagus flordanus*	
Ochotonidae			*Ochotona collaris*			

Point #	25	26	27	28	29	30
Lat	63.966	39.9702	55.5015	52.1975	71.3147	58.8526
Long	-133.936	-105.979	-69.0055	-104.875	-81.2864	-135.725
Castoridae	*Castor canadensis*	*Castor canadensis*	*Castor canadensis*	*Castor canadensis*		*Castor canadensis*
Cricetidae	*Dicrostonys nunatakensis, Lemmus trimucronatus, Microtus longicaudus, Microtus miurus, Microtus oeconomus, Microtus pennsylvanicus, Microtus xanthognathus, Myodes rutilus, Ondatra zibethicus, Synaptomys borealis*	*Lemmiscus curtatus, Microtus longicaudus, Microtus montanus, Microtus pennsylvanicus, Myodes gapperi, Neotoma cinerea, Ondatra zibethicus, Peromyscus boylii, Peromyscus maniculatus, Peromyscus truei*	*Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Phenacomys ungava, Synaptomys borealis*	*Microtus ochrgaster, Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Onychomys leucogaster, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Dicrostonyx groenlandicus, Lemmus trimucronatus*	*Microtus longicaudus, Microtus oeconomus, Microtus pennsylvanicus, Myodes rutilus, Peromyscus keeni, Peromyscus maniculatus, Synaptomys borealis*
Cuniculidae						
Dasyproctidae						
Dipodidae	*Zapus hudsonius*	*Zapus hudsonius, Zapus princeps*		*Zapus hudsonius, Zapus princeps*		*Zapus hudsonius, Zapus princeps*
Erethizontidae	*Erethizon dorsatum*	*Erethizon dorsatum*	*Erethizon dorsatum*	*Erethizon dorsatum*		*Erethizon dorsatum*
Geomyidae		*Thomomys talpoides*		*Thomomys talpoides*		
Heteromyidae						
Leporidae	*Lepus americanus*	*Lepus americanus, Lepus californicus, Lepus townsendii, Sylvilagus audubonii, Sylv nuttallii*	*Lepus americanus*	*Lepus americanus, Lepus townsendii*	*Lepus arcticus*	*Lepus americanus*
Ochotonidae	*Ochotona collaris*	*Ochotona princeps*				

Point #	31	32	33	34	35	36
Lat	71.8876	48.6968	46.2	54.6169	64.8296	63.5378
Long	-89.2333	-66.6384	-97.7436	-115.506	-76.565	-122.041
Castoridae		*Castor canadensis*	*Castor canadensis*	*Castor canadensis*		*Castor canadensis*
Cricetidae	*Dicrostonyx groenlandicus, Lemmus trimucronatus*	*Microtus chrotorrhinus, Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Synaptomys borealis, Synaptomys cooperi*	*Microtus ochrogaster, Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Onychomys leucogaster, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys megalotis*	*Microtus ochrogaster, Microtus pennsylvanicus, Microtus xanthognathus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Dicrostonyx groenlandicus, Lemmus trimucronatus*	*Microtus pennsylvanicus, Microtus xanthognathus, Myodes rutilus, Ondatra zibethicus, Phenacomys ungava, Synaptomys borealis*
Cuniculidae						
Dasyproctidae						
Dipodidae		*Napaeozapus insignis, Zapus hudsonius*	*Zapus hudsonius, Zapus princeps*	*Zapus hudsonius, Zapus princeps*		
Erethizontidae		*Erethizon dorsatum*	*Erethizon dorsatum*	*Erethizon dorsatum*		*Erethizon dorsatum*
Geomyidae			*Geomys bursarius*			
Heteromyidae			*Perognathus fasciatus, Perognathus flavescens*			
Leporidae	*Lepus articus*	*Lepus americanus*	*Lepus townsendii, Sylvilagus floridanus*	*Lepus americanus*	*Lepus articus*	*Lepus americanus*
Ochotonidae						

Point #	37	38	39	40	41	42
Lat	48.8416	50.9227	63.419	62.7813	13.3113	39.6933
Long	-54.7269	-63.6203	-138.298	-99.6104	-83.7115	-87.1657
Castoridae		*Castor canadensis*	*Castor canadensis*			*Castor canadensis*
Cricetidae	*Ondatra zibethicus*	*Microtus chrotorrhinus, Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Lemmus trimucronatus, Microtus longicaudus, Microtus miurus, Microtus oeconomus, Microtus pennsylvanicus, Microtus xanthognathus, Myodes rutilus, Ondatra zibethicus, Peromyscus maniculatus, Synaptomys borealis*	*Dicrostonyx richardsoni, Lemmus trimucronatus, Microtus pennsylvanicus, Myodes rutilus*	*Oryzomys couesi, Sigmodontomys alfari, Sigmodon hispidus*	*Microtus ochrogaster, Microtus pennsylvanicus, Microtus pinetorum, Ondatra zibethicus, Peromyscus leucopus, Peromyscus maniculatus, Synaptomys cooperi*
Cuniculidae					*Cuniculus paca*	
Dasyproctidae					*Dasyprocta punctata*	
Dipodidae		*Zapus hudsonius*	*Zapus hudsonius*			*Zapus hudsonius*
Erethizontidae		*Erethizon dorsatum*	*Erethizon dorsatum*			
Geomyidae						
Heteromyidae						
Leporidae	*Lepus americanus*	*Lepus americanus*	*Lepus americanus*	*Lepus articus*		*Sylvilagus flordanus*
Ochotonidae			*Ochotona collaris*			

Point #	43	44	45	46	47	48
Lat	66.5677	33.6253	34.4073	42.5358	66.8795	53.6569
Long	-63.7105	-92.89	-103.421	-76.4142	-86.4902	-83.1383
Castoridae		*Castor canadensis*	*Castor canadensis*	*Castor canadensis*		*Castor canadensis*
Cricetidae	*Dicrostonyx groenlandicus, Lemmus trimucronatus*	*Microtus pinetorum, Neotoma floridana, Ochrotomys nuttalli, Ondatra zibethicus, Oryzomys palustris, Peromyscus gossypinus, Peromyscus leucopus, Peromyscus maniculatus, Sigmodon hispidus*	*Neotoma leucodon, Neotoma micropus, Ondatra zibethicus, Onychomys leucogaster, Peromyscus boylii, Peromyscus leucopus, Peromyscus maniculatus, Peromyscus truei, Reithrodontomys megalotis, Reithrodontomys montanus, Sigmodon hispidus*	*Microtus pennsylvanicus, Microtus pinetorum, Myodes gapperi, Ondatra zibethicus, Peromyscus leucopus, Peromyscus maniculatus, Synaptomys cooperi*	*Dicrostonyx groenlandicus, Lemmus trimucronatus, Myodes rutilus*	*Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*
Cuniculidae						
Dasyproctidae						
Dipodidae				*Napaeozapus insignis, Zapus hudsonius*		*Zapus hudsonius*
Erethizontidae			*Erethizon dorsatum*	*Erethizon dorsatum*		*Erethizon dorsatum*
Geomyidae			*Cratogeomys castanops, Geomys arenarius*			
Heteromyidae			*Chaetodipus hispidus, Dipodomys ordii, Dipodomys spectabilis, Perognathus flavescens, Perognathus merriami*			
Leporidae	*Lepus articus*	*Sylvilagus aquaticus , Sylvilagus floridanus*	*Lepus californicus, Sylvilagus audubonnii, Sylvilagus floridanus*	*Lepus americanus, Sylvilagus floridanus*	*Lepus arcticus*	*Lepus americanus*
Ochotonidae						

Point #	49	50	51	52	53	54
Lat	54.7904	70.2197	62.8299	17.2393	48.9863	61.4986
Long	-76.8974	-105.139	-67.8412	-90.6701	-94.1981	-142.093
Castoridae	*Castor canadensis*				*Castor canadensis*	*Castor canadensis*
Cricetidae	*Dicrostonyx hudsonius, Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Lemmus trimucronatus*	*Dicrostonyx groenlandicus, Lemmus trimucronatus*	*Oligoryzomys fulvescens, Oryzomys couesi, Oryzomys rostratus, Sigmodon hispidus, Tylomys nudicaudus*	*Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Synaptomys borealis, Synaptomys cooperi*	*Microtus longicaudus, Microtus miurus, Microtus oeconomus, Microtus pennsylvanicus, Myodes rutilus, Ondatra zibethicus, Synaptomy borealis*
Cuniculidae				*Cuniculus paca*		
Dasyproctidae				*Dasyprocta punctata*		
Dipodidae					*Napaeozapus insignis, Zapus hudsonius*	*Zapus hudsonius*
Erethizontidae	*Erethizon dorsatum*			*Sphiggurus mexicanus*	*Erethizon dorsatum*	*Erethizon dorsatum*
Geomyidae				*Orthgeomys hispidus*		
Heteromyidae				*Heteromys desmarestianus, Heteromys gaumeri*		
Leporidae	*Lepus americanus*	*Lepus articus*	*Lepus articus*		*Lepus americanus*	*Lepus americanus*
Ochotonidae						*Ochotona collaris*

Point #	55	56	57	58	59	60
Lat	48.0673	56.256	34.2095	31.1176	66.7157	75.6663
Long	-115.156	-120.884	-99.2939	-97.0083	-139.985	-91.7647
Castoridae	*Castor canadensis*	*Castor canadensis*	*Castor canadensis*	*Castor canadensis*	*Castor canadensis*	
Cricetidae	*Microtus longicaudus, Microtus pennsylvanicus, Microtus richardsoni, Myodes gapperi, Neotoma cinerea, Ondatra zibethicus, Peromyscus maniculatus, Synaptomys borealis*	*Microtus pennsylvanicus, Microtus xanthognathus, Myodes gapperi, Neotoma cinerea, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Neotoma micropus, Ondatra zibethicus, Onychomys leucogaster, Peromyscus attwateri, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys fulvescens, Reithrodontomys montanus, Sigmodon hispidus*	*Baiomys taylori, Microtus pinetorum, Neotoma floridana, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys fulvescens, Reithrodontomys montanus, Sigmodon hispidus*	*Lemmus trimucronatus, Microtus longicaudus, Microtus miurus, Microtus oeconomus, Microtus pennsylvanicus, Microtus xanthognathus, Myodes rutilus, Ondatra zibethicus, Synaptomys borealis*	
Cuniculidae						
Dasyproctidae						
Dipodidae	*Zapus princeps*	*Zapus hudsonius, Zapus princeps*				
Erethizontidae	*Erethizon dorsatum*	*Erethizon dorsatum*			*Erethizon dorsatum*	
Geomyidae	*Thomomys talpoides*		*Geomys bursarius*	*Geomys breviceps*		
Heteromyidae			*Chaetodipus hispidus, Dipodomys ordii, Perogathus flavescens*	*Chaetodipus hispidus*		
Leporidae	*Lepus americanus, Lepus townsendii*	*Lepus americanus*	*Lepus californicus, Sylvilagus audubonii, Sylvilagus floridanus*	*Lepus californicus, Sylvilagus aquaticus, Sylvilagus floridanus*	*Lepus americanus*	*Lepus articus*
Ochotonidae	*Ochotona princeps*				*Ochotona collaris*	

Point #	61	62	63	64	65	66
Lat	52.1912	56.7053	75.1983	61.231	66.3686	55.9775
Long	-110.718	-73.2094	-103.679	-163.505	-97.4325	-125.325
Castoridae	*Castor canadensis*	*Castor canadensis*		*Castor canadensis*		*Castor canadensis*
Cricetidae	*Lemmiscus curtatus, Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus*	*Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Phenacomys ungava, Synaptomys borealis*		*Dicrostonyx nelsoni, Lemmus trimucronatus, Microtus oeconomus, Myodes rutilus, Ondatra zibethicus, Synaptomys borealis*	*Dicrostonyx groenlandicus, Lemmus trimucronatus, Myodes rutilus*	*Lemmus trimucronatus, Microtus longicaudus, Microtus pennsylvanicus, Myodes gapperi, Neotoma cinerea, Ondatra zibethicus, Peromyscus maniculatus, Synaptomys borealis*
Cuniculidae						
Dasyproctidae						
Dipodidae	*Zapus hudsonius, Zapus princeps*					*Zapus hudsonius, Zapus princeps*
Erethizontidae	*Erethizon dorsatum*	*Erethizon dorsatum*				*Erethizon dorsatum*
Geomyidae	*Thomomys talpoides*					
Heteromyidae						
Leporidae	*Lepus americanus, Lepus townsendii*	*Lepus americanus*		*Lepus americanus, Lepus othus*	*Lepus articus*	*Lepus americanus*
Ochotonidae						

Point #	67	68	69	70	71	72
Lat	57.8135	30.3245	54.3373	44.0039	82.6206	35.038
Long	-93.6807	-109.178	-95.4028	-118.066	-70.9819	-118.352
Castoridae	*Castor canadensis*		*Castor canadensis*	*Castor canadensis*		
Cricetidae	*Dicrostonyx richardsoni, Lemmus trimucronatus, Microtus pennsylvanicus, Microtus xanthognathus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Microtus mexicanus, Neotoma albigula, Neotoma mexicana, Onychomys torridus, Peromyscus boylii, Peromyscus eremicus, Peromyscus gratus, Peromyscus leucopus, Reithrodontomys fulvescens, Reithrodontomys montanus, Sigmodon arizonae, Sigmodon fulviventer, Sigmodon ochrognathus*	*Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Lemmiscus curtatus, Microtus longicaudus, Microtus montanus, Microtus richardsoni, Myodes gapperi, Neotoma cinerea, Neotoma lepida, Ondatra zibethicus, Onychomys leucogaster, Peromyscus crinitus, Peromyscus maniculatus, Peromyscus truei, Reithrodontomys megalotis*		*Microtus californicus, Neotoma lepida, Neotoma macrotis, Onychomys torridus, Peromyscus boylii, Peromyscus californicus, Peromyscus maniculatus, Peromyscus truei, Reithrodontomys megalotis*
Cuniculidae						
Dasyproctidae						
Dipodidae	*Zapus hudsonius*		*Zapus hudsonius*	*Zapus princeps*		
Erethizontidae		*Erethizon dorsatum*	*Erethizon dorsatum*	*Erethizon dorsatum*		
Geomyidae		*Thomomys umbrinus*		*Thomomys talpoides*		*Thomomys bottae*
Heteromyidae		*Chaetodipus hispidus, Chaetodipus penicillatus, Dipodomys merriami, Dipodomys ordii*		*Dipodomys ordii, Perognathus parvus*		*Dipodomys agilis, Dipodomys merriami, Dipodomys panamintinus, Perognathus alticola, Perognathus longimembris*
Leporidae	*Lepus americanus, Lepus arcticus*	*Lepus californicus, Lepus callotis, Sylvilagus audubonii, Sylvilagus floridanus*	*Lepus americanus*	*Brachylagus idahoensis, Lepus townsendii, Sylvilagus nuttallii*	*Lepus articus*	*Lepus californicus, Sylvilagus audubonii, Sylvilagus bachmani*
Ochotonidae						

Point #	73	74	75	76	77	78
Lat	65.2374	39.0348	51.3959	64.9653	40.2361	31.8451
Long	-103.864	-120.494	-98.951	-69.5502	-109.935	-111.095
Castoridae		*Castor canadensis*	*Castor canadensis*		*Castor canadensis*	*Castor canadensis*
Cricetidae	*Dicrostonyx groenlandicus, Lemmus trimucronatus, Myodes rutilus*	*Microtus californicus, Microtus longicaudus, Microtus montanus, Neotoma cinerea, Neotoma fuscipes, Ondatra zibethicus, Onychomys leucogaster, Peromyscus maniculatus, Phenacomys intermedius, Reithrodontomys megalotis*	*Microtus ochrogaster, Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Dicrostonyx groenlandicus, Lemmus trimucronatus*	*Microtus longicaudus, Microtus montanus, Microtus richardsoni, Myodes gapperi, Neotoma cinerea, Ondatra zibethicus, Onychomys leucogaster, Peromyscus boylii, Peromyscus crinitus, Peromyscus maniculatus, Phenacomys intermedius*	*Neotoma albigula, Neotoma mexicana, Onychomys torridus, Peromyscus eremicus, Peromyscus leucopus, Peromyscus maniculatus, Peromyscus merriami, Reithrodontomys fulvescens, Reithrodontomys megalotis, Reithrodontomys montanus, Sigmodon arizonae, Sigmodon fulviventer, Sigmodon ochrognathus*
Cuniculidae						
Dasyproctidae						
Dipodidae		*Zapus princeps*	*Zapus hudsonius*		*Zapus princeps*	
Erethizontidae		*Erethizon dorsatum*	*Erethizon dorsatum*		*Erethizon dorsatum*	
Geomyidae		*Thomomys monticola*			*Thomomys talpoides*	*Thomomys bottae, Thomomys umbrinus*
Heteromyidae					*Dipodomys ordii, Perognathus flavescens, Perognathus parvus*	*Chaetodipus baileyi, Chaetodipus hispidus, Chaetodipus intermedius, Chaetodipus penicillatus, Dipodomys merriami, Dipodomys ordii, Dipodomys spectabilis, Perognathus amplus, Perognathus flavus*
Leporidae	*Lepus articus*	*Lepus americanus, Lepus californicus, Lepus townsendii, Sylvilagus nuttallii*	*Lepus americanus, Lepus townsendii, Sylvilagus floridanus*	*Lepus articus*	*Lepus americanus, Lepus townsendii, Sylvilagus audubonii, Sylvilagus nuttallii*	*Lepus alleni, Lepus californicus, Sylvilagus audubonii, Sylvilagu sfloridanus*
Ochotonidae		*Ochotona princeps*			*Ochotona princeps*	

Point #	79	80	81	82	83	84
Lat	47.8863	44.2512	39.8777	44.5562	52.3927	27.943
Long	-105.634	-101.628	-117.95	-71.9642	-57.5331	-81.3302
Castoridae	*Castor canadensis*		*Castor canadensis*	*Castor canadensis*	*Castor canadensis*	
Cricetidae	*Lemmiscus curtatus, Microtus ochrogaster, Microtus pennsylvanicus, Myodes gapperi, Neotoma cinerea, Ondatra zibethicus, Onychomys leucogaster, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys megalotis*	*Microtus ochrogaster, Microtus pennsylvanicus, Neotoma cinerea, Ondatra zibethicus, Onychomys leucogaster, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys megalotis, Reithrodontomys montanus*	*Lemmiscus curtatus, Microtus longicaudus, Microtus montanus, Neotoma cinerea, Neotoma lepida, Ondatra zibethicus, Onychomys leucogaster, Onychomys torridus, Peromyscus crinitus, Peromyscus maniculatus, Peromyscus truei, Reithrodontomys megalotis*	*Microtus chrotorrhinus, Microtus pennsylvanicus, Microtus pinetorum, Myodes gapperi, Ondatra zibethicus, Peromyscus leucopus, Peromyscus maniculatus, Synaptomys borealis, Synaptomys cooperi*	*Microtus chrotorrhinus, Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys ungava, Synaptomys borealis*	*Neofiber alleni, Neotoma floridana, Ochrotomys nuttalli, Oryzomys palustris, Peromyscus gossypinus, Peromyscus polionotus, Podomys floridanus, Reithrodontomys humilis, Sigmodon hispidus*
Cuniculidae						
Dasyproctidae						
Dipodidae	*Zapus princeps*	*Zapus hudsonius*		*Napaeozapus insignis, Zapus hudsonius*	*Napaeozapus insignis, Zapus hudsonius*	
Erethizontidae	*Erethizon dorsatum*	*Erethizon dorsatum*	*Erethizon dorsatum*	*Erethizon dorsatum*	*Erethizon dorsatum*	
Geomyidae	*Thomomys talpoides*	*Thomomys talpoides*				
Heteromyidae	*Dipodomys ordii, Perognathus fasciatus*	*Chaetodipus hispidus, Dipodomys ordii, Perognathus fasciatus*	*Dipodomys merriami, Dipodomys microps, Dipodomys ordii, Perognathus longimembris, Perognathus parvus*			
Leporidae	*Lepus townsendii, Sylvilagus audubonii, Sylvilagus nuttallii*	*Lepus townsendii, Sylvilagus audubonii, Sylvilagus floridanus*	*Brachylagus idahoensis, Lepus californicus, Lepus townsendii, Sylvilagus nuttallii*	*Lepus americanus*	*Lepus americanus, Lepus arcticus*	*Sylvilagus floridanus, Sylvilagus palustris*
Ochotonidae						

Point #	85	86	87	88	89	90
Lat	28.5269	33.9501	72.4123	51.4877	71.6478	45.5063
Long	-106.258	-86.99	-123.183	-119.718	-113.116	-62.9438
Castoridae		*Castor canadensis*		*Castor canadensis*		*Castor canadensis*
Cricetidae	*Baiomys taylori, Neotoma albigula, Neotoma mexicana, Onychomys arenicola, Peromyscus boylii, Peromyscus eremicus, Peromyscus leucopus, Peromyscus maniculatus, Peromyscus truei, Reithrodontomys fulvescens, Reithrodontomys megalotis, Reithrodontomys montanus, Sigmodon fulviventer, Sigmodon hispidus, Sigmodon ochrognathus*	*Microtus pinetorum, Neotoma floridana, Ochrotomys nuttalli, Ondatra zibethicus, Oryzomys palustris, Peromyscus gossypinus, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys humilus, Sigmodon hispidus*	*Lemmus trimucronatus*	*Microtus longicaudus, Microtus pennsylvanicus, Myodes gapperi, Neotoma cinerea, Ondatra zibethicus, Peromyscus maniculatus, Phenacomys intermedius, Synaptomys borealis*	*Lemmus trimucronatus*	*Microtus pennsylvanicus, Myodes gapperi, Ondatra zibethicus, Peromyscus maniculatus, Synaptomys cooperi*
Cuniculidae						
Dasyproctidae						
Dipodidae				*Zapus princeps*		*Napaeozapus insignis, Zapus hudsonius*
Erethizontidae				*Erethizon dorsatum*		*Erethizon dorsatum*
Geomyidae	*Cratogeomys castanops*					
Heteromyidae	*Chaetodipus hispidus, Chaetodipus intermedius, Dipodomys ordii, Dipodomys spectabilis, Perognathus flavus*					
Leporidae	*Lepus californicus, Sylvilagus audubonii, Sylvilagus floridanus*	*Sylvilagus aquaticus, Sylvilagus floridanus*	*Lepus articus*	*Lepus americanus*	*Lepus articus*	*Lepus americanus*
Ochotonidae						

Point #	91	92	93	94	95	96
Lat	65.0418	65.508	80.9356	60.8535	35.9927	68.3351
Long	-73.3738	-145.664	-69.0427	-105.645	-95.7234	-137.655
Castoridae		*Castor canadensis*			*Castor canadensis*	*Castor canadensis*
Cricetidae	*Dicrostonyx groenlandicus, Lemmus trimucronatus*	*Dicrostonyx groenlandicus, Lemmus trimucronatus, Microtus oeconomus, Microtus pennsylvanicus, Microtus xanthognathus, Myodes rutilus, Ondatra zibethicus, Synaptomys borealis*		*Microtus pennsylvanicus, Microtus xanthognathus, Myodes gapperi, Ondatra zibethicus, Phenacomys ungava, Synaptomys borealis*	*Microtus ochrogaster, Microtus pinetorum, Neotoma floridana, Ondatra zibethicus, Oryzomys palustris, Peromyscus attwateri, Peromyscus leucopus, Peromyscus maniculatus, Reithrodontomys humilis, Reithrodontomys montanus, Sigmodon hispidus*	*Dicrostonyx groenlandicus, Lemmus trimucronatus, Microtus miurus, Microtus oeconomus, Microtus pennsylvanicus, Microtus xanthognathus, Myodes rutilus*
Cuniculidae						
Dasyproctidae						
Dipodidae					*Zapus hudsonius*	
Erethizontidae		*Erethizon dorsatum*		*Erethizon dorsatum*		
Geomyidae						
Heteromyidae					*Chaetodipus hispidus*	
Leporidae	*Lepus articus*	*Lepus americanus*	*Lepus articus*	*Lepus americanus*	*Sylvilagus aquaticus, Sylvilagus floridanus*	
Ochotonidae		*Ochotona collaris*				*Ochotona collaris*

Point #	97	98	99	100
Lat	66.3757	70.3529	44.7879	16.7566
Long	-70.8618	-87.0184	-113.838	-94.7347
Castoridae			*Castor canadensis*	
Cricetidae	*Dicrostonyx groenlandicus, Lemmus trimucronatus*	*Dicrostonyx groenlandicus, Lemmus trimucronatus*	*Lemmiscus curtatus, Microtus longicaudus, Microtus montanus, Microtus pennsylvanicus, Microtus richardsoni, Myodes gapperi, Neotoma cinerea, Ondatra zibethicus, Peromyscus maniculatus*	*Baiomys musculus, Neotoma mexicana, Nyctomys sumichrasti, Oligoryzomys fulvescens, Oryzomys alfaroi, Oryzomys couesi, Oryzomys rostratus, Peromyscus beatae, Peromyscus leucopus, Peromyscus megalops, Peromyscus melanophrys, Peromyscus mexicanus, Reithrodontomys fulvescens, Reithrodontomys mexicanus, Rheomys mexicanus, Sigmodon hispidus, Sigmodon mascotensis, Tylomys nudicaudus*
Cuniculidae				
Dasyproctidae				
Dipodidae			*Zapus princeps*	
Erethizontidae			*Erethizon dorsatum*	*Sphiggurus mexicanus*
Geomyidae			*Thomomys talpoides*	
Heteromyidae			*Perognathus parvus*	*Liomys pictus*
Leporidae	*Lepus articus*	*Lepus articus*	*Lepus americanus, Lepus californicus, Lepus townsendii, Sylvilagus nuttallii*	*Sylvilagus floridanus*
Ochotonidae			*Ochotona princeps*	

Appendix B. Chart of Localities listed by region including name, total taxa (total), number brachydont (bra), number mesodont (Mes), number hypsodont (hyp), number hypselodont (hys), mean crown height (MeanCH), age of site in million years, state, latitude, longitude, predicted Annual Precipitation (AP), and predicted Mean Annual Temperature (MAT).

Locality	Locality Name	Total	Bra	Mes	Hyp	Hys	MeanCH	Age (Ma)	State	Lat	Long	AP	MAT
CP39D	White River Formation	12	10	2	0	0	1.167	36.5-35.7	WY	43.030	-106.809	1848.38	29.12
CP39E	White River Formation	13	10	2	1	0	1.308	36.5-34.7	WY	43.030	-106.809	1779.05	26.87
CP39B	White River Formation	17	11	4	2	0	1.471	36.5-34.7	WY	43.030	-106.809	1698.98	24.26
CP39C	White River Formation	15	10	2	2	1	1.600	35.7-34.7	WY	43.030	-106.809	1571.91	22.19
CP98B	Chadron Formation	18	13	4	1	0	1.333	35.7-34.7	NE	41.126	-100.751	1766.45	26.46
CP98C	Chadron Formation	15	8	4	3	0	1.667	34.7-33.7	NE	41.126	-100.751	1602.58	21.13
CP46	Wiggins Formation	14	8	3	3	0	1.643	33.7-32	WY	41.146	-104.802	1614.29	21.51
CP68C	White River Formation	22	16	3	3	0	1.409	33.7-32	CO	40.579	-103.358	1729.21	25.25
CP99A	Brule Formation	40	29	7	4	0	1.375	33.7-32	NE	40.810	-96.675	1745.97	25.79
CP84A	Brule Formation	21	12	6	3	0	1.571	33.7-32	SD	45.600	-103.600	1649.40	22.65
CP99B	Brule Formation	14	8	3	3	0	1.643	32-30	NE	40.810	-96.675	1614.29	21.51
CP84B	Brule Formation	23	14	6	3	0	1.522	32-30	SD	44.500	-100.000	1673.83	23.45
CP101	Gering Formation	22	8	10	4	0	1.818	30-28.1	NE	41.615	-103.251	1528.10	18.71
CP85C	Sharps Formation	28	9	9	10	0	2.036	30-28.1	SD	43.083	-102.333	1421.16	15.23
CP85D	Sharps Formation	20	13	6	1	0	1.400	30-23	SD	43.083	-102.333	1733.68	25.39
CP86B	Rosebud Formation	21	8	6	6	2	2.190	28.1-23	SD	43.180	-102.420	1218.19	12.75
CP103A	Harrison Formation	18	6	3	9	0	2.167	23-19.5	NE	42.419	-103.801	1356.79	13.14
CP86D	Rosebud Formation	15	2	6	5	2	2.467	19.5-18.8	SD	43.390	-102.465	1082.41	8.34
CP105	Runningwater Formation	17	2	9	5	1	2.294	18.8-17.5	NE	42.751	-102.022	1230.68	11.10
CP114A	Valentine Formation	24	8	9	5	2	2.042	14.8-12.5	NE	42.784	-100.035	1291.34	15.13
CP114B	Valentine Formation	27	6	8	9	4	2.407	14.8-12.5	NE	42.827	-97.636	984.65	9.29
CP45E	Colter Formation	11	2	6	3	0	2.091	14.8-12.5	WY	43.762	-110.555	1394.03	14.35
CP116B	Ash Hollow Formation	26	7	5	10	4	2.423	12.1-9	NE	42.694	-100.856	976.95	9.04
CP116F	Ash Hollow Formation	12	0	4	3	5	3.083	5.9-4.9	NE	42.816	-97.725	588.92	-1.52

CP118	Kiem Formation	16	2	4	7	3	2.688	4.9-2.5	NE	40.810	-96.675	910.40	4.81
CP128A	Rexroad Formation	19	8	3	7	1	2.053	4.9-2.5	KS	39.056	-95.689	1349.40	14.96
CP128A	Rexroad Formation	20	5	6	6	3	2.350	4.9-2.5	KS	39.056	-95.689	1076.32	10.20
CP128B	Rexroad Formation	12	2	2	4	4	2.833	4.9-2.5	KS	39.056	-95.689	775.27	2.48
CP128C	Rexroad Formation	25	3	6	8	8	2.840	4.9-2.5	KS	39.056	-95.689	518.20	2.37
CP131	Belleville Formation	20	2	3	10	5	2.900	2.5-1.9	KS	39.924	-97.821	679.05	1.41
CP132B	Crooked Creek Formation	16	1	5	4	6	2.938	2.5-1.9	KS	39.056	-95.689	597.16	0.81

SB44D	Chambers Tuff Formation	12	6	5	1	0	1.583	36.5-35.7	TX	29.561	-104.366	1643.55	22.46
SB60	Unnamed Unit	11	4	3	2	2	2.182	5.9-4.9	MEX	28.500	-108.250	1222.44	12.89
SB12	Verde Formation	11	5	3	3	0	1.818	4.9-2.5	AZ	34.562	-112.383	1528.10	18.71
SB14A	St David Formation Sequence	10	2	1	3	4	2.900	4.9-2.5	AZ	32.114	-109.921	742.49	1.41
SB15A	Gila Conglomerate	12	4	2	3	3	2.417	4.9-2.5	AZ	33.102	-109.269	1043.54	9.14
SB14D	St David Formation Sequence	15	3	5	5	2	2.400	2.5-1.9	AZ	32.114	-109.921	1115.19	9.41
SB18B	Bila Conglomerate	13	4	0	4	5	2.769	2.5-1.9	AZ	33.448	-112.074	743.33	3.50

PN6C2	John Day Formation	15	4	4	6	1	2.267	31.42-29.09	OR	44.651	-119.638	1244.18	11.54
PN6D1	John Day Formation	11	4	2	4	1	2.182	29.07-26.58	OR	44.693	-119.637	1285.89	12.89
PN6D2	John Day Formation	19	7	3	7	2	2.211	29.07-26.59	OR	44.693	-119.637	1208.33	12.43
PN6D3	John Day Formation	25	8	5	11	1	2.200	29.07-26.60	OR	44.707	-119.630	1276.95	12.60
PN6E	John Day Formation	12	3	2	6	1	2.417	26.57-23.79	OR	44.931	-123.029	1170.44	9.14
PN6F	John Day Formation	27	10	6	10	1	2.074	26.57-23.79	OR	44.931	-123.029	1338.86	14.62
PN6G	John Day Formation	15	4	4	5	2	2.333	23.79-18.7	OR	44.931	-123.029	1147.96	10.47
PN7	Mascall Formation	11	4	2	2	3	2.364	19-17.5	OR	44.492	-119.536	1069.61	9.99
PN11B	Drewsey Formation	14	5	3	5	1	2.143	7.6-6.8	OR	43.747	-118.419	1305.04	13.52

PN14	Shutler Formation	22	4	10	5	3	2.318	6.8-5.9	OR	45.596	-118.785	1091.96	10.71
PN15	Chalk Butte Formation	10	3	2	5	1	2.600	6.8-5.9	OR	44.931	-123.029	1080.31	6.21
PN3C	Ringold Formation	10	2	1	4	3	2.800	4.9-2.5	WA	47.043	-122.893	855.10	3.01
PN23A	Glenns Ferry Formation	22	4	5	9	4	2.591	4.18-3.11	ID	43.614	-116.238	894.44	6.35

NP10B	Cypress Hills Formation	16	10	4	2	0	1.500	37-36.5	CAN	54.500	-105.681	1684.52	23.79
NP24C	Renova Formation	18	7	8	2	1	1.833	35.7-34.7	MT	46.596	-112.027	1457.20	18.46
NP24D	Renova Formation	11	4	4	2	1	2.000	35.7-33.7	MT	46.596	-112.027	1375.27	15.80
NP29D	Unmapped Beds	10	6	2	2	0	1.600	34.7-33.4	MT	46.596	-112.027	1635.36	22.19
NP32C	Cook Ranch Formation	13	9	2	2	0	1.462	32.5-32	MT	46.596	-112.027	1703.42	24.41
NP10C	Cypress Hills Formation	20	8	6	4	2	2.000	28.1-23	CAN	54.500	-105.681	1311.82	15.80
NP41B	Madison Valley Formation	12	3	3	6	0	2.250	16-14.8	MT	45.667	-111.300	1315.82	11.80
NP11	Wood Mountain Formation	17	4	4	7	2	2.412	14.8-12.5	CAN	54.500	-105.681	1109.40	9.22

NB6C	Barstow Formation	11	3	5	2	1	2.091	16-14.8	CA	35.098	-116.620	1330.58	14.35
NB6E	Barstow Formation	18	11	3	3	1	1.667	14.8-12.5	CA	35.032	-117.040	1539.14	21.13
NB23C	Esmerelda Formation	11	4	1	5	1	2.273	12.1-10.1	NV	38.604	-117.843	1241.20	11.44
NB31	Thousand Creek Formation	11	1	3	6	1	2.636	9-7.6	NV	41.925	-118.836	1062.44	5.63
NB33A	Panaca Formation	17	1	2	9	5	3.059	4.9-2.5	NV	37.640	-114.880	600.97	-1.13
NB13C	Palm Springs Formation	12	0	1	1	10	3.750	2.5-.85	CA	38.556	-121.469	-56.05	-12.18

CC22B	Cajon Formation	17	8	4	4	1	1.882	18-17.5	CA	34.323	-117.486	1433.11	17.68
CC22A	Crowder Formation	13	8	1	3	1	1.769	17.5-17	CA	34.298	-117.469	1488.72	19.49
CC22A	Crowder Formation	12	8	4	0	0	1.333	17.5-16	CA	34.298	-117.469	1766.45	26.46
CC17G	Caliente Formation	11	6	2	1	2	1.909	12.1-10.1	CA	34.821	-119.337	1356.51	17.25

SP1F	Ogallala Formation	21	6	4	5	6	2.524	4.9-2.5	TX	32.519	-96.381	800.53	7.43
SP1H	Ogallala Formation	10	1	5	2	2	2.500	2.5-1.9	TX	34.970	-101.900	1066.03	7.81

GC15C	Inglis 1A-1G	11	4	1	1	5	2.636	2.5-1.9	FL	28.133	-81.632	808.65	5.63

VITA

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