MAMMALIAN COMMUNITY RECOVERY FROM VOLCANIC ERUPTIONS IN THE CENOZOIC OF NORTH AMERICA

by

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DISSERTATION ABSTRACT

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It is clear that ecosystems are devastated after a volcanic eruption coats the landscape with a layer of ash; however, the ecological recovery of mammalian communities after eruptions is poorly understood. Volcanic eruptions vary with magnitude and type and only a fraction of them have been analyzed for effects on mammalian communities. To better understand mammalian community recovery, I investigated three different lines of evidence. First, I created a new numeric metric for statistically analyzing reproductive strategies in mammals and tested the impact of diet and body size on reproductive strategies within a phylogenetic framework as proof of concept. The trend of lower reproductive rates and larger body size hold true for herbivores and omnivores, but different trajectories exist for carnivores. Second, I investigated how species richness, evenness, and similarity change across volcanic boundaries in the 1980 Mount St. Helens (MSH), Washington, and 1914-1917 Mount Lassen, California, eruptions. Richness and evenness remain unchanged in Lassen. MSH saw an immediate drop in richness followed by an increase over five years to pre-eruptive levels. Chord distance analysis suggests no long-term change in the Lassen fauna. The pre- and post-MSH fauna are different from one another. The post-eruptive fauna was more similar to neighboring regions. Lastly, I tested whether the Oligocene horse *Miohippus* demonstrated morphological changes across the volcanic Picture Gorge ignimbrite (PGI; 29.069 Ma) in the John Day Formation of Oregon. Variation in upper and lower teeth was first tested to define a single species in the assemblage. Length, width, and wear of teeth were compared across the PGI and there were no significant differences between pre- and post-PGI assemblages. It is clear from my results that larger eruptions tend to have a greater impact on mammalian community recovery than smaller eruptions, but ultimately, mammalian populations are robust and the presence of neighboring communities is important for recolonizing devastated areas.

There are two supplemental files associated with this dissertation, a CSV file of raw data downloaded for Chapter III and an excel file of raw data and coefficient of variation calculations for Chapter IV. This dissertation includes both unpublished and co-authored material.

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CHAPTER I

GENERAL INTRODUCTION

It is evident that ecosystems have been disrupted in the wake of volcanic activity, but the evolutionary and ecological mechanisms governing mammalian recovery are poorly understood. Many volcanoes are found in regions with high biodiversity, making the potential for devastation of ecosystems and humanity a real possibility. Volcanic eruptions vary from tiny, nearly unnoticeable eruptions to massive ones that can dramatically change landscapes and alter global climate. Rarely do they result in the annihilation of all living things in their path (Crisafulli et al. 2015). Submerged eruptions tend not to have as much of an apparent negative impact on life as eruptions which occur, at least partially, within the atmosphere. Some volcanic activity creates new habitats and ecosystems, such as those volcanoes that create new landforms (*e.g.*, the volcanoes associated with Iceland and Hawai‘i) to be colonized by the first species to arrive. Even volcanoes perceived as destructive (*e.g.*, Mount Saint Helens, Krakatoa, and Mount Vesuvius) introduce new nutrients and trigger environmental change (Crisafulli et al. 2015). Although there has been a great deal of work focused on ecology around volcanic eruptions, most of that work has been done on a few iconic eruptions, limiting our understanding of global processes, therefore more examples must be investigated (Crisafulli et al. 2015).

Understanding the impacts of volcanic eruptions on the ecological and evolutionary processes governing recovery can be difficult because of the convoluted nature of their relationship. The influence of the eruption on these biological processes can be difficult to distinguish from other factors, such as local and global climate and biotic interactions. Changes in taxonomic opinions over time can also confound our understanding of volcanic disturbance ecology by artificially increasing or decreasing the number of species present in a devastated area.

Research on volcano ecology, a subdiscipline of disturbance ecology, was first developed while focusing on iconic volcanic eruptions, including: 1883 Krakatau (Indonesia), 1963 Sertsey (Iceland), and 1980 Mount Saint Helens (Washington, USA) eruptions. Each of these events set the stage for new communities of organisms to colonize the disturbed area, and allowed for the study of succession, or the direction of ecosystem assembly over time (Crisafulli et al. 2015). Ecological studies have focused on the plants and animals in disturbed environments within the context of soil and landform development (Vitousek 2004).

Studies of succession have primarily focused on decadal to century level time scales, as a result of timing of volcanic eruptions and the ability to collect biological samples. These studies have given great insight into plant, fish, bird, and limited mammal succession in volcanically disturbed areas (Bisson et al. 1988, del Moral and Wood 1988, Franklin et al. 2000, del Moral and Magnússon 2014, Crisafulli et al. 2015). These studies benefited from collecting samples immediately after the eruption. Unfortunately, the information collected, while useful, only includes a small percentage of the volcanic events in earth history. The fossil record must be used to get at the data associated with eruptions from before modern data collection methods were established. One such eruption is the 1850 Taupo eruption in New Zealand that deposited an ignimbrite, or an explosive pyroclastic flow. Studies utilized macrofossils and pollen in lake cores to investigate fine scale changes in succession of forests in response to the eruption (Clarkson et al. 1995, Wilmshurst and McGlone 1996). Volcano ecology of mammals has been investigated in the fossil record associated with the last eruption of Toba, but found little to no effect on the mammalian community (Louys 2007). The Toba study system suffers from a poor record of species occurrences after the eruption, which could be too coarse a record to pick up nuanced changes in the fauna after the event. Again, much has been learned, but still more volcanic events can be accessed through deep time in the fossil record.

Mammals are an excellent study system to investigate volcano ecology during the Cenozoic because of their importance to human society, role in the ecosystem, and the similarity of preservation between the modern and fossils records. Besides the obvious fact that humans are mammals, the role of mammals is essential to the stability of some ecosystems, and they have an important role in human society. In the context of resource management, a better understanding of terrestrial mammalian response to volcanic events will help fill in gaps to facilitate development of more holistic management policies. In the fossil record, the Cenozoic record of terrestrial mammals also tends to be better preserved than any other group of vertebrates, allowing for a much deeper and more complete understanding of their paleoecology. The modern record of field collected specimens and the fossil record relatively similar because of the inherent biases of both collection, taphonomy, and preservation (Andrews et al. 1979).

Modern and fossil data must be used in concert with one another to provide better insight into ecological and evolutionary processes governing mammalian community response in volcanically active areas. The benefits of the modern record include: 1) more precise taxonomic identifications (derived from skeletal, soft tissue, and molecular data), 2) more precise timing for presence in the ecosystem, and 3) a better understanding of ecological and behavioral patterns from observations. With these data, we can be more confident about which processes are associated with each pattern of ecological recovery in volcanic settings. The fossil record provides an increased diversity of study systems to investigate volcano ecology and longer time scales to investigate recovery than the modern record. The modern record is used to develop a series of hypotheses and predictions about volcano ecology that can then be tested in the fossil record on much larger eruptions than have been seen in recorded human history (*sensu* McGuire and Davis 2014).

Fossils are more common in areas of volcanic devastation than one might expect, because of the high heat associated with the deposition of volcanic rock. It is commonly thought that fossils are never found in rocks of volcanic origin, but ~ 2% of known bone beds are preserved within this rock type (Behrensmeyer 2007). The major factor in preserving fossils in igneous rocks is the temperature of the rock when it comes in contact with the organic material. If the rock is over 400–450°C, the organic materials will be destroyed (Antoine et al. 2012). One such occurrences is the Blue Lake Rhino in Washington state; a rhino (*Diceratherium* sp.) carcass which was floating in a lake and was enveloped by a lava flow from the Columbia River Basalts about 16 million years ago (Chappell et al. 1951). The water of the lake cooled the lava enough to not incinerate the carcass. More commonly, fossils are found in cooler deposits like airfall tuffs, lahars, or volcaniclastic sediments but can also be found in superheated ignimbrites (Table 1.1). Fossils found in volcanic rocks have the unique distinction of having an absolute age associated with them and relatively high levels of preservation. A great deal can be learned about the ecology (*e.g.*, diet from stomach contents like the rhinos of Ashfall Fossil Beds) and even soft tissue morphology like the vulture from the Alban Hills (Table 1.1). Often, volcanically active areas preserve more than one volcanic event, as in the Turtle Cove Member of the John Day Formation of Oregon, and the numerous tuffs allow for precise dating in the fossil record (Fremd 2010).

Table 1.1. Exemplar fossil localities found within volcanically derived rocks.

Locality	Geography	Matrix	Fossils	Age	Reference
Alban Hills	Italy	Ignimbrite	Vulture and plants	0.0297 Ma	Iurino et al. (2014)
Laetoli Beds	East Africa	Tuffs, volcanoclastics	Ichnofossils	3.7 Ma	Hay (1986)
Karacaşar	Turkey	Ignimbrite	Rhino	9.2 Ma	Antoine et al. (2012)
Ashfall Fossil Beds	Nebraska, USA	Airfall tuff (ash)	Waterhole Community; plants and animals, ichnofossils	11.83 Ma	Voorhies (1985)
Blue Lake Rhino	Washington, USA	Basalt	“Bloat and Float” Rhino	16-15 Ma	Chappell et al. (1951)
Turtle Cove Member, John Day Formation	Oregon, USA	Volcaniclastics, tuffs, and ignimbrite	Animal communities, some isolated occurrences of trees and mammals in tuffs and ignimbrite	31-25 Ma	Fremd (2010)
Clarno Formation	Oregon, USA	Lava flows and lahars	Plant and animal communities	45-40 Ma	Dillhoff et al. (2009)
Jehol biota	China	Volcaniclastics	Invertebrates, vertebrates, and plants	129-120 Ma	Jiang et al. (2014)

In this dissertation, I aim to better understand the processes that underlie mammalian community recovery from volcanic events. I intend to explore several measurable ecological characteristics with communities which have been impacted by volcanism within recorded history.

To develop a quantitative method to better understand how reproductive strategies are impacted by volcanic events, I explore the relationship between reproductive strategies, body size, and diet in Chapter II. Many quantitative ecological metrics have been used to explore disturbance ecology in mammals, but reproductive strategies have only been qualitatively investigated, primarily focusing on the broadly-defined concepts of *r*- and *K*-selection. Taxa which are *r*-selected tend to produce many offspring with little parental investment, while *K*-selected taxa have fewer offspring and a relatively large amount of parental investment. With the help of co-authors Drs. Samantha S. B. Hopkins and Edward Byrd Davis, we quantified the reproductive strategy continuum based on several behavioral characters and performed some basic tests as a proof-of-concept. The quantified reproductive strategies for each mammalian species can then be applied to historic occurrence records of mammals in volcanically disturbed areas, providing a prediction to look for in the fossil record. It is also possible to now estimate the reproductive strategies of fossil taxa within an evolutionary context, as well as with some skeletal indicators, and apply these estimates to fossil assemblages. From qualitative observations, I expect that there will be a higher proportion of *r*-selected taxa immediately after the eruption followed by an increase in the proportion of *K*-selected taxa (Anderson and Macmahon 1985, Del Moral 1998). This chapter will be published with Drs. Samantha S. B. Hopkins and Edward Byrd Davis as co-authors.

In Chapter III, I investigate the evenness and richness of mammalian communities disturbed by the 1980 Mount Saint Helens eruption in Washington, USA, and the 1914-1916 Mount Lassen eruption in California, USA, using the historic field collections of mammals to better understand the underlying processes. The modern record of field collected mammals has similar biases to the fossil record making it a good analog for exploring patterns of volcano ecology. This study explores patterns of mammalian community recovery on the decadal scale at Mount St. Helens and centennial scale at Mount Lassen, in two very different eruptions. We can then take these predictions from the modern into the fossil record to gain more insight into volcano ecology on much longer time scales and with types of volcanoes that have not been seen in human history. The effects of volcanic eruptions are highly variable from one event to the next, making it necessary to investigate as many examples as possible to produce a complete understanding of volcano ecology (Crisafulli et al. 2015). This chapter will be authored souly be me.

Chapter IV looks for morphological changes in the Oligocene horse, *Miohippus*, across the Picture Gorge ignimbrite, a supervolcanic eruption preserved within the Turtle Cove Member of the John Day Formation. First, the confounding effects of taxonomy must be addressed with this species. Up to eight species of *Miohippus* have been described from the Turtle Cove Member, mostly from the late 1800's and early 1900's (Osborn 1918). A different species concept from that of today was in use when these species were described (Simpson 1951, Cracraft 1987). Modern concepts of fossil species attempt to more accurately mimic what we think of as a modern species and often involve comparisons of variation in morphological characters between modern and fossil populations (Gingrich 1985, Emery 2016). Fossil species concepts from the turn of the century were based more upon describing unique morphology and were less statistically rigorous. This difference in species concepts requires modernization of the taxonomy of *Miohippus* from the Turtle Cove Member for comparison with what we would find in modern data. If the Turtle Cove *Miohippus* has been over-split or over-lumped, then we might miss a real ecological signal. It is therefore necessary to first quantify and statistically analyze the variation seen in the *Miohippus* population in the Turtle Cove Member to establish the number of species. From there, ecological processes associated with volcano ecology can be investigated. I focused on tooth width and length to look for possible shifts in body size and wear, searching for shifts in wear stage or unusual wear patterns that might be indicative of changes in diet or the introduction of abrasive exogenous grit. These morphological characters add new facets to our understanding of volcano ecology and the underlying evolutionary processes operating within. This chapter will be authored souly be me.

In the end, understanding the volcano ecology of mammals in as many unique eruptions as possible will benefit a multitude of conservation and humanitarian efforts around the world. There are still many types of eruptions that we have not seen in recorded human history (*e.g.*, supervolcanic eruptions), which can only be investigated in the fossil record. Understanding the underlying processes in these events will better inform conservation efforts when these types of eruptions eventually do occur, allowing human society to be better prepared for the ecological impact.

CHAPTER II

HOW DOES DIET AND BODY MASS DRIVE REPRODUCTIVE STRATEGIES IN MAMMALS?

The data collection and data analysis were all performed by me. Samantha S. B. Hopkins and Edward Byrd Davis provided assistance with statistical methodology and general context for the study. The writing is entirely mine as was the initial idea for the project and the numerical index. Samantha S. B. Hopkins and Edward Byrd Davis also provided editorial assistance.

2.1 Main Text

The tempo and mode of reproduction in mammals is the consequence of natural selection acting on ecological pressures and physiological constraints. Two end-member reproductive strategies have been classically identified: *K*-selected, those taxa producing few offspring with intensive parental care, and *r*-selected, those producing many offspring with little parental care (*1*, *2*). *K*-selected strategies require allocating a considerable amount of energy and resources to the rearing of young and are categorized as competitors, as opposed to *r*-selected strategies, which require relatively little energy and resources and are generally considered colonizers (*1*, *2*).

The relationship between body size and life history traits in mammals is well understood (*3*–*8*), but quantitative methods have yet to explore the effects of diet on this relationship. This gap in knowledge leads us to ask, how does diet impact the relationship between body size and life history in mammals? To answer this question we used phylogenetic comparative methods to investigate the effects of diet on the relationship between body size and reproductive life history in extant mammals.

Six life history traits (litter size, litters per year, gestation age, weaning age, total lifespan, and age of sexual maturity) of mammals, including volant (flying) and marine species, were used to calculate three variables that were then transformed with a Principal Components Analysis (PCA) to create the Reproductive Strategy Index (RSI). This index is a numerical proxy for reproductive strategy where larger values increase along a spectrum from K-selection to r-selection. We found that reproductive strategies are highly phylogenetically conserved ($\lambda = 0.995$). There is a negative, significant relationship between RSI and body mass independent of diet ($p < 0.001$) as well as for herbivores ($p < 0.0001$) and omnivores ($p = 0.0323$). A non-significant relationship exists between the index of reproductive strategy and body mass for organisms with a carnivorous diet ($p = 0.5217$); however, the slope of the linear relationship for this group is comparable to that for the others (Fig. 2.1, Appendix A). Other summary statistics are presented in Appendix A. When volant and marine mammals are included, the overall model is still significant and the carnivores are also not significant.

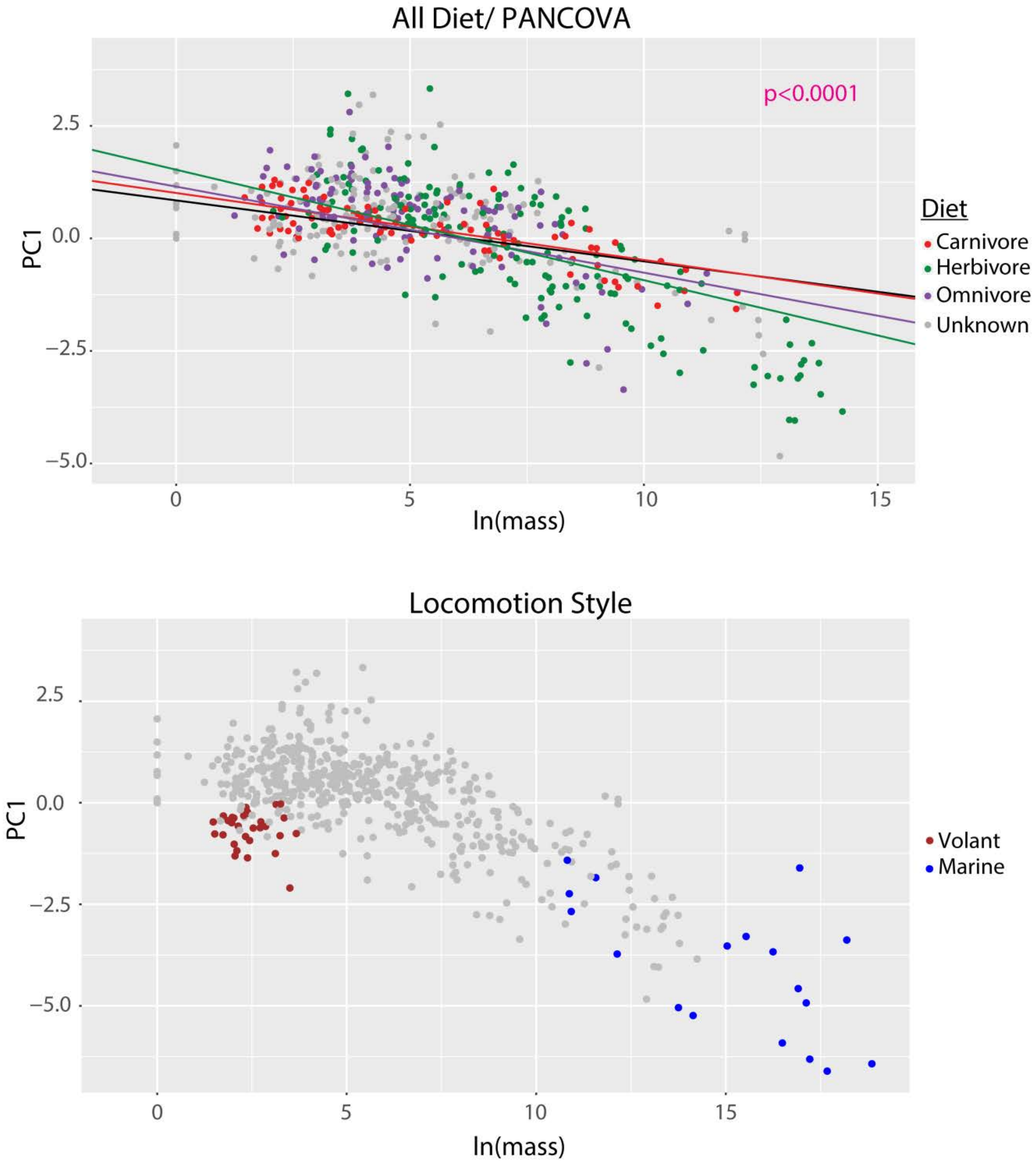


Figure 2.1. Plot of RSI vs. body mass. Each point represents a single species. The upper plot shows all data used for the final PANCOVA. The entire model was significant (*p*<0.0001) as was the herbivore (*p*<0.0001) and omnivore (*p*=0.0323) diets. However, the carnivore diet was not significant (*p*=0.5217). The slope and intercept values for each line are presented in Appendix A. The lower plot shows where the volant and marine mammals used in this study plot in relation to the other mammals. Volant mammals tend to be more *K*-selected than expected for their body mass and the carnivorous marine mammals are on a similar trend with herbivores.

Reproductive strategy in mammals is partially driven by the three factors investigated in this study: phylogenetic relatedness, diet, and body mass. It is clear that higher values of RSI (*r*-selection) are the ancestral state for all mammals, with lower values (*K*-selection) evolving several times throughout the tree (Fig. 2.2). This evolutionary trajectory fits with the known history of mammals, evolving from small-bodied omnivores in the Mesozoic (*9*), which would be expected to be *r*-selected under this analysis. Although only about 10% of mammal species are included in this study, those species belong to about 77% of orders and about 59% of families. *K*-selection originated twice in marsupials, twice in bats, and three times in rodents. All other orders appear to have only evolved *K*-selection once. Interestingly, the crown-group perissodactyls (*e.g.*, horses, rhinos, and tapirs) in this study are entirely *K*-selected (Fig. 2.2), though it is likely that extinct perissodactyls exhibited the ancestral trait of *r*-selection. Early perissodactyls exhibited small body size (*10*), and we see strong correlation between small body size and *r*-selection in our results.

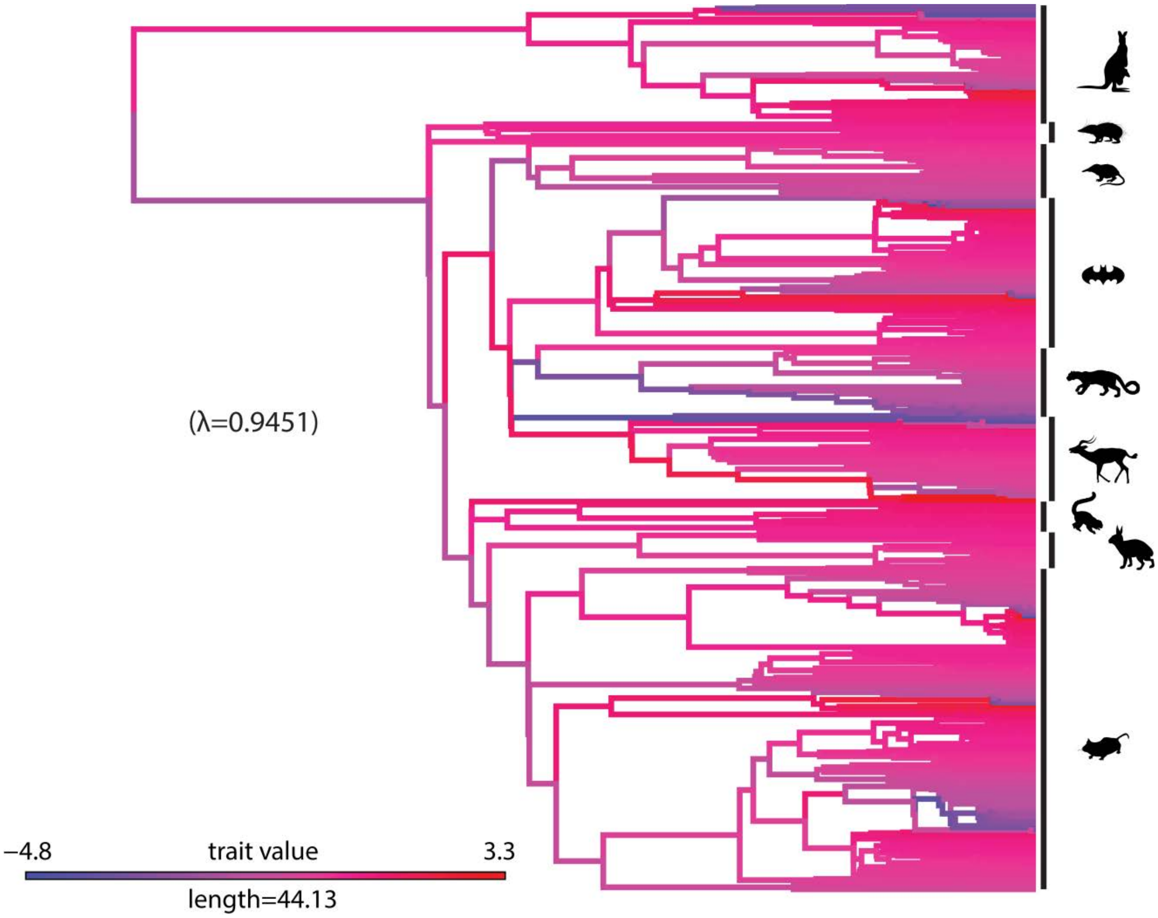


Figure 2.2. Phylogeny with RSI mapped on the tree. Hot colors represent more *r*-selected taxa. Symbols on the right represent major mammalian clades and their position on the phylogeny. From top to bottom they are: Marsupialia, Afrosoricida, Eulipotyphla, Chiroptera, Carnivora, ungulates, Primates, Lagomorpha, and Rodentia.

Diet has a strong relationship with reproductive strategy in mammals. The importance of diet on reproductive strategy varies among species. Metabolic rate is known to constrain the production of offspring with respect to body size (*11*). Increasing body size leads to niche shifts that decrease mortality or increase fecundity through exploiting new food sources (*11*). The distribution of resources between carnivores that feed on vertebrate and invertebrate prey is drastically different, as well as the amount energy available from the food sources, with invertebrate meat possessing less energy than vertebrate, possibly from the presence of indigestible chitin (*12*). Additionally, invertebrates are both hard- and soft-bodied, which leads to morphological differences in taxa that specialize for one or the other(*13*). Likely there are two distinctly different ecological trends between these two subdivisions of mammalian carnivore ecologies. There may also be a difference in life history and its relationship with mass between social vs. solitary carnivores. Social carnivores could be more *K*-selected because of the energetic and resource distribution among members of the social group (*14*, *15*). In further analysis, a significant result may be yielded by subdividing the carnivore diet category into vertebrate and invertebrate feeders. This was not possible with this study as the diet data used were not subdivided in that way, so additional data collection will be necessary.

Our results confirm the conclusion that mammals with larger body size are more likely to be *K*-selected. The limits on mammalian body size and size of the offspring at birth are directly tied to energetics such that metabolic rate dictates body size (*11*). Females of mammalian species that produce many offspring have reduced life spans because so much of their energy is devoted to gestation and rearing (*16*). Dedication of resources to producing offspring would also mean less time and resources available to increase body size. The origin of *K*-selected strategies, which are correlated with larger body sizes, are likely related to niche shifts and exploiting new food sources.

Interestingly, marine and volant mammals tend to be more *K*-selected than expected for their body size (Fig. 2.1). Marine mammals in this study, which all happen to be carnivores, plot on the same trend as herbivores, and the reduced effects of gravity on body size in water and more dense distribution of food sources in the marine realm (*17*) likely contribute to the similarity. Most marine mammals in this study are cetaceans and include some of the largest body masses of extant mammals. Whales are essentially falling back onto the bulk eating strategies of their artiodactyl ancestors but are feeding on animal proteins rather than plant material. Thus, it is not surprising that the marine mammals have a similar relationship between these two characters to terrestrial herbivores of similar body size, supporting the major role of body size in reproductive strategies.

Flying mammals (*i.e.*, bats) are on a completely different trajectory from terrestrial mammalian carnivores (Fig. 2.1). Body size in volant mammals is controlled by different constraints than in terrestrial and marine mammals. Parental care in bats is high in some species because young bats are unable to fly until they have reached 90 per cent of the adult wing span, and pups commonly fall from roosts and need to be recovered by their parents (*18–20*). It is common in larger bat species to transport offspring while foraging, but this behavior is less common in smaller species (*18*). The additional parental investment for flying is the best explanation for why volant mammals are more *K*-selected than expected.

In the end, diet does have an impact on the relationship between body size and reproductive strategy. The effect is far more nuanced in carnivores than in herbivores and omnivores, likely in response to the varying distribution of resources between carnivores which feed on vertebrates and invertebrates. This new method of quantifying reproductive strategy is a powerful tool for exploring the relationships between life history traits and various aspects of ecology.

2.2 Materials and Methods

We downloaded life history from 5,417 taxa from the PanTHERIA database (*21*). We calculated three variables derived from six life history variables. We only used female life history variables in this study. Number of offspring per year is simply the litter size multiplied by the number of litters per year. Percentage of year dedicated to parental care adds the gestation age and weaning age and determined what percentage of the year is devoted to those two variables. This variable will be greater than 100 percent in cases where more than a year is dedicated to these variables. Sexual lifespan is the total lifespan minus the age of sexual maturity. Only 560 mammal species (~10% of species) have all necessary variables. This results in 77% of of mammal orders and about 59% of mammal families being represented. Most families in this study have more than one species present and sample a normal distribution of life history variables. We ran a Principal Components Analysis (PCA) on these three variables to orient the data in a way that minimized the number of variables and maximize the variance. Principal component one was extracted (proportion of variance explained = 64.13% and eigenvalue = 0.6413275) and used as the Reproductive Strategy Index (RSI), a numerical proxy for reproductive strategy where larger values represent *r*-selection.

We used a phylogenetically-informed analysis of covariance (PANCOVA) to test whether diet, body mass, and phylogeny drive the evolution of reproductive strategy. PANCOVA was performed using the caper package version 0.5.2 (*22*) in R version 3.2.3 (*23*). Diet data are available from Price and Hopkins et al. (*24*) while body mass data are from PanTHERIA (*21*). Phylogenetic signal for RSI was also calculated in caper. We used 101 all-mammal trees based on the topology of Fritz et al. (*25*), which had polytomies resolved using a constant rates birth-death process following the methods of Kuhn et al. (*26*). Marine and volant mammals have distinctly different body masses and life history from non-volant terrestrial mammals (*17*, *24*) therefore we removed them from the PANCOVA. R code is presented in Appendix B.

2.3 Bridge

In this chapter, we investigated how diet and body size impact the reproductive strategies of mammals within a phylogenetic framework using RSI, an index for reproductive strategy. Through a proof-of-concept analysis, we have shown the RSI does quantitatively represent reproductive strategies in a way that coinsides with qualitative predictions. There is now a way to analyse reproductive strategies in future statistical ecological studies. RSI can be used alongside the ecological analyses of volcano ecology presented in Chapter III, although that has not yet been done. The classic ecological methods presented in Chapter III must be investigated first before RSI can be confidently applied.

CHAPTER III

MAMMALIAN COMMUNITY RESPONSE TO HISTORIC VOLCANIC ERUPTIONS

3.1 Introduction

While it seems obvious that ecosystems will be devastated after a volcanic eruption coats the landscape with a layer of ash, the ecological recovery of mammalian communities after eruptions is poorly understood. To date, the response of mammalian communities to eruptions has only been studied in one study system, a problematic situation which limits the effectiveness of land management policies in disturbed areas. Modern ecosystems disrupted by recent volcanism, *e.g.*, the 1980 Mount St. Helens eruption in southern Washington, have been studied on short time scales (10^1 years) with a primary focus on plant, fish, bird, and limited mammal communities (Bisson et al. 1988, del Moral and Wood 1988, Franklin et al. 2000, Crisafulli et al. 2015). Mammalian ecosystem recovery from volcanic eruptions has only been investigated in two study systems, one modern and one fossil (Mount St. Helens and the 77-69 ka Toba super-eruption, Indonesia [Louys 2007]). Modern mammalian studies have only focused on the impacts of Mount St. Helens; however, volcanic perturbations are highly variable in their effects on ecosystems, necessitating investigation of additional eruptions to elucidate a more complete picture of ecological processes in volcanic reassembly in diverse ecosystems (Crisafulli et al. 2015). What research has been done using the fossil record is plagued by poor sampling and preservation before and after the eruption, leaving little chance to detect changes in faunal composition. To understand how volcanic events impact mammalian ecosystems, the modern records of continental eruptions in North

America can be used to create predictions of how mammalian communities can reassemble after eruptions which can then be applied to other study systems. The information gleaned from this analysis can be used to understand whether and, if so, how volcanic events impact local mammalian communities.

The impacts of volcanism on ecosystems are either minor and short term or profound and enduring in tested study systems (*e.g.*, birds, fish, and plants; Crisafulli et al. 2015). These biota are rarely annihilated after eruptions and either most taxa survive in a devastated area or endemic taxa survive in small refuge populations (Crisafulli et al. 2015). The tempo and mode of reassembly is often driven by the presence of the surviving population, characteristics of the new deposits, climate, and biotic interactions (Crisafulli et al. 2015). Of course, these predictions are primarily informed by volcanic events which occurred after the 1980 eruption of Mount St. Helens and can only give predictions of recovery after, at most, 37 years.

Mount St. Helens produced geologic results that mimic aridity with no long-term climate change, called 'mock aridity' by Harris and Van Couvering (1995), and altered the local soil chemistry through pyroclastic flows, mudflows, and avalanches (Dale et al. 2005). The non-mammalian fauna appears to be robust to these environmental changes (Bisson et al. 1988, del Moral and Wood 1988, Franklin et al. 2000). In the fossil record associated with Toba, long-term effects on mammal communities (10^2 to 10^3 years) were not observed after the eruption, an event which deposited large quantities of ash over the region (Louys 2007, Global Volcanism Program 2013, Williams 2012). As a result of poor sampling after the Toba eruption, we still do not know whether the ecosystem of the devastated area returned to a pre-eruption composition on larger time scales (*e.g.*, 100 years). The 1914-1917 Mount Lassen eruption differs from these other eruptions by impacting the ecosystem exclusively through mudflows; though only impacts on plant communities have been studied there (Dale et al. 2005).

Study systems for volcano ecology will need to have a rich record of field collected specimens if long term effects are to be investigated. The historic record around the 1980 eruption of Mount St. Helens in southern Washington and the 1914-1917 eruption of Mount Lassen in northern California are both rich in field collected specimens. Mount St. Helens offers a glimpse at short term recovery, while Mount Lassen's record can elucidate recovery on the century scale.

3.1.1 Eruptive History and Climatic Differences

It is important to understand the differences in the eruptive history of the volcanic systems if proper predictions are to be drawn regarding mammalian community recovery. The 1980 eruption of Mount St. Helens and the 1914-1917 eruption of Mount Lassen are different in character, and these differences may impact the communities around them differently.

3.1.1.1 Mount St. Helens

The May 1980 eruption of Mount St. Helens was characterized by steam-blasts, landslides, ashfall, pyroclastic flows, and lahars (Christiansen and Peterson 1981). About 600 km^2 of the devastated area was blanketed by hot debris from this dacitic eruption (Christiansen and Peterson 1981). A great deal of water was incorporated into the landslides from the Toutle River, Spirit Lake, and the melting glaciers on the flanks of the volcano to produce large mudslides eventually deposited into the Cowlitz River (Christiansen and Peterson 1981). The additional water likely caused the landslides and mudflows to be larger than expected. The initial part of the eruption, which consisted of landslides, initial blast, and mudflows, caused the most loss of life. The subsequent Plinian eruption column (with a column of gas and ash) spread about 200 km from the volcano and produced lightning which started several fires over this wide area (Christiansen and Peterson 1981). The eruption continued to produce toxic gas and ash for two weeks following the eruption (Christiansen and Peterson 1981).

3.1.1.2 Mount Lassen

The last eruption of Mount Lassen occurred between May 1914 and May 1917, with the strongest event occurring on May 22, 1915 (Clynne et al. 2012). The eruption covered 0.107 km^2 and produced 0.007 km^3 of proximal volcanic material with lahars and pyroclastic flows covering an additional 8 km^2 (Clynne et al. 2012). The eruption was andesitic to dacitic in composition and included intermittent steam expositions prior to the May 1915 eruption (Clynne et al. 2012). It is important to note here that the 1914-1915 winter included unusually high snowfall which likely added to the volume of lahars (Clynne et al. 2012).

3.1.2 Collecting History

Field notes and field reports are the key to validating collection methods and identifying biases for the historical collections used in this study. The Lassen Transect was originally surveyed by Joseph Grinnell and Museum of Vertebrate Zoology (MVZ) crews between 1911 and 1934 and was resurveyed between 2003 and 2010 by the MVZ (Grinnell et al. 1930, Rowe et al. 2015). Mount Lassen was included in the Lassen Transect which was a 3,000 square mile swath of northern California between the Sacramento River and the Nevada border. Both of these surveys were aimed at discovering the general fauna in the area, but the resurvey did differ from the original survey by using pit fall traps, no guns, and not trapping in rough terrain where pika tend to live (Rowe et al. 2015, C. J. Conroy Pers. Comm. 2016). The resurvey also relied on student crews from mammalogy classes to trap mammals, unlike the original survey which relied on professional trappers. The field notes also indicated that intervening years between the two surveys saw several taxon-specific expeditions to collect bats, gophers, chipmunks, or other small mammals (*e.g.*, Sutton and Patterson 2000). At Mount Shasta, the collecting intensity was much more consistent over the past 100 years, so we do not see the same peaks in collecting like we see with Mount Lassen. The collecting around Mount Shasta, like Mount Lassen, involved several mammalogy classes collecting around the mountain. Collections around Mount Lassen and Mount Shasta also included several roadkill and hunted specimens from throughout the collecting history. These isolated collections represent a random sample of taxa from the ecosystem and were not collected with standard methods like the transect samples.

Collecting around Mount St. Helens was not nearly as formal as the collections around Mount Lassen. Several of the specimens were collected by mammalogy classes both before and after the eruption. By far the most prolific collector was the University of Washington College of Forest Resources, which were conducting small mammal biodiversity surveys in the area. The US Forest Service and National Park Service also conducted several collecting expeditions in the area around both Mount Rainier and Mount St. Helens. These collections were intended to be surveys. The common general small mammal surveys at both Mount Rainier and Mount St. Helens utilized guns, live traps, and snap traps, while little to no specimens were collected from pit fall traps. As expected, there were also various salvaged roadkill specimens and hunter donated specimens. Some specimens were even confiscated poached specimens. There were some taxon-specific collections such as charred specimens collected after the eruption as part of a deer survey to evaluate the effects of the St. Helens eruption (Lyman 1989). These taxon-specific collections were not common at either Mount St. Helens or Mount Rainier.

3.1.3 Objectives and Hypotheses

Although fish, bird, and plant community recovery has been extensively studied after modern eruptions, no one has studied mammalian community recovery from volcanic eruptions other than Mount St. Helens. I attempt to address this gap in knowledge by answering the question, “what processes underlie mammalian community reassembly after volcanic perturbations?” in multiple study systems.

3.1.3.1 Hypotheses

Null hypothesis: ecosystems are robust and will exhibit no change across the volcanic boundary, indicating a short term (10^1 years) full recovery to the pre-eruption ecosystem. Alternative hypothesis: ecosystems will be destabilized by eruptions resulting in distinctly different pre- and post-eruption mammalian faunas. Sub-hypotheses: A) Eruptions will eliminate local refugia allowing non-native species the opportunity to colonize the disturbed region. The larger the eruption the more non-native species will be found in the recovery fauna. B) An increased volume of ash will cause aridity, decreasing the total number of species and increasing the abundance of colonizing species (*i.e.*, species with short individual lifespans and high reproductive rates). C) Community reassembly will be driven by random dispersal rather than habitat filtering, causing the resulting community to be composed of a random assembly of species from the nearby area.

3.2 Methods

To answer my question, I must establish how modern mammal communities have reassembled after-well documented eruptions. I focused on the large historical collection of mammals associated with the 1980 Mount St. Helens eruption and the 1914-15 Mount Lassen eruption. To account for regional climate changes that may be responsible for any changes in the fauna, I used the coeval communities from two ecologically-analogous volcanoes as control systems: Mount Rainier (last erupted 1894; n=3,413 specimens) in west-central Washington and Mount Shasta (last erupted 1786; n= 1,180 specimens) in northern California. Control systems are necessary to evaluate the role of climate in post-volcanic reassembly. Both control ecosystems had time to recover from their previous eruptions at the time of the Mount St. Helens and Mount Lassen eruptions. The sample associated with Mount St. Helens (n= 636 specimens) was collected between 1929 and 1999, allowing an investigation of the pre- and post-eruption faunal relationship (Fig. 3.1). The sample associated with Mount Lassen (n=2,520 specimens) records a relatively continuous 96 year record (1915-2011) of the mammal community, providing insight into longer term impacts (Fig. 3.1). I used occurrence data from within a 30 km radius of the peak of each of these volcanoes because this is approximately the area that was devastated by the eruption of Mount St. Helens. I kept this area consistent among all study sites to control for potential species area effect where larger areas would be expected to have more species represented (Godron 1971, Rosenzweig 1995, Barnosky et al. 2005). Mammal occurrence data associated with these volcanoes were downloaded from the VertNet portal (http://vertnet.org/) on April 27, 2015 and represent 18 museum collections (Supplemental Table S3.1). Human observations were excluded from this study, leaving only vouchered museum specimens.

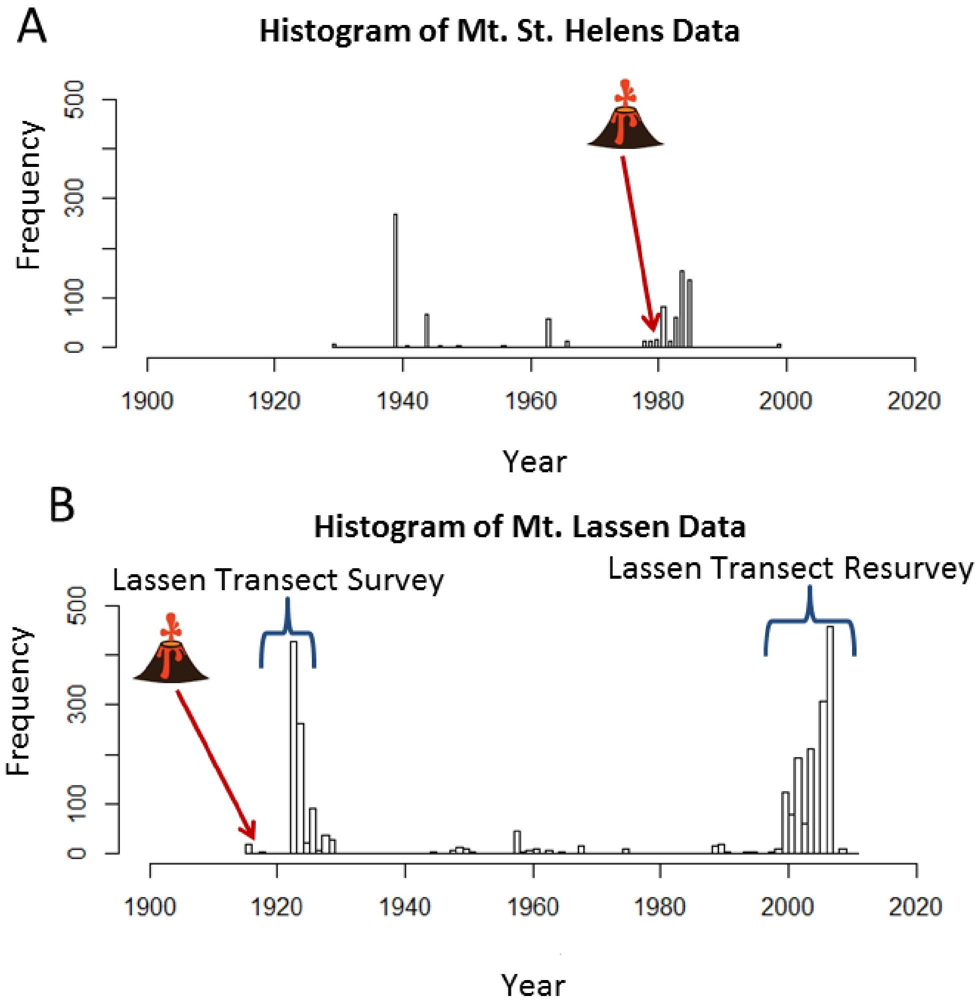


Figure 3.1. Distribution of mammalian occurrence data. A) Distribution around Mount St. Helens. B) Distribution around Mount Lassen. Volcano symbol represents the eruptive event.

I read over field notes related to the specimens downloaded from VertNet to account for any collection bias (*e.g.*, a field expedition collecting only ground squirrels yielding a disproportionately large sample relative to the actual population in the system). Historic notes and field catalogs have important information regarding the collecting techniques that can help determine if there were collecting biases. This information helps inform interpretations of the data, and may help to explain aberrant results from data analysis if collecting biases are present.

To determine whether the number and abundance of species change after eruptions, I calculated ecological metrics of richness (number of species) and evenness (the percentage of the community belonging to each species). Richness is measured with Chao richness which uses sample size to estimate the number of species that should be represented (Chao et al. 2009). Evenness is measured using the Hurlburt Index, which measures how unequal the abundances of species in a community are (Hurlbert 1971) as well as the classic Shannon Index which uses both richness and abundance (Poole 1974). To describe the similarity of the pre- and post-eruption communities, I used a chord distance analysis which is a measure of the number of species shared between populations (Faith et al. 1987, Calede et al. 2011). Nonmetric Multidimensional Scaling (NMDS) was also computed to visualize the distance between the different communities (Kruskal 1964). All statistical methods were performed using the vegan package version 2.3-5 (Oksanen et al. 2016) implemented in R version 3.2.3 (R Core Team 2015) and can be found in Appendix C.

3.2.1 Institutional Abbreviation

ASNHC= Angelo State University Natural History Collections, San Angelo, Texas, USA; **CAS**= California Academy of Sciences, San Francisco, California, USA; **CUMV**= Cornell University Museum of Vertebrates, Ithaca, New York, USA; **FMNH**= Field Museum of Natural History, Chicago, Illinois, USA; **KU**= University of Kansas Biodiversity Institute, Lawrence, Kansas, USA; **LACM**= Natural History Museum of Los Angeles County, Los Angeles, California, USA; **LSU**= Louisiana State University

Museum of Natural Science, Baton Rouge, Louisiana, USA; **MSU**= Michigan State University, East Lansing, Michigan, USA; **MVZ**= Museum of Vertebrate Zoology, University of California-Berkeley, Berkeley, California, USA; **OMNH**= Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma, USA; **PSM**= Slater Museum of Natural History, University of Puget Sound, Tacoma, Washington, USA; **ROM**= Royal Ontario Museum, Toronto, Ontario, Canada; **SBMNH**= Santa Barbara Museum of Natural History, Santa Barbara, California, USA; **TTU**= Museum of Texas Tech University, Lubbock, Texas, USA; **UAM**= University of Alaska Museum of the North, Fairbanks, Alaska, USA; **UCLA**= University of Californa-Los Angeles, Donald R. Dickey Bird and Mammal Collection, Los Angeles, California, USA; **UMMZ**= University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA; **UWBM**= Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, USA.

3.3 Results

The pre- and post-eruption communities at Mount St. Helens were extremely disparate according to the chord distance analysis (cd=1.2409286). The richness was lower after the eruption and there were more unequally distributed abundances of species (Table 3.1). When the 5 years after the Mount St. Helens are investigated each year at a time, we see that richness is low for the first three years and after 5 years returns to a level comparable to the pre eruption level (Table 3.2, Fig. 3.2). Over the 100 years after the eruption of Mount Lassen, the community is relatively stable (Fig. 3.3, Table 3.3, 3.4). It is clear that the Mount Lassen 1930-1980 time bin is quite disparate from the other time bins (Fig. 3.2, Table 3.4). There are fewer species and more unevenness, but the community immediately after the eruption and 100 years later are not nearly as different as the pre- and post-Mount-St.-Helens-eruption communities. It appears that once the eruptions occurred, the recovery fauna was established and upon its stabilization, that community persists.

Table 3.1. Ecological statistics for Washington. In this table, s.e. = standered error and n = sample size.

	n	Raw Richness	Chao Richness	Chao s.e.	Shannon Index	Hurlburt Index
St. Helens Pre-eruption	167	28	37.33	8.84	2.9470	0.9397
St. Helens Post-eruption	450	25	26.00	1.58	2.1600	0.8212
Rainier Pre-eruption	1597	76	84.75	6.04	2.9826	0.9019
Rainier Post-eruption	1816	47	53.43	5.46	2.4676	0.8716

Table 3.2. Yearly ecological statistics for post-eruption Washington. In this table, s.e. = standered error and n = sample size.

Year	System	Raw	Chao	Chao s.e.	Shannon Index	Hurlburt Index	n
1980	Helens	11	14.30	4.10	0.5623	0.5000	33
1981	Helens	11	13.50	3.14	0.2967	0.1617	33
1982	Helens	10	17.50	8.09	0.2868	0.1667	32
1983	Helens	12	26.00	13.13	1.9184	0.8197	32
1984	Helens	10	20.00	10.17	1.6439	0.6633	32
1985	Helens	11	32.00	17.26	1.9466	0.8131	32
1999	Helens	12	17.50	5.35	1.0549	0.8000	32
1980	Rainier	9	37.00	21.22	2.0228	0.9091	12
1981	Rainier	9	12.75	4.18	2.1383	0.9545	12
1982	Rainier	9	10.00	1.80	1.3758	0.6189	69
1983	Rainier	5	8.00	4.09	1.5607	0.9333	6
1984	Rainier	23	23.14	0.49	1.9193	0.7752	747
1985	Rainier	20	20.25	0.73	2.4419	0.8964	509
1999	Rainier	NA	NA	NA	NA	NA	NA

Table 3.3. Ecological statistics for California. In this table, S.E. = standered error and n = sample size.

	n	Raw Richness	Chao Richness	Chao S.E.	Shannon Index	Hurlburt Index
Lassen 1910-1920’s	888	64	70.00	4.54	3.3130	0.9473
Lassen 1930-1980’s	154	40	61.90	13.88	3.1960	0.9490
Lassen 1990-2000’s	1478	45	48.50	3.66	2.6330	0.8732
Shasta 1910-1920’s	248	46	56.10	7.19	3.2162	0.9428
Shasta 1930-1980’s	894	72	89.50	10.11	3.3991	0.9509
Shasta 1990-2000’s	38	8	14.00	7.10	1.7150	0.8151

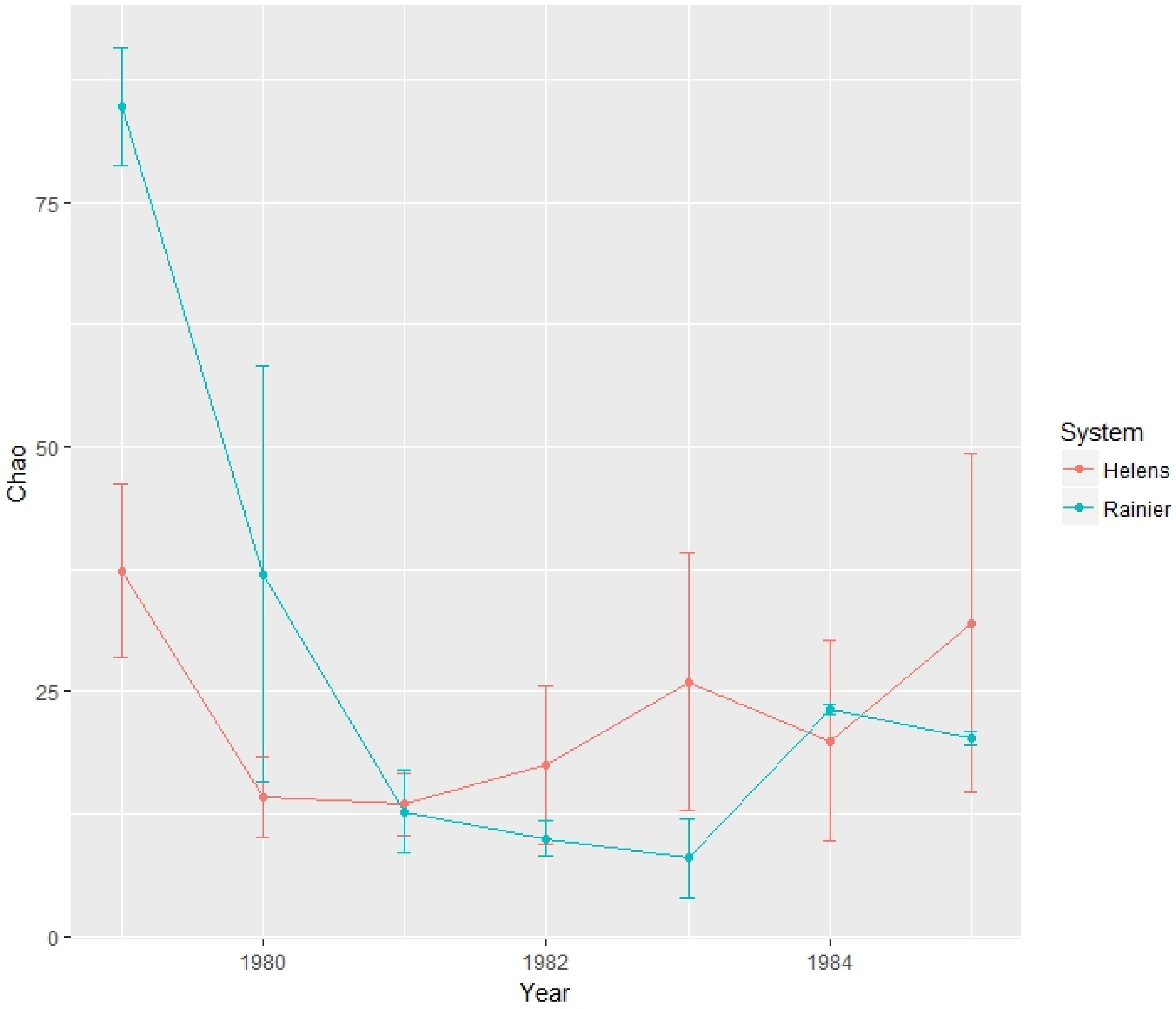


Figure 3.2. Plot of Chao Richness for five years after the 1980 Mount St. Helens eruption. The plot shows the relationship between of the control system (Mount Rainier) compared to Mount St. Helens. In general, there is an increase in the number of species present after the euption for 3-5 years at Mount St. Helens.

Table 3.4. Chord Distance table for all volcanoes and bins.

	Pre Helens	Post Helens	Lassen 1910s-1920s	Lassen 1930s-1980s	Lassen 1990s-2000s	Rainier Pre	Rainier Post	Shasta 1910s-1920s	Shasta 1930s-1980s	Shasta 1990s-2000s
Pre Helens	--	1.2393	1.4139	1.3998	1.4057	1.0294	1.1451	1.4072	1.3895	1.3940
Post Helens	--	--	1.4142	1.4099	1.4142	0.8302	0.7787	1.4142	1.4073	1.4076
Lassen 1910s-1920s	--	--	--	1.1479	0.8951	1.4138	1.4142	0.8274	0.9396	1.2313
Lassen 1930s-1980s	--	--	--	--	1.2189	1.3899	1.4033	1.2294	1.1988	1.3918
Lassen 1990s-2000s	--	--	--	--	--	1.4127	1.4137	0.8587	1.1156	1.3688
Rainier Pre	--	--	--	--	--	--	0.5808	1.4129	1.3750	1.3922
Rainier Post	--	--	--	--	--	--	--	1.4138	1.3887	1.3756
Shasta 1910s-1920s	--	--	--	--	--	--	--	--	0.9762	1.2764
Shasta 1930s-1980s	--	--	--	--	--	--	--	--	--	1.2505

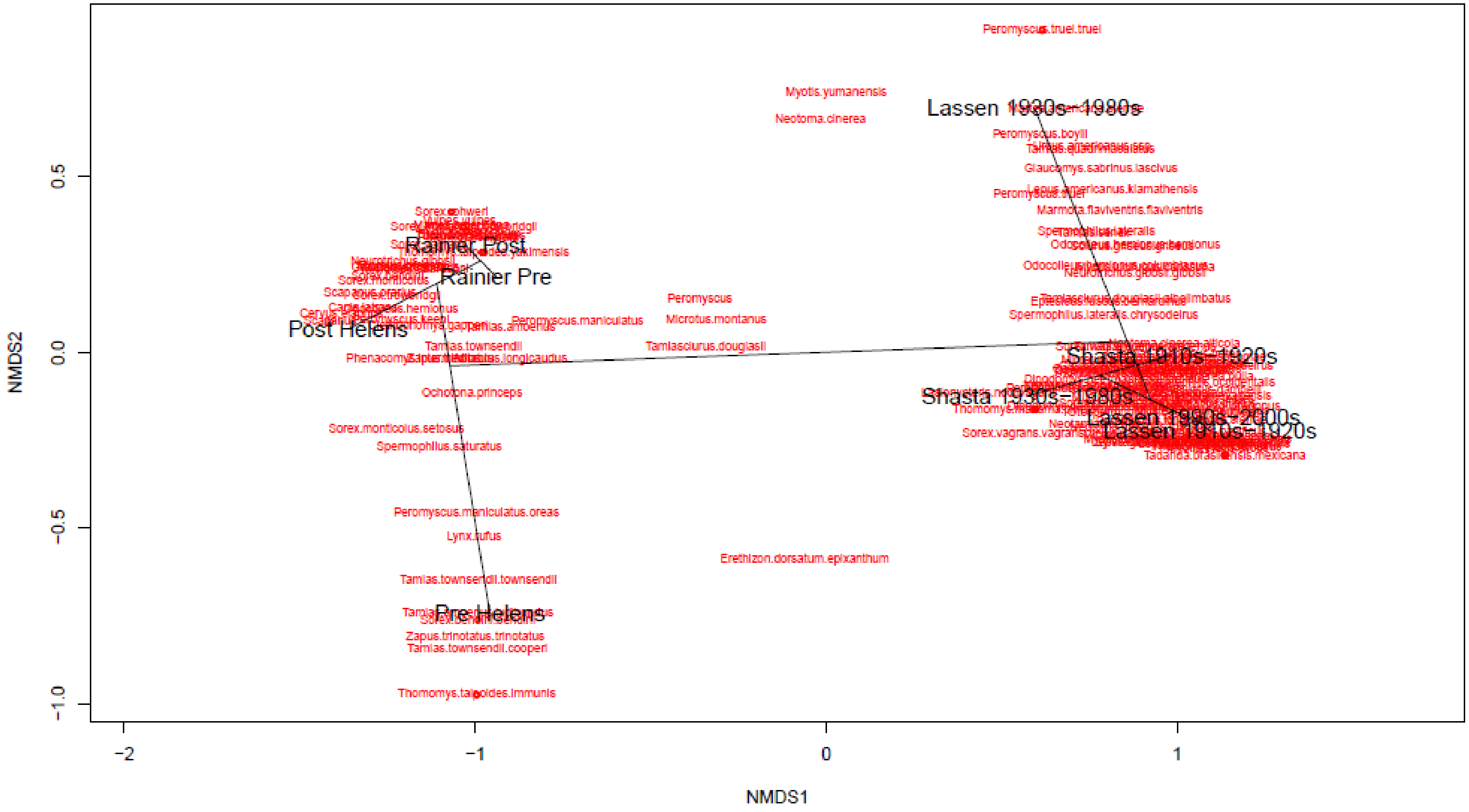


Figure 3.3. NMDS of all volcanoes and bins. The taxa on the plot are important taxa driving the differences for each bin. The longer the line connecting the points, the more different the bins are. The obvious major difference is between California and Washington sites. All of the Califonia bins are very similar to eachother other than Lassen 1930-1980, which was biased by several taxon specific field collections. The pre-St. Helens bin is very different from the other Washington bins, indicating that the pre- and post-eruption faunas at St. Helens are different from one another. The post-eruption fauna at St. Helens is more similar to the fauna at Rainer. Stress = 0.00009573504 and R^2 = 1

3.4 Discussion

The ecological metrics calculated from historical occurrence data show unique patterns between the two study areas. Firstly, the NMDS shows that there is a strong regional effect separating the Washington and California study areas, as expected (Fig. 3.2). The two regions are separated by approximately 500 km in the N-S direction. The two study areas would not be expected to have the same fauna because they represent different environments.

With regard to Mount Lassen, there appears to be no noticeable change in the mammalian fauna on the 100-year time scale. The Mount Lassen 1930-1980 time bin suffers from a small sample size and its disparity is a result of differing collecting methods from other time bins and does not reflect a real ecological signal (Fig. 3.1). From reviewing field notes at the MVZ, it is clear that a majority of the collecting trips that were done in the Mount Lassen 1930-1980 time bin were for specific taxa (*e.g.*, bats or gophers) and not for general faunal diversity studies. Overall, the fauna at Mount Lassen is not very different from the fauna seen at Mount Shasta, suggesting that the smaller Mount Lassen eruption had a minor impact on the local fauna and the devastated areas were able to repopulate quickly with local taxa. Mount Lassen only produced mudflows and disturbed a relatively small area (Dale et al. 2005). Mount Lassen does not have pre-eruption data, making it impossible to truly gauge the full impact of the eruption on the existing fauna; however, the historical record at Mount Lassen does allow for an in-depth examination of the long-term assembly of the recovery fauna. The assembly of the recovery fauna was fast, within the 20 years immediately after the first eruption, and remained stable with respect to climate over the following 100 years.

The pattern seen at Mount St. Helens suggests that the fauna around the volcano prior to the eruption was different from the fauna after the eruption, and we can therefore reject the null hypothesis of no change post-eruption. The NMDS (Fig. 3.3) suggests that the fauna at Mount St. Helens after the eruption was more similar to the fauna seen at Mount Rainer both before and after the eruption (Fig. 3.3, Table 3.1). Field collections from the pre-eruptive fauna appear to have been collected through standard biodiversity field trips. The eruption of Mount St. Helens was much more powerful than that of Mount Lassen, covering a larger area with pyroclastic flows, mudflows, and avalanches (Dale et al. 2005).

The yearly data after the Mount St. Helens eruption shows that the first five years after the eruption are very disparate, but eventually stabilize. The Chao richness steeply drops after the eruption but has returned to a level similar to the pre-eruption landscape by 1985 (Table 3.2, Fig. 3.2). However, the post-fauna is more uneven than the pre-fauna (Table 3.2). As with richness, we see a fast recovery in evenness within about 5 years post-eruption. The lack of museum data in the 2000s prohibits the investigation of long-term recovery post-eruption, but the data can give insight into the short-term faunal recovery, an area that could not be studied with the Mount Lassen eruption.

It would be worth continuing field work in any area that has been volcanically disturbed or to begin in areas with the potential to be disturbed. Field collections present direct and reproducible evidence of ecological change especially with modern field note methods. A good sample both before and after the eruption is imperative to understanding mammalian ecological response to volcanism.

The differences in size of the devastated areas and general eruptive behavior between these two eruptions may also explain the mammalian community responses. The relatively quick recovery and stabilization time after the Mount Lassen eruption may result from simply less perturbation and destruction of habitat. It would have presumably been easier for taxa in surrounding areas to return to the devastated areas. It is also likely that local fauna would have survived the eruption at similar sites nearby and could quickly recover the population. Mount St. Helens’ larger devastated area would have made it more difficult for recovery taxa to be introduced and likely would have seen the extirpation of some local fauna, explaining the similarity between the Mount Rainier and Mount St. Helens recovery faunas. It is important to note here that the museum collections used in this study do not represent the complete fauna of either area, but rather can be characterized as a faunal assemblage similar to the fossil record. This similarity makes it possible to apply the predictions of the modern record to the fossil record and gain access to an entirely new set of volcanic study systems. The fossil record has the added benefit of including larger scale eruptions than the modern record, thus elucidating a more complete picture of mammalian community response to volcanism.

With the data in the Mount Lassen dataset, I cannot reject the null hypothesis of robust communities that fully recover after the eruption. The data in the Mount St. Helens dataset support the alternative hypothesis of destabilization through the elimination of local communities and recolonization of non-native species from other regions, namely Mount Rainier. These data also shows that there was a decrease in the total number of species for the five years post-eruption suggesting increased aridity. The support of different hypotheses in each study system is likely the result of the eruptive behavior and size of the two systems. Again, every volcanic eruption has different characteristics making it necessary to investigate as many as possible. Mount St. Helens was a larger eruption than Mount Lassen, suggesting that scale may play an important role in the mammalian ecological recovery in volcanically disturbed area.

Though it may seem obvious that larger eruptions will have a greater impact on the mammalian community, a five-- to ten-year period of recovery can now be established for a

Mount St. Helens sized eruption. Larger volcanoes may cause longer recovery times, but additional field collections in these study systems will be needed to shed light on the relationship. It is also evident that volcanic eruptions create a more arid environment from the pre-eruptive one given sufficient scale through eliminating local populations thus permitted recolonization by neighboring communities.

In the end, all of the bins in the study, with the exception of Mount Lassen 1930-1980, have very similar collecting histories. They were dominated by small mammal surveys with periodic small collections from donation, salvage, or taxon-specific collecting. The similar collecting histories mean that these bins have similar biases and are directly comparable.

3.5 Conclusion

Mammalian communities recovered differently at Mount Lassen and Mount St. Helens. Mammal communities at Mount St. Helens are very disparate 1-5 years after the eruption compared to the pre-eruption fauna, but eventually stabilize. The fauna in the volcanically devastated regions may never fully return to the pre-eruption community, but after 5-10 years the community appears to stabilize. The mammal community at Mount Lassen persisted on the 100-year scale after the initial stabilization. The eruption of Mount St. Helens appears to have fundamentally changed the abiotic component of the surrounding ecosystem, resulting in a different fauna that may have been introduced from neighboring areas like Mount Rainier. The smaller scale of the Mount Lassen eruption clearly had little to no long-term effect compared to the larger Mount St. Helens eruption on the mammalian communities. It is clear that the larger the eruption the longer it takes for mammalian communities to recover. Not only are the eruptions larger, but they open the door for arid adapted taxa and refuge taxa from nearby regions to recolonize the devastated area. Land managers should be prepared to encourage arid adapted colonizing species to help stabilize the devastated area for at least five to ten years after the eruption if the eruptions is similar in size to Mount St. Helens. However, if the eruption is more similar in size to Mount Lassen, little to no management is necessary. There is no point when the ecology at Mount St. Helens fully returns to the pre-eruption composition; therefore, land users within the devastated area of Mount St. Helens sized eruptions must be prepared for more arid environments and to deal with immigration from neighboring communities.

3.6 Bridge

In this chapter, the modern record of mammals associated with the 1980 Mount Saint Helens and the 1914-1916 Mount Lassen eruptions was used to investigate how mammalian communities recovered after they were disturbed by their respective eruptions. Classic ecological metrics have now been established with respect to volcano ecology, utilizing two case studies. We now better understand how larger eruptions impact mammalian community recovery after volcanic events. However, studies using the fossil record will be needed to address volcano ecology for events not seen in human history, such as supervolcanic eruptions. The faunal assemblage associated with the Turtle Cove Member of the John Day Formation was subject to many volcanic events including the supervolcanic Picture Gorge ignimbrite. The time scale represented in the fossil record is very course with respect to modern volcano ecology; therefore, analyzing morphological change in response to volcanic events on evolutionary time scales is best studied with this study sytem. Chapter IV investigates morphological changes in the Oligocene horse, *Miohippus*, of the Turtle Cove Member after identifying a single species.

3.7 Supplemental Files

Table S3.1: raw data files from VertNet

CHAPTER IV

STATISTICAL ANALYSIS OF DENTAL VARIATION IN THE OLIGOCENE EQUID *MIOHIPPUS* (MAMMALIA, PERISSODACTYLA) OF OREGON

4.1 Introduction

Quantifying variation in extinct species is an important first step in understanding the paleoecology of extinct organisms; the number of species present in an assemblage must be known before testing for changes in paleoecological relationships such as rates of turnover and extinction. Quantifying variation in species of terrestrial fossil vertebrates can be exceptionally difficult as large sample sizes and complete skeletal material are rarely recovered. Utilizing taxa that are phylogenetically related, ecologically similar, and known from more complete material can improve understanding of population variation.

Historically, eight species of the equid genus *Miohippus* Marsh, 1874 have been named from the Turtle Cove Member of the John Day Formation (Osborn, 1918). Recent work has suggested that a smaller genus of equid, *Mesohippus* Marsh, 1875, is also present in this section (Albright et al., 2008). Most recently, authors have refrained from identifying species, instead identifying genera of equids from this section (Albright et al., 2008). However, little work has been done to examine, quantify, and statistically test the level of variation seen within the equid assemblage in the John Day Basin. This emphasizes the need to determine the number of verifiable species in the Turtle Cove assemblage. If a single species of equid is present in an assemblage then the variation in linear morphological measurements would be similar to that observed for extant perissodactyl species. Additionally, dental characters should be stable within species regardless of the animal’s individual age.

Equid dental material in the John Day Formation consists of skulls, partial palates, complete and partial jaws, and isolated teeth, which are common and easily identifiable. This material was reexamined from the Turtle Cove Member comparing the coefficients of variation (V) with a t test to determine if the variation seen in John Day *Miohippus* is similar to variation seen in extant species of perissodactyls. The hypostyle condition, an important dental character used to distinguish species in *Miohippus*, was tested using an ordered logistic regression to determine if it varies with wear. The hypostyle is an enamel structure located on the distal end of the second premolar through third molar and has three morphological states, or conditions, including a ridge, an anterior projection, and an enamel lake (Prothero and Shubin, 1989). John Day *Miohippus* was compared to related extant taxa and well-studied extinct taxa. Once these morphological characters have been analyzed for variation, it will be possible to investigate the influence of paleoecological changes (*e.g.*, volcanic events) on them. These influences must be analyzed on a single species. Specifically, in the Turtle Cove Member, the effects of the Picture Gorge ignimbrite, a supervolcanic eruption, can be investigated for morphological changes in *Miohippus*. If there is no impact on the ecology of *Miohippus* from volcanic events then we should not see any change in morphological traits across the volcanic boundary. There may be a rapid increase in dental characters following a volcanic event as seen with Miocene Argentinian marsupials and rodents which resulted from speciation (Anderson et al., 1995).

4.1.1 Geologic Setting

The John Day Formation is distributed throughout eastern and central Oregon (Fig. 4.1) and is currently subdivided into seven members: Big Basin, Turtle Cove, Kimberly, Haystack Valley, Balm Creek, Johnson Canyon, and Rose Creek (Retallack et al., 2000; Hunt and Stepleton, 2004; Albright et al., 2008; Fig. 4.2). This study focuses primarily on the equid faunal assemblage of the Turtle Cove Member (~32-25.9 Ma), which consists of approximately 400 m of section that Albright et al. (2008) divided into 14 lithostratigraphic subunits (A-K2; Fig. 4.2). Included within the member are several dated tuffs and the Picture Gorge ignimbrite, a super-volcanic event related to the Yellowstone hotspot (Seligman et al., 2014).The faunas of the Turtle Cove Member are assigned to the Whitneyan and Arikareean (subages Ar1 and Ar2) North American Land Mammal Ages (Albright et al., 2008). The Turtle Cove Member provides an excellent opportunity to investigate paleoecological change in a volcanically active region and time. Several types and scales of eruptions are preserved in this lithostratigraphic unit from the tiny unnamed tuffs to the immense Picture Gorge ignimbrite. Few specimens from the lower Big Basin Member, and the higher Kimberly and Haystack Valley Members are also included in this study; these samples are much smaller than that of the Turtle Cove Member.

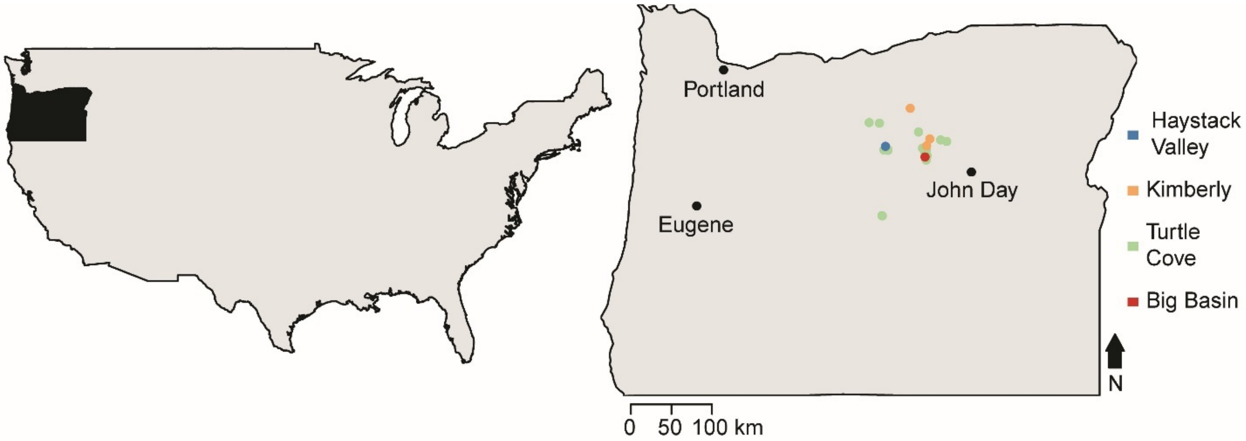


Figure 4.4. Distribution of localities utilized in this study. Localities are color coded by member; localities with unknown stratigraphy are not mapped. The locations of Portland, Eugene, and John Day are marked. Oregon is highlighted in black on the map of the United States of America.

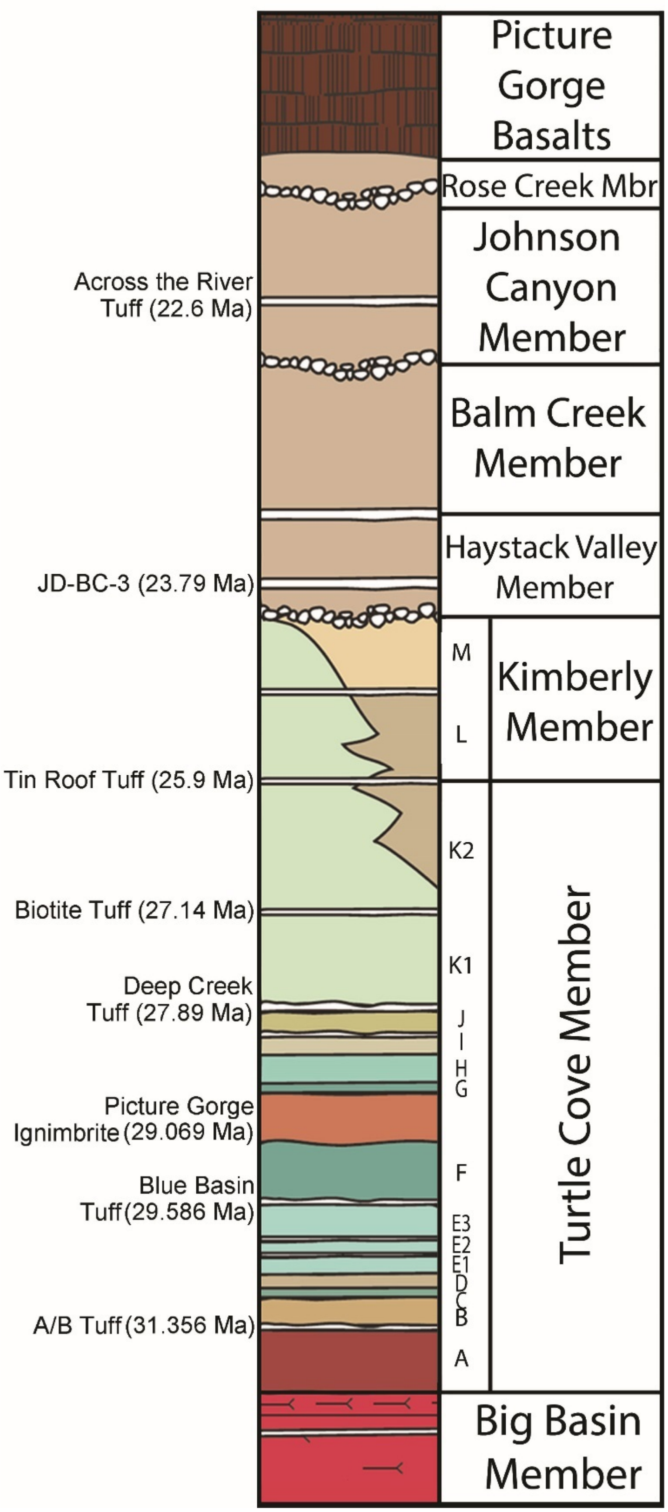
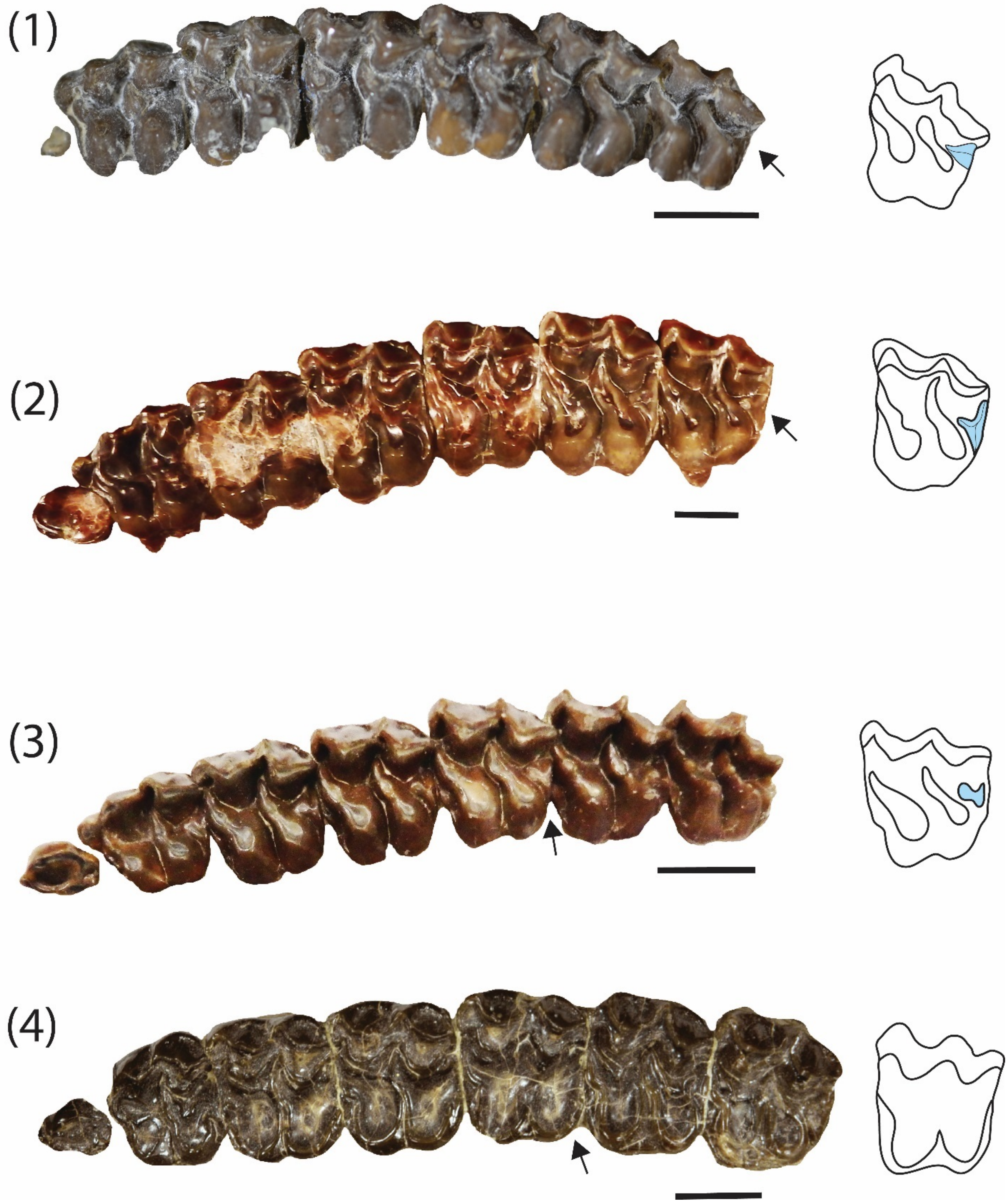


Figure 4.5. Composite stratigraphic section of the John Day Formation used in this study. Specimens are from the upper portion of the Big Basin, Turtle Cove, Kimberly, and Haystack Valley Members. Data for this study are from the Big Basin, Turtle Cove, Kimberly, and Haystack Valley Members.

4.1.2 Taxonomic Background

Miohippus is a genus of relatively moderate sized equid (~ 53.8 kg, M1-3 length = 34-50 mm) belonging to the paraphyletic subfamily "Anchitheriinae" Leidy, 1869 (MacFadden, 1986; Prothero and Shubin, 1989; MacFadden 1998). *Miohippus* is coeval with the smaller *Mesohippus* and the larger *Kalobatippus,* Osborn, 1915, all of which are members of "Anchitheriinae" (MacFadden, 1998). *Miohippus* is considered to be distinct from *Mesohippus* based on the presence and condition of the articular facet on the third metatarsal which articulates with the cuboid, larger hypostyles (Fig. 4.3), a longer face, and a deeper facial fossa (Prothero and Shubin, 1989; MacFadden, 1998); however, these two genera are difficult to distinguish (Stirton, 1940). Species within *Miohippus* in the Great Plains are diagnosed primarily on the basis of tooth row length and hypostyle condition (Prothero and Shubin, 1989). Often, multiple hypostyle conditions can be observed in the same individual (Fig. 4.3; Prothero and Shubin, 1989). The Great Plains species have been the subject of more intensive study than the John Day species. However, this does not mean that the currently recognized Great Plains species are more likely to be valid than the John Day species. Further character and variation analyses of the Great Plains material may reduce the number of recognized species.

Figure 4.6. (next page). Representative examples of hypostyle conditions in Oligocene horses of the Turtle Cove Assemblage of Oregon. Hypostyle condition follows the terminology of Prothero and Shubin (1989). (1) Type 1 hypostyles (UOMNH F-58207) are thin thin ridges which have no cusps or spurs projecting anteriorly; (2) Type 2 hypostyles (JODA 1086) exhibit a small spur which projects anteriorly from the hypostyle ridge; (3) Type 3 hypostyles (UCMP 75274) are characterized by a small distinct ovoid or triangular pocket between a posterior ridge and an anterior spur. I have added the additional condition, (4) none (UCMP 75279), which I define as the lack of hypostyle in heavily worn teeth. Note that there are multiple hypostyle conditions contained within an individual tooth row. Arrows point to exemplar hypostyles on each tooth row that exhibit the specific condition. Line drawings of exemplar teeth are to the right of the photographs with the hypostyle highlighted in blue.


(1)
(2)
(3)
(4)

There are currently 16 species of *Miohippus* considered valid in North America. Of these, eight species have been named from the John Day Formation (*Miohippus annectens* Marsh, 1874; *M. condoni* [=*Anchitherium*; Leidy, 1870]; *M. anceps* [Marsh, 1874]; *M. equiceps* [Cope, 1878]; *M. primus* Osborn, 1918; *M. quartus* Osborn, 1918; *M. acutidens* [Sinclair, 1905]; and *M. equinanus* Osborn, 1918) (Prothero and Shubin, 1989; MacFadden, 1998). Many of the characters which diagnose these species are present in the molars and premolars. These characters include the anterior-posterior length and transverse width of molars and premolars, the texture of the enamel, and the morphology of the protoconules, metaconules, hypostyles, cingula, tubercle, paracone, metacone, hyperconulid, medivallum cusps, protoloph, protoconule, metaloph, ectoloph and parastyle (Osborn, 1918; Prothero and Shubin, 1989). The relative size of the M3 versus the M1-2and the morphology of the incisors and canines have also been invoked as a diagnostic character (Osborn, 1918). The position of the orbit, dorsal preorbital fossa (DPOF) depth, lacrimal fossa depth, position of the infraorbital foramen, malar morphology, and muzzle shape have also been used to diagnose species (Osborn, 1918). The morphology of postcrania is only described in *M. equinanus,* and includes the metatarsals and cuboid (Osborn, 1918). Geometric morphometric analyses can aid in determining the validity of these characters and variation studies are the first step in this course of study. It is important to note that *M. condoni* is only known from a partial dp^3 that is about the same size as *M. annectens* and *M. anceps* (Osborn, 1918). Osborn (1918) states that Marsh's (1874) description of *Miohippus* (=*Anchitherium*) *anceps* does not follow the morphology of the type specimen.

Only dental characters can be compared among these eight species and most species do not have descriptions of cranial or postcranial morphology (Osborn, 1918; Prothero and Shubin, 1989). It is well known that dental characters vary with wear and great care must be taken to sample taxa from medial stages of wear when comparing morphology (MacFadden, 1998). Of all of the dental characters, hypostyle condition can be determined in all unbroken upper molars and premolars and its differential morphology has been given the most emphasis when diagnosing species (Prothero and Shubin, 1989). *Miohippus* species from the Great Plains are primarily distinguished by anterior-posterior length of the tooth row and hypostyle condition when there is a lack of cranial and post-cranial material (Prothero and Shubin, 1989). Taphonomic processes in the John Day Formation tend to eliminate non-dental characters (*e.g.*, skulls and post-crania), which tend to be more reliable in determining species-level identity, making it difficult or impossible to make such a determination on a majority of specimens. Furthermore, the validity of the presence and morphology of the facial fossa as valid characters has been debated for more derived equids (Alberdi, 1987; MacFadden 1997) and has been called into question for early anchitherine equids (Masciale, 2010), therefore it should not be the sole basis of taxonomic assignment in *Miohippus*-grade equids. Prothero and Shubin (1989) focused on updating the taxonomy of the equids from the Oligocene White River Group of the Great Plains while no taxonomic analyses has been conducted on those from the Oligocene John Day Formation of Oregon since Osborn (1918).

There is an ongoing debate regarding the presence of *Mesohippus* in the John Day Basin (Osborn, 1918; Fremd et al., 1994; Albright et al., 2008; Fremd 2010). Most recently, Albright et al. (2008) recognized *Mesohippus* from the Big Basin Member to Turtle Cove Member Unit A, and *Miohippus* from Turtle Cove Unit A to the Haystack Valley Member. In their study, Albright et al. (2008) never identify either taxon to species. *Miohippus annectens* from the John Day is the genotype and was also the first equid to be named from the John Day Basin (Marsh, 1874). *M.*

condoni, although named before *M. annectens*, was originally assigned to the genus *Anchitherium* and later assigned to *Miohippus* after the genus was named in 1874.

4.2 Materials and Methods

I measured and examined 202 equid teeth (173 original specimens and 29 casts) at John Day Fossil Beds National Monument and the University of Oregon Museum of Natural and Cultural History (Table 4.1; Appendix D). Specimens included have been identified as *Miohippus*, *Mesohippus*, and *Archaeohippus* Gidley, 1906 (Appendix D). Additionally, measurements of the type specimen of *Miohippus annectens* and one additional specimen, held in the collections of the Yale Peabody Museum of Natural History, were taken from high-quality digital photographs using ImageJ (http://imagej.nih.gov/ij/). Removing these two specimens from my dataset does not change the outcome of the analysis. ImageJ is an open source program designed for analyzing images, including measuring length and area of structures and has become commonly used (*e.g.*, Samuels, 2009; Meachen-Samuels and Van Valkenburgh, 2010; Meachen-Samuels, 2012; Famoso et al., 2013; Farke and Wilridge, 2013; Vanderven et al., 2014; Vendrasco and Checa, 2015). Specimens come from throughout the exposures of the Big Basin, Turtle Cove, Kimberly, and Hasystack Valley Members of the John Day Formation in eastern Oregon (Fig. 4.1; Table 4.1). Precise stratigraphic position for each specimen is recoded in Appendix D when known. The anterior-posterior length (APL) and the transverse width (TW) of individual upper and lower molars and premolars and the mesostyle crown height were measured with a Mitutoyo Absolute Solar Digimatic CD-54”c digital caliper and a Pittsburgh 8” electronic digital caliper. The morphology of the hypostyle was also recorded.

Table 4.1. Sample size of equid teeth for each stratigraphic unit in this study.

Tooth Position	John Day Formation	Big Basin Member	Turtle Cove Member	Kimberly Member	Haystack Valley Member
Upper (Indeterminate)	27	1	21	3	1
P2	12	0	6	2	0
P3	11	0	5	2	0
P4	14	0	8	2	0
M1	16	0	9	3	0
M2	19	0	12	3	0
M3	20	0	12	4	0
Lower (Indeterminate)	19	1	16	0	1
p1	0	0	1	0	0
p2	8	0	5	1	0
p3	5	0	1	2	0
p4	6	0	3	0	0
m1	12	0	8	1	0
m2	15	0	12	1	0
m3	18	0	12	2	0
Total	202	2	131	26	2

The hypostyle is present in all unbroken upper teeth unlike most other dental characters used to diagnose species. Furthermore, hypostyle morphology has been emphasized when diagnosing *Miohippus* species (Prothero and Shubin, 1989). Hypostyle condition follows the terminology of Prothero and Shubin (1989), but I have added the additional category "none", defined here as the lack of a hypostyle in heavily worn teeth (Fig. 4.3). Type 1 hypostyles are thin ridges which have no cusps or spurs projecting anteriorly. Type 2 hypostyles exhibit a small spur which projects anteriorly from the hypostyle ridge. Type 3 hypostyles are characterized by a small distinct ovoid or triangular pocket between a posterior ridge and an anterior spur. Wear stage was approximated by using the mesostyle crown height and APL in a similar way to Hyposodonty Index (HI) of Van Valen (1960) for upper cheek teeth.

All raw data are presented in Appendix D and Supplemental Table S4.1. All other characters that have been used to differentiate genera and species (*i.e.*, the articulation between the cuboid and third metatarsal, a longer face, and a deeper facial fossa) are not present in a majority of equid specimens from the John Day Formation. The taphonomy of the John Day Formation has resulted in a faunal assemblage where the most diagnostic skeletal elements for generic and specific identification are generally not preserved.

A Shapiro-Wilk W test (Shapiro and Wilk, 1965) was used to determine if APL and TW values were normally distributed (Gaussian distribution), an assumption of the parametric tests used in this study. Violations of this assumption would increase the possibility of Type II error. The coefficient of variation (*V*), a metric used to test whether there is more variance than expected for a single species in fossil communities (Simpson and Roe 1939, Cope and Lacey 1992, 1995), was calculated for APL and TW of upper and lower teeth to determine whether the amount of variation present was compatible with a single population. Miller (1991) developed a method for comparing the fractional coefficients of variation (*CV*) of two samples using the *t* statistic.

The upper first molar (M1) of the sample of John Day *Miohippus* was compared to the published values for the modern equid *Equus quagga* Boddaert, 1785, the well-studied Oligocene equid *Mesohippus bairdii* Leidy, 1850 (MacFadden 1989), the coeval equid *Miohippus equinanus* (Prothero and Shubin, 1989), and the modern South American tapir *Tapirus terrestris* Linnaeus, 1758 (Colbert, 2006), a taxon also classified as a browser. Additionally, the lower first molar (m1) of the John Day *Miohippus* was compared to *Tapirus terrestris*. This study is constrained to the use of the M1 and m1 because of the availability of comparative data in the literature. The modern equid *E. quagga*, was chosen as a comparative species because it is considered a decendant of John Day *Miohippus*, although from different subfamilies. *E. quagga* allows for modern species variation of a closely related species to be directly compared to that of fossil assemblages. *M. bairdii* and *M. equinanus* are both extinct horses that would have been coeval with John Day *Miohippus*. Both species looks fairly similar to John Day *Miohippus*, suggesting similar ecologies, and are also closely related. The modern South American tapir, *T. terrestris*, was chosen because it is a modern ecological analog to John Day *Miohippus*. Both are browsers and perissodactyls. They may not be as closely related as the other analog horse species, but they do share a relatively close ancestor compared to other modern browsers. Like *E. quagga, T. terrestris* allows for direct comparison of modern species variation to that of a fossil assemblage, although this is an ecological analog rather than direct descendent.

When calculating *V*s on populations with small sample sizes ($n<5$) it is necessary to correct for small samples (Sokal and Braumann, 1980; MacFadden, 1989). If the calculated t statistic is smaller than the critical t statistic, I cannot reject the null hypothesis that the two *V*s are the same. The p-value was also calculated for the t tests.

Hypostyle morphology was investigated using an ordered logistic regression with the ordinal package 2014.11-14 (Christensen, 2014) in R (R Core Team, 2013). The ordered logistic regression is a type of logistic regression where the order of the dependent variable matters. A logistic regression uses a nominal dependent variable and a continuous independent variable to determine if the variation in the continuous variable is responsible for the variation in the nominal variable, unlike a linear regression where the dependent variable is continuous. The ordered logistic regression is slightly different in that it uses an ordinal dependent variable and tests for differences between ordered pairs of the dependent variable. Hypsodonty Index (HI; a proxy for wear stage) was used as the independent variable and hypostyle condition as the ordinal dependent variable. For this analysis, all tooth positions in the upper tooth row were used. Previous work has shown that occlusal enamel complexity, and by extension the occlusal enamel morphology like the hypostyle morphology, is statistically similar in all molariform tooth positions in equids (Famoso and Davis 2014). As such, this study assumes that hypostyle morphology is serially homologous between tooth positions at the same state of wear. Hypostyle condition type 1 should be less developed than type 2. Likewise, type 2 appears less developed than type 3, and type 3 appears less developed than the final stage designated as none. If hypostyle condition is related to wear stage, then the hypostyle condition should be ordered and each ordered pair should be significantly different. However, if hypostyle condition is not related to tooth wear, then there would be no significant relationship between the ordered hypostyle condition pairs. R code is provided in Appendix E.

To test if there is a change in linear tooth morphology or in tooth wear in response to the super-volcanic Picture Gorge ignimbrite eruption, a series of statistical tests were performed on the APL, TW, and HI (a proxy for wear). A *t* test was performed on each of the three variables between the pre and post eruption populations and separated by upper and lower dentition where applicable. The upper and lower dentition have very different morphology, especially in the TW, making it necessary to separate the populations. These analyses were performed in R using version 3.3.2 (R Core Team 2016). The raw data for these analyses is available in Appendix D and Supplemental Table S4.1 and the R code is provided in Appendix E.

4.2.1 Repositories and Institutional Abbreviations

AMNH FM: Frick Collection, American Museum of Natural History, Division of Paleontology, New York, NY, USA; **JODA**: John Day Fossil Beds National Monument, United

States National Park Service, Kimberly, OR, USA; **UCMP**: University of California Museum of Paleontology, Berkeley, CA, USA; **UOMNH F-**: University of Oregon Museum of Natural and Cultural History, Condon Fossil Collection, Eugene, OR, USA; **UWBM**: Burke Museum of Natural History and Culture, University of Washington, Seattle, WA, USA; **YPM VP**: Yale Peabody Museum of Natural History, Division of Vertebrate Paleontology, New Haven, CT, USA.

4.3 Results

None of the datasets violated the assumption of Gaussian distribution. The *V* values for the APL and TW of the M1 of the John Day *Miohippus*, *M. equinanus*, *Mesohippus bairdii*, *Equus quagga*, and *Tapirus terrestris* are presented in Table 4.2. The *p* values for each of the M1 *t* testtests are in Table 4.3. Interestingly, when all of the John Day equid material was lumped, the *t* test was significant, suggesting more than one species was present. However, when specimens that were identified as *Mesohippus*, those from the Kimberly Member, and one specimen with uncertain locality and lithologic information were excluded, the *t* test was not significant, suggesting only one species is present among those remaining specimens. The remaining specimens are only from the Turtle Cove Member. Each group as defined earlier was removed one at a time. The *V* values for the APL and TW of the m1 of the Turtle Cove *Miohippus* and *T. terrestris* are also presented in Table 4.2. The *p* values for the m1 *t* testtests are in Table 4.3. The calculations of *V* and the *t* statistic are provided in Supplemental Table S4.1. Only the calculated *t* statistics for the m1 TW between the Turtle Cove *Miohippus* and *T. terrestris* was significant. There is no significant difference between the *V* in the Turtle Cove *Miohippus* and *M. bairdii*, *M. equinanus*, *E. quagga*, and *T. terrestris* with the exception of the TW of the m1 as noted above (Table 4.3).

Table 4.2. Summary statistics for *t* test. *V* = Coefficent of variation, *V'* = Coefficent of Variation (small sample size correction), *n* = sample size, APL = anterior-posterior length, TW = transverse width, M1 = upper molar, m1 = lower molar, N/A = not available. Mean values are in mm.

Species	Measurnment	*n*	*V*	*V'*	*SD*
Equus quagga	M1 APL	42	5.827	N/A	1.29
Equus quagga	M1 TW	42	4.805	N/A	1.12
Turtle Cove *Miohippus*	M1 APL	11	6.425	N/A	0.911
Turtle Cove *Miohippus*	M1 TW	8	4.326	N/A	0.718
Turtle Cove *Miohippus*	m1 APL	5	6.156	N/A	0.818
Turtle Cove *Miohippus*	m1 TW	5	12.305	N/A	1.191
Mesohippus bairdii	M1 APL	27	9.821	N/A	1.1
Mesohippus bairdii	M1 TW	24	8.262	N/A	1.16
Miohippus equinanus	M1 APL	3	N/A	5.856	0.6
Miohippus equinanus	M1 TW	3	N/A	4.012	0.5
Tapirus terrestris	M1 APL	29	5.52	N/A	N/A
Tapirus terrestris	M1 TW	28	3.891	N/A	N/A
Tapirus terrestris	m1 APL	29	6.553	N/A	N/A
Tapirus terrestris	m1 TW	29	3.931	N/A	N/A

Table 4.3. Summary of *p*-values for *t* tests between the Turtle Cove *Miohippus* and analog species. APL = anterior-posterior length, TW = transverse width, M1 = upper molar, m1 = lower molar, N/A = not available.

Analog Species	M1 APL	M1 TW	m1 APL	m1 TW
Equus quagga	0.345	0.636	N/A	N/A
Mesohippus bairdii	0.921	0.955	N/A	N/A
Miohippus equinanus	0.436	0.448	N/A	N/A
Tapirus terrestris	0.276	0.359	0.563	< 0.001

The ordered logistic regression was significant for all hypostyle condition pairs (Table 4.4). The ordered logistic regression was also significant when the M3 was removed. Each hypostyle condition was significantly different from the next advanced stage indicating that hypostyle condition is dependent on wear stage.

Table 4.4. Summary statistics for ordered logistic regression. Wear = Wear stage as approximated by Hypsodonty Index and represents the overall relationship between wear stage and hypostyle condition, 1|2 = ordered test of hypostyle condition 1 and 2, 2|3 = ordered test of hypostyle condition 2 and 3, 3|none = ordered test of hypostyle condition 3 and none, * = dependent variable. Hypostyle condition and wear stage appear as independent variables because the logistic regression tests both for a relationship with wear stage and for differences among ordered pairs.

Variable	Value	Std. Error	*t*-value	*p*-value
Wear	-16.197	2.903	-5.580	<0.0001
1|2 *	-9.717	1.407	-6.907	<0.0001
2|3 *	-7.192	1.192	-6.031	<0.0001
3|none *	-4.436	1.004	-4.417	<0.0001

None of the paleoecological *t* tests for APL, TW, and HI were significant (Table 4.5). There was no significant difference in these measurements between the pre- and post-Picture Gorge ignimbrite eruption populations of the single species of *Miohippus* present in the Turtle Cove assemblage.

Table 4.5. Summary statistics from paleoecological *t* tests.

Test	Sum	Mean Square	*F* value	*p* value
HI Pre v. Post	< 0.001	< 0.001	0.054	0.816
APL Upper Pre v. Post	< 0.001	0.002	0.002	0.968
APL Lower Pre v. Post	4.320	4.323	0.890	0.351
TW Upper Pre v. Post	1.190	1.191	0.357	0.553
TW Lower Pre v. Post	2.120	2.124	1.051	0.311

4.4 Discussion

The *V* values found in the sample of the of Turtle Cove *Miohippus* population are not significantly different from the *V* of any other sample of comparative taxa investigated in this study. Because the samples of comparative taxa used in this study are considered to be from populations containing a single species, these results suggest that the length and width of teeth observed in the Turtle Cove sample is what would be expected from a single horse population, or species concept. Species level diagnoses for *Miohippus* and *Mesohippus* use the APL as an important character (Prothero and Shubin, 1989), and it is clear from my results that more than one species of Turtle Cove *Miohippus* cannot be distinguished based upon the APL or TW. However, specimens of *Mesohippus* that were included in this study are smaller than what is identified as *Miohippus* (Appendix D and Supplemental Table S4.1), suggesting a second species is present. The Kimberly Member specimens also represent a different species from the other *Miohippus* specimens.

The m1 TW of John Day *Miohippus* has a significantly different and relatively higher V than that of *Tapirus terrestris*, the only other taxon in this study with V for the lower dentition (Table 4.2). Both the TW and APL are measured at the base of the crown eliminating wear as a confounding factor. MacFadden (1989) found that the TW and APL of the M1 were not consistently related and concluded that the variation of fossil equids is similar in a majority of cases. Therefore, it is not unusual to have the TW be more variable than the APL.

The data suggest that there are at least two species of horse present in the Turtle Cove Member, There is a larger morph, *Miohippus*, and a smaller morph, *Mesohippus*. There is not enough material to justify a species level identification for the *Mesohippus* material. The species level identification of *Miohippus* is likely to be *M. annectens*. Provinciality and taxonomic priority can be invoked to support this identification. Additionally, the type specimen of *M. annectens* was included in the analysis further justifying this taxonomic assignment. *M. annectens* is the genotype species of *Miohippus* and is the first valid equid species described from the John Day Formation.

The ordered logistic regression demonstrated that the hypostyle condition was dependent on wear stage for John Day *Miohippus*. The spread in the variance may be the result of including all tooth positions in the analysis; however, when M3 is removed the result is unchanged. Further analysis with a larger sample size should consider tooth position as it has been shown to be a significant factor in occlusal morphology of ungulates (Famoso et al., 2013). This is an interesting result as the hypostyle condition has been used as a character to differentiate between species of *Miohippus* and even between *Miohippus* and *Mesohippus* in the Great Plains (Prothero and Shubin, 1989). As a result, the validity of the hypostyle as a character is called into doubt. Future work to resolve the number of species in the "Anchitheriinae" will need to take wear into account as wear stage is an important factor when dealing with ungulate dentition.

The identification of equid teeth is often confounded by the wear stage of the tooth. For example, the occlusal morphology of hypsodont equid teeth is often used to diagnose tribes, genera, and species. The two major tribes of hypsodont equids, Hipparionini and Equini, are often diagnosed by whether the protocone is connected (Equini) or isolated (Hipparionini). The hipparionine genus *Pseudhipparion* has a protocone which is isolated in early wear and connected in late stages of wear, and in the equine genus *Protohippus* the protocone is isolated in relatively early wear and connected in later wear (MacFadden, 1998). In this case, identification at the tribal-level is far from trivial without considering wear stage. Attention to tooth wear is paramount when identifying teeth from these taxa as they are coeval in the Miocene of North America (MacFadden, 1998, Famoso and Pagnac, 2011). It is not surprising that wear stage is also important to the identification of dental material from lower crowned anchitherine equids like *Miohippus*. Consideration of wear in these low crowned taxa should be adopted when considering the ubiquitous dental characters used to diagnose equids of *Miohippus*-grade.

Some species of *Miohippus* are distinguished based on non-dental characters which were not present in this analysis. It may be possible to analyze the John Day *Miohippus* population more completely once sufficient non-dental material is acquired and appropriate methods are developed. However, these characters may prove to be less useful in light of statistical methods. Future work should focus on non-dental morphology if sufficient material is collected.

Statistical methods will better inform analyses which address the continent-wide issue of distinguishing *Mesohippus* from *Miohippus*. These two genera are difficult to distinguish (Stirton, 1940), but are considered distinct based on the presence and condition of the articular facet on the third metatarsal which articulates with the cuboid, larger hypostyles, a longer face, and a deeper facial fossa (Prothero and Shubin, 1989; MacFadden, 1998). The paleopopulation of John Day *Miohippus* is not adequate in addressing this issue as there are only five occurrences of *Mesohippus* in the entire assemblage. Very few specimens from the Turtle Cove assemblage were identified as *Mesohippus*, and those that were identified as such were determined to be different from the specimens of *Miohippus*. In the end, a larger sample size of all equid taxa from the John Day Formation would be necessary to get at more nuanced differences between these genera and species. In the geographically limited area of this study where many species have previously been reported there is no statistically significant evidence for the presence of more than a single species of *Miohippus*. Applying these techniques to the *Miohippus* recovered from the Great Plains would likely lead to reduction in the number of species. Statistical analyses of dental variation have shown great utility in assessing species-level diversity in the small, geographically constrained, paleopopulation of the Turtle Cove assemblage, therefore the application of these methods to the continent-wide issue seems promising.

The influence of the Picture Gorge ignimbrite on the three traits in the Turtle Cove *Miohippus* is not statistically significant, suggesting the eruptions had no influence on the morphology of these horses. It is clear that speciation did not occur as expected from the Argentinian marsupial and rodent example of Anderson et al. (1995) as there is not any change in dental morphology. Although *Miohippus* is smaller than the modern horse and likely filled a different ecological role (MacFadden, 1998), it was still capable of migrating relatively large distances. The local Turtle Cove *Miohippus* population may have been eradicated by the Picture Gorge ignimbrite, but neighboring populations of the same species outside of the devastated area could have easily migrated to the devastated area and recolonized.

The dental variation of *Miohippus* considered herein from the Turtle Cove Member is not statistically different from other populations of similar perissodactyls, both extinct and extant. The hypostyle condition cannot be used to differentiate species in this population as it is dependent on wear. It is clear that the confounding effects of wear on dental morphology need to be considered even in low-crowned equids like *Miohippus*. Two species of equid in the Turtle Cove Member of the John Day Formation can be recognized based on analysis of dental characters which have been used to diagnose species of *Miohippus* and *Mesohippus* in the Great Plains. Based on the available dental material, there is no statistical or morphological variation in the sample of Turtle Cove *Miohippus* in excess of the variation seen in a single analog species. Specimens of *Mesohippus* do represent a different species, as do the specimens from the Kimberly Member which include both *Archaeohippus* and *Miohippus longiceps*. As a result, only *Miohippus annectens*, the genotype and first species recognized in the Turtle Cove Member, can be recognized as the sole species of *Miohippus* in the Turtle Cove assemblage (Marsh, 1874). Also, the Picture Gorge ignimbrite did not have a large enough impact on this population of equids to cause speciation detectable by changes in dental morphology.

4.5 Supplemental Material

Table S4.1 Raw Data Table and Coefficient of Variation Calculations

CHAPTER V

CONCLUDING SUMMARY

My work has made it evident that volcano ecology requires both the modern and fossil record to gain a complete understanding of the underlying processes. Mammals provide an excellent study system to investigate volcano ecology during the Cenozoic because of their importance to human society, role in the ecosystem, and the similarity of preservation between the modern and fossil records. As part of this dissertation, additional ecological tools have been created, and predictions of mammalian reassembly have been established, both of which greatly enhance our understanding of mammalian volcano ecology.

Chapter II investigated how diet and body size impact the reproductive strategies of mammals within a phylogenetic framework using an index for reproductive strategy. The Reproductive Strategy Index (RSI) utilizes six life history traits of 560 mammal species to create three variables that were then transformed using a Principal Components Analysis (PCA). Specifically, RSI is the first principle component (PC1) extracted from the PCA. For all three diet categories (*i.e.*, herbivores, omnivores, and carnivores), larger mammals tend to be more *K*-selected. This relationship is significant for herbivores and omnivores, but not for carnivores, although the relationship for carnivores is comparable to that for the other diet categories. The relationship is non-linear in carnivores and may be a consequence of the differences in resource distribution between insect and vertebrate predators and the energy available from their respective food sources. In the end, the trend of lower reproductive rates with larger body size holds true for herbivores and omnivores, but different trajectories exist for carnivores depending on their diet preferences. From here, the RSI can be applied to volcanically disturbed ecosystems to answer questions about the relationship and distribution of *r*- and *K*-selected mammals before and after volcanic eruptions.

In Chapter III, the modern record of mammals associated with the 1980 Mount Saint Helens and the 1914-1916 Mount Lassen eruptions was used to investigate how mammalian communities recovered after they were disturbed by their respective eruptions. Mount Saint Helens has a modern mammal record that covers both before and after the disturbance, allowing for investigation of the short-term recovery after the eruption, while Mount Lassen has a record that begins right after the eruption and continues for about 100 years, elucidating more long-term effects. The size and characteristics of the two eruptions are also different, with Mount Saint Helens being much larger with greater variety in deposits than Mount Lassen. The record at Mount Saint Helens shows an immediate destabilization of the mammalian population, which then stabilized after five years. Richness was low, eventually returning to the same level as before, but the species present in the system are significantly different. The post-eruption fauna is more similar to the fauna at Mount Rainier than to the pre-eruption fauna, and suggests that a neighboring population recolonized the devastated area. At Mount Lassen, there is little change in the fauna over the century post-eruption, suggesting that the volcanic eruption was too small to have a lasting effect on the ecosystem. It is clear that the size of the eruption matters when it comes to mammalian recovery, but ultimately, mammalian populations are robust and the presence of refugia and neighboring populations is important for recolonizing devastated areas.

In Chapter IV, taxonomic consistency needed to be applied to taxa in the fossil record before volcano ecology could be investigated. I statistically analyzed the dental variation in Oligocene horses of the Turtle Cove Member of the John Day Formation in Oregon and determined that two genera of horse are present in the fossil assemblage. Each species is monotypic in the assemblage, with *Miohippus annectens* being the most common equid taxon. There is no statistical difference between the pre- and post-Picture Gorge ignimbrite eruption populations of *M. annectens* when *t*-tests are performed on the length, width, and wear stage of teeth. This result suggests that the Picture Gorge ignimbrite had little effect on the ecology or evolution of this horse species. That is, the eruption likely wiped out endemic populations, but refuge populations that were morphologically similar to the eradicated endemic population were able to reclaim the devastated area. Additionally, the ecology of the devastated area recovered enough by the time the refuge population returned as to not select for different morphologies.

The stage has been set for future analyses of volcano ecology in both the modern and fossil records. Investigating multiple volcanic settings has led to a deeper understanding of volcano ecology, and with further analyses, the role neighboring populations play in the mammalian community recovery can be better understood. The size of an eruption clearly has an impact on recovery, possibly because large eruptions result in fewer neighboring populations that are farther away from the devastated area, making it difficult for recolonization. Even supervolcanic eruptions do not appear to have had a long-term effect on the large mammal populations that recolonized devastated areas in the deep past. In the end, mammalian communities appear to be robust to volcanic disturbances seen in human history, recovering within a five- to ten-year timeframe. The larger eruptions in the fossil record analyzed herein have yet to show indication of adverse effects on morphological characters of mammalian taxa. Understanding the relationship between ecology and volcanism will better prepare land managers for responding to a greater variety of volcanic events in the future.

APPENDIX A

SUPPLEMENTAL TABLES FOR CHAPTER II

Table S1. Summary statistics from phylogenetically-informed analysis of covariance (PANCOVA). All reported values are means from 101 analyses.

	Value	*t*-value	*p*-value
Intercept	0.8061	1.798	0.07353
Body Mass	-0.1305	-6.728	<0.0001
Carnivore Intercept	0.1534	0.8600	0.3910
Herbivore Intercept	0.6795	4.661	<0.0001
Omnivore Intercept	0.3312	2.043	0.04308
Carnivore Slope	-0.01703	-0.5417	0.5894
Herbivore Slope	-0.1146	-5.230	<0.0001
Omnivore Slope	-0.06432	-2.197	0.02947
Multiple R^2	0.2221	NA	NA
Multiple adjusted R^2	0.2112	NA	NA

Table S2. Phylogenetic signal for RSI. All reported values are means from 101 analyses. CI = confidance interval, ML = Maximum Likeleyhood, λ = Pagel’s lambda.

	ML λ	95% CI upper limit	95% CI lower limit
Value	0.9451	0.0000	0.0000

APPENDIX B

R CODE FOR CHAPTER II

```
#Code written by Nicholas A. Famoso for the r/K selected index on 2/2/2017

#clear the memory
rm(list=ls())

data<-read.csv('PanTHERIA.csv')


long<-data$MaxLongevity
mat<-data$SexualMaturityAge

wean<-data$WeaningAge
gust<-data$GestationLen
litsize<-data$LitterSize
litperyear<-data$LittersPerYear

sexlife<-((long/12)-(mat/365))
precentyear<-((gust+wean)/365)*100
offspringyear<-(litsize*litperyear)

newdata<-cbind(sexlife, precentyear, offspringyear)
newdata<-data.frame(newdata)
rownames(newdata)<-data$MSW05_Binomial

newdata[newdata == 0] <- NA
newdata<-na.omit(newdata)

plot(newdata$precentyear~newdata$sexlife)
plot(newdata$offspringyear~newdata$sexlife)

#I want to do a PCA
ir.pca <- prcomp(newdata, center = TRUE,scale. = TRUE)

print(ir.pca)

plot(ir.pca, type = "l")

summary(ir.pca)

PC1<-ir.pca$x[,1]
hist(PC1)

#just doing the raw data in the PCA
pca2<-cbind(long, mat, wean,gust,litsize,litperyear)
pca2<-data.frame(pca2)
rownames(pca2)<-data$MSW05_Binomial
```

```
pca2[pca2 == 0] <- NA
pca2<-na.omit(pca2)

#I want to do a PCA
ir.pca2 <- prcomp(pca2, center = TRUE,scale. = TRUE)

print(ir.pca2)

plot(ir.pca2, type = "l")

summary(ir.pca2)

PC12<-ir.pca2$x[,1]
hist(PC12)

#just on two variables
newdata2<-cbind(sexlife, offspringyear)
newdata2<-data.frame(newdata2)
rownames(newdata2)<-data$MSW05_Binomial

newdata2[newdata2 == 0] <- NA
newdata2<-na.omit(newdata2)

#I want to do a PCA
ir.pca3 <- prcomp(newdata2, center = TRUE,scale. = TRUE)

print(ir.pca3)

plot(ir.pca3, type = "l")

summary(ir.pca3)

PC13<-ir.pca3$x[,1]
hist(PC13)

#data for the analyses
diet<-read.csv("pcdietmassnew.csv")

#take out the marine mammals
dietnowhale<-diet[which(diet$group!="whale"),]

#take out the flying mammals
dietnowhalenbat<-diet[which(diet$group!="whale" & diet$group!="bat"),]

#only carnivores w/o whales and bats
```

```
carnowhalenbat<-diet[which(diet$group!="whale" & diet$group!="bat" &
diet$Diet=="Carnivore"),]

#making the comparison data frame that is in the same order as the tip labels
DF.taxa <-  data.frame(dietnowhalenbat)
DF.taxa

DF.taxa2 <- data.frame(diet)

#create a list of taxa in this study to be pruned later
specname<-row.names(newdata)

#create a column with Taxon name for the analysis
DF.taxa$Taxon<-specname

DF.taxa2$Taxon<-specname
#phylogenetic analysis

#libraries
library(picante)
library(caper)
#read yer tree from yer nexus file
tree<-read.nexus("alltaxontreefritz.txt")
fixedtree <- read.nexus("FritzTree.rs200k.100trees.tre")
#prune the tree to these taxa
species<- c(specname)



#make a for loop to look at all trees!
rk_signal<- rk_p_low<- rk_p_upp<- ml_list<- CI_upper <- CI_lower <- intercept_list<-
int.tstat_list<- int.pval_list<- mass.slope_list<- mass.tstat_list<- mass.pval_list<-
carn.intercept_list<- carnInt.tstat_list<- carnInt.pval_list<- herb.intercept_list<-
herbInt.tstat_list<- herbInt.pval_list<- omn.intercept_list<- omnInt.tstat_list<- omnInt.pval_list<-
carn.slope_list<- carnSlope.tstat_list<- carnSlope.pval_list<- herb.slope_list<-
herbSlope.tstat_list<- herbSlope.pval_list<- omn.slope_list<- omnSlope.tstat_list<-
omnSlope.pval_list<- multiRsq_list<- multiRsq_list <- multiadjRsq_list <-
matrix(0,length(fixedtree))



for(i in 1:length(fixedtree)){
  tryCatch({
  #pruning the tree for each iteration of the loop
  pruned.trees<-drop.tip(fixedtree[[i]], setdiff(fixedtree[[i]]$tip.label, species))
  #class(pruned.trees)<-"multiPhylo"
```

```
  #run the analysis
  taxa <- comparative.data(phy = pruned.trees, data = DF.taxa,
                           names.col = Taxon , vcv = TRUE,
                           na.omit = FALSE, warn.dropped = TRUE)

  #Do the Maximum Likelyhood PGLS
  #use the * rather than +, this gives me the cross and the interaction term
  MLmodel.pgls <- pgls(PC1 ~ lnmass * Diet,data = taxa, lambda = "ML")
  ml.summary<-summary(MLmodel.pgls)

  #testing for signal
  est_rk.lambda <- pgls(PC1 ~ 1, data = taxa, lambda = "ML", bounds = list(delta = c(1e-04, 3),
lambda = c(1e-06,  1), kappa = c(1e-04, 3)))
  rk.summary<-summary(est_rk.lambda)

  #

  intercept_list[i] <- ml.summary$coefficients[1,1]
  int.tstat_list[i]<-ml.summary$coefficients[1,3]
  int.pval_list[i]<-ml.summary$coefficients[1, 4]

  mass.slope_list[i] <- ml.summary$coefficients[2,1]
  mass.tstat_list[i]<-ml.summary$coefficients[2,3]
  mass.pval_list[i]<-ml.summary$coefficients[2, 4]

  carn.intercept_list[i]<- ml.summary$coefficients[3,1]
  carnInt.tstat_list[i]<-ml.summary$coefficients[3,3]
  carnInt.pval_list[i]<-ml.summary$coefficients[3, 4]

  herb.intercept_list[i]<- ml.summary$coefficients[4,1]
  herbInt.tstat_list[i]<-ml.summary$coefficients[4,3]
  herbInt.pval_list[i]<-ml.summary$coefficients[4, 4]

  omn.intercept_list[i]<- ml.summary$coefficients[5,1]
  omnInt.tstat_list[i]<-ml.summary$coefficients[5,3]
  omnInt.pval_list[i]<-ml.summary$coefficients[5, 4]

  carn.slope_list[i]<- ml.summary$coefficients[6,1]
  carnSlope.tstat_list[i]<-ml.summary$coefficients[6,3]
  carnSlope.pval_list[i]<-ml.summary$coefficients[6, 4]

  herb.slope_list[i]<- ml.summary$coefficients[7,1]
  herbSlope.tstat_list[i]<-ml.summary$coefficients[7,3]
  herbSlope.pval_list[i]<-ml.summary$coefficients[7, 4]

  omn.slope_list[i]<- ml.summary$coefficients[8,1]
```

```
  omnSlope.tstat_list[i]<-ml.summary$coefficients[8,3]
  omnSlope.pval_list[i]<-ml.summary$coefficients[8, 4]

  ml_list[i]<-ml.summary$param.CI$lambda$opt
  CI_lower[i]<-ml.summary$param.CI$lambda$ci.val[1]
  CI_upper[i]<-ml.summary$param.CI$lambda$ci.val[2]

  multiRsq_list[i] <- ml.summary$r.squared
  multiadjRsq_list[i] <- ml.summary$adj.r.squared

  rk_signal[i]<- rk.summary$param.CI$lambda$opt
  rk_p_low[i]<- rk.summary$param.CI$lambda$bounds.p[1]
  rk_p_upp[i]<- rk.summary$param.CI$lambda$bounds.p[2]
  }, error=function(e){cat("ERROR :", conditionMessage(e), "/n")})

}

#plot the results
rk_signal
rk_p_low
rk_p_upp

mass.tstat_list
mass.pval_list
ml_list
CI_lower
CI_upper

ml.sig<-pval_list[pval_list <0.05]
ml.sig


#Make some figures

library(ggplot2)

carslope<-(MLmodel.pgls$model$coef[2,])+(MLmodel.pgls$model$coef[6,])
carinter<-(MLmodel.pgls$model$coef[1,])+(MLmodel.pgls$model$coef[3,])

omnislope<-(MLmodel.pgls$model$coef[2,])+(MLmodel.pgls$model$coef[8,])
omniinter<-(MLmodel.pgls$model$coef[1,])+(MLmodel.pgls$model$coef[5,])

herbslope<-(MLmodel.pgls$model$coef[2,])+(MLmodel.pgls$model$coef[7,])
herbinter<-(MLmodel.pgls$model$coef[1,])+(MLmodel.pgls$model$coef[4,])

taxa2 <- comparative.data(phy = pruned.trees, data = DF.taxa2,
```

```
                        names.col = Taxon , vcv = TRUE,
                        na.omit = FALSE, warn.dropped = TRUE)
taxa <- comparative.data(phy = pruned.trees, data = DF.taxa,
                         names.col = Taxon , vcv = TRUE,
                         na.omit = FALSE, warn.dropped = TRUE)

#plot of the diets together
sp<-qplot(lnmass, PC1, data=taxa$data, colour=Diet)
sp + scale_color_manual(breaks = c( "Other", "Carnivore", "Herbivore", "Omnivore"),
values=c("grey70","red", "green4", "purple"))+
  ggtitle("All Diet")+
  geom_point(size=3)+
  geom_abline(intercept=MLmodel.pgls$model$coef[1,] ,
slope=MLmodel.pgls$model$coef[2,])+
  geom_abline(intercept=carinter, slope=carslope, colour="red")+
  geom_abline(intercept=omniinter, slope=omnislope, colour="purple")+
  geom_abline(intercept=herbinter, slope=herbslope,colour="green4")+
  theme(legend.title = element_text(size=12), legend.text = element_text(size = 10), plot.title =
element_text(size = 20), axis.title = element_text(size = 15), axis.text = element_text(size =
15))+
  expand_limits(x=c(-1,15) ,y=c(-5,4))

sp8<-qplot(lnmass, PC1, data=taxa2$data, colour = group)
sp8 + scale_color_manual(breaks = c( "Terrestrial", "Volant", "Marine"), values =
c("grey","brown", "blue"))+
  ggtitle("Locomotion Style")+
  geom_point(size=3)+
  xlab("ln(mass)")+
  theme(legend.title = element_blank(), legend.text = element_text(size = 10), plot.title =
element_text(size = 20), axis.title = element_text(size = 15), axis.text = element_text(size =
15))+
  expand_limits(x=c(-1,15) ,y=c(-5,4))

#Lets see what the lines the lm model pulls out look like
sp2<-qplot(lnmass, PC1, data=taxa$data, colour=Diet)+geom_point(aes(size=3))
sp2 + scale_color_manual(breaks = c( "Other", "Carnivore", "Herbivore", "Omnivore"),
                       values=c("grey70","red", "green4", "purple"))+
  ggtitle("All Diet")+
  geom_smooth(method = "lm", se= FALSE)

#qplot(Diet, PC1, data=taxa$data, colour=Diet)

#ggplot(taxa$data, aes(x = logmass, y = PC1, color = Diet))+
  #geom_point(aes(size=3))

#plot of just the carnivores
```

```
car<-ggplot(taxa$data, aes(x = lnmass, y = PC1, color = Diet)) +
  geom_point(data = subset(taxa$data, Diet %in% c("Carnivore")),colour="red", size=3)
car+ggtitle("Carnivores")+
  geom_abline(intercept=carinter, slope=carslope, colour="red")+
  expand_limits(x=c(-1,15) ,y=c(-5,4))+
  theme(plot.title = element_text(size = 20), axis.title = element_text(size = 15), axis.text =
element_text(size = 15))

#plot of just the Omnivores
omn<-ggplot(taxa$data, aes(x = lnmass, y = PC1, color = Diet)) +
  geom_point(data = subset(taxa$data, Diet %in% c("Omnivore")),colour="purple",size=3)
omn+ggtitle("Omnivores")+
  geom_abline(intercept=omniinter, slope=omnislope, colour="purple")+
  expand_limits(x=c(-1,15) ,y=c(-5,4))+
  theme(plot.title = element_text(size = 20), axis.title = element_text(size = 15), axis.text =
element_text(size = 15))

#plot of just the herbivores
herb<-ggplot(taxa$data, aes(x = lnmass, y = PC1, color = Diet)) +
  geom_point(data = subset(taxa$data, Diet %in% c("Herbivore")),colour="green4", size=3)
herb+ggtitle("Herbivores")+
  geom_abline(intercept=herbinter, slope=herbslope, colour="green4")+
  expand_limits(x=c(-1,15) ,y=c(-5,4))+
  theme(plot.title = element_text(size = 20), axis.title = element_text(size = 15), axis.text =
element_text(size = 15))

#plot(PC1~logmass, data = taxa$data, pch=16)
#abline(MLmodel.pgls)

plot(PC1~Diet, data = taxa$data, pch=16)

taxa$dropped$tips
taxa$dropped$unmatched.rows

#make a figure showing the r/K index on the tree
library(phytools)

#map characters on tree
#plotBranchbyTrait(pruned.trees,DF.taxa$PC1, mode="edges", palette = "gray")
plotBranchbyTrait(pruned.trees,DF.taxa$PC1, mode="edges",show.tip.label = FALSE,
no.margin = FALSE, palette = "heat.colors")
#plotBranchbyTrait(pruned.trees,DF.taxa$logmass, method="tips", palette = "gray")


#PCA figure
library(devtools)
```

```
#install_github("ggbiplot", "vqv")

library(ggbiplot)
g <- ggbiplot(ir.pca, obs.scale = 1, var.scale = 1, ellipse = TRUE, circle = TRUE, varname.size = 10)+
  geom_point(size = 3)
print(g)

g2<-ggbiplot(ir.pca2, obs.scale = 1, var.scale = 1, ellipse = TRUE, circle = TRUE)
print(g2)

g3<-ggbiplot(ir.pca3, obs.scale = 1, var.scale = 1, ellipse = TRUE, circle = TRUE)
print(g3)


#Get some data
summary(rk_signal[rk_signal != 0])
summary(ml_list[ml_list != 0])
summary(mass.pval_list[mass.pval_list != 0])

#summary(carnInt.pval_list[carnInt.pval_list != 0])
#summary(herbInt.pval_list[herbInt.pval_list != 0])
#summary(omnInt.pval_list[omnInt.pval_list != 0])
summary(carnSlope.pval_list[carnSlope.pval_list != 0])

summary(intercept_list[intercept_list != 0])
summary(int.tstat_list[int.tstat_list != 0])
summary(int.pval_list[int.pval_list != 0])

summary(mass.slope_list[mass.slope_list != 0])
summary(mass.tstat_list[mass.tstat_list != 0])
summary(mass.pval_list[mass.pval_list != 0])

summary(carn.intercept_list[carn.intercept_list != 0])
summary(carnInt.tstat_list[carnInt.tstat_list != 0])
summary(carnInt.pval_list[carnInt.pval_list != 0])

summary(herb.intercept_list[herb.intercept_list != 0])
summary(herbInt.tstat_list[herbInt.tstat_list != 0])
summary(herbInt.pval_list[herbInt.pval_list != 0])

summary(omn.intercept_list[omn.intercept_list != 0])
summary(omnInt.tstat_list[omnInt.tstat_list != 0])
summary(omnInt.pval_list[omnInt.pval_list != 0])
```

```
summary(carn.slope_list[carn.slope_list != 0])
summary(carnSlope.tstat_list[carnSlope.tstat_list != 0])
summary(carnSlope.pval_list[carnSlope.pval_list != 0])

summary(herb.slope_list[herb.slope_list != 0])
summary(herbSlope.tstat_list[herbSlope.tstat_list != 0])
summary(herbSlope.pval_list[herbSlope.pval_list != 0])

summary(omn.slope_list[omn.slope_list != 0])
summary(omnSlope.tstat_list[omnSlope.tstat_list != 0])
summary(omnSlope.pval_list[omnSlope.pval_list != 0])

summary(multiRsq_list[multiRsq_list != 0])
summary(multiadjRsq_list[multiadjRsq_list != 0])

summary(rk_signal[rk_signal != 0])
summary(rk_p_low[rk_p_low != 0])
summary(rk_p_upp[rk_p_upp != 0])

summary(rk_p_low)
summary(rk_p_upp)
```

APPENDIX C

R CODE FOR CHAPTER III

```
#Code written by Nicholas A. Famoso to do ecological analyses, written on 1/11/2017

#clear the memory
rm(list=ls())

#load the libraries
library(vegan)
library(dplyr)
library(plyr)
library(analogue)
library(primer)
library(MASS)

#Bring in the data
lasdata<-read.csv('Mt_Lassen_post_eruptions_about_30_km_radius.csv')
lasdata<-data.frame(lasdata)
count(lasdata$order)

preheldata<-read.csv('Mt_St_Helens_pre-1980_eruption_about_30_km_radius.csv')
preheldata<-data.frame(preheldata)
count(preheldata$order)

postheldata<-read.csv('Mt_St_Helens_post-1980_eruption_about_30_km_radius.csv')
postheldata<-data.frame(postheldata)
count(postheldata$order)

MtShasta <- read.delim("C:/Users/NickF/Dropbox/U Oregon/Dissertation things/Modern
Data/Modern Turnover/Mt_Shasta_post_eruption_about_30_km_radius-
56433d8ae7b94ce1ad4c7fb59055038c.txt")
hist(MtShasta$year, breaks=122, xlim=c(1893,2015), ylim=c(0, 800))

count(MtShasta$order)

MtRainier <- read.delim("C:/Users/NickF/Dropbox/U Oregon/Dissertation things/Modern
Data/Modern Turnover/Mt_Rainier_post_eruption_about_30_km_radius-
a9f69c9740ec43cc953d13c5ef16ed0a.txt")
hist(MtRainier$year, breaks=122, xlim=c(1893,2015), ylim=c(0, 800))

count(MtRainier$order)

#St Helens pre-eruption
prehelrich<-count(preheldata, 'scientificname')
rownames(prehelrich)<-prehelrich$scientificname
prehelrich$scientificname<-NULL
colnames(prehelrich)<-NULL
prehelrichT<-t(prehelrich)
```

```
prehelrichT<-data.frame(prehelrichT)

#St Helens post-eruption
posthelrich<-count(postheldata, 'scientificname')
rownames(posthelrich)<-posthelrich$scientificname
posthelrich$scientificname<-NULL
colnames(posthelrich)<-NULL
posthelrichT<-t(posthelrich)
posthelrichT<-data.frame(posthelrichT)

#Rainier pre-eruption
rainnowhale<-MtRainier[MtRainier$order!='Cetacea',]
rainbinpre<-rainnowhale[rainnowhale$year>=1929 & rainnowhale$year<=1980,]
prerainrich<-count(rainbinpre, 'scientificname')
rownames(prerainrich)<-prerainrich$scientificname
prerainrich$scientificname<-NULL
colnames(prerainrich)<-NULL
prerainrichT<-t(prerainrich)
prerainrichT<-data.frame(prerainrichT)
count(rainbinpre$institutioncode)

#Rainier post-eruption
rainbinpost<-rainnowhale[rainnowhale$year>=1980 & rainnowhale$year<=1999,]
postrainrich<-count(rainbinpost, 'scientificname')
rownames(postrainrich)<-postrainrich$scientificname
postrainrich$scientificname<-NULL
colnames(postrainrich)<-NULL
postrainrichT<-t(postrainrich)
postrainrichT<-data.frame(postrainrichT)
count(rainbinpost$institutioncode)

#Lassen 1910-1920s
lasbin1020<-lasdata[lasdata$year>=1910 & lasdata$year<=1929,]
lasrich1020<-count(lasbin1020, 'scientificname')
rownames(lasrich1020)<-lasrich1020$scientificname
lasrich1020$scientificname<-NULL
colnames(lasrich1020)<-NULL
lasrich1020T<-t(lasrich1020)
lasrich1020T<-data.frame(lasrich1020T)

#Lassen 1930-1980s
lasbin3080<-lasdata[lasdata$year>=1930 & lasdata$year<=1989,]
lasrich3080<-count(lasbin3080, 'scientificname')
rownames(lasrich3080)<-lasrich3080$scientificname
lasrich3080$scientificname<-NULL
colnames(lasrich3080)<-NULL
```

```
lasrich3080T<-t(lasrich3080)
lasrich3080T<-data.frame(lasrich3080T)

#Lassen 1990-2000s
lasbin9000<-lasdata[lasdata$year>=1990 & lasdata$year<=2015,]
lasrich9000<-count(lasbin9000, 'scientificname')
rownames(lasrich9000)<-lasrich9000$scientificname
lasrich9000$scientificname<-NULL
colnames(lasrich9000)<-NULL
lasrich9000T<-t(lasrich9000)
lasrich9000T<-data.frame(lasrich9000T)

#Shasta 1910-1920s
shasbin1020<-MtShasta[MtShasta$year>=1910 & MtShasta$year<=1929,]
shasrich1020<-count(shasbin1020, 'scientificname')
rownames(shasrich1020)<-shasrich1020$scientificname
shasrich1020$scientificname<-NULL
colnames(shasrich1020)<-NULL
shasrich1020T<-t(shasrich1020)
shasrich1020T<-data.frame(shasrich1020T)
count(shasbin1020$institutioncode)

#Shasta 1930-1980s
shasbin3080<-MtShasta[MtShasta$year>=1930 & MtShasta$year<=1989,]
shasrich3080<-count(shasbin3080, 'scientificname')
rownames(shasrich3080)<-shasrich3080$scientificname
shasrich3080$scientificname<-NULL
colnames(shasrich3080)<-NULL
shasrich3080T<-t(shasrich3080)
shasrich3080T<-data.frame(shasrich3080T)
count(shasbin3080$institutioncode)

#Shasta 1990-2000s
shasbin9000<-MtShasta[MtShasta$year>=1990 & MtShasta$year<=2015,]
shasrich9000<-count(shasbin9000, 'scientificname')
rownames(shasrich9000)<-shasrich9000$scientificname
shasrich9000$scientificname<-NULL
colnames(shasrich9000)<-NULL
shasrich9000T<-t(shasrich9000)
shasrich9000T<-data.frame(shasrich9000T)
count(shasbin9000$institutioncode)

#create matrix for just pre and post
HelensLassentmatrix<-rbind.fill(prehelrichT, posthelrichT, lasrich1020T,
lasrich3080T,lasrich9000T)
#get rid of the NA's and replace them with 0
```

```
HelensLassentmatrix[is.na(HelensLassentmatrix)] <- 0
#change the row names so they make sence
rownames(HelensLassentmatrix)<-c("Pre", "Post", "1910s-1920s","1930s-1980s", "1990s-2000s")

#create matrix for 4 volcanoes
allmatrix<-rbind.fill(prehelrichT, posthelrichT, lasrich1020T, lasrich3080T,lasrich9000T, prerainrichT, postrainrichT, shasrich1020T, shasrich3080T,shasrich9000T)
#get rid of the NA's and replace them with 0
allmatrix[is.na(allmatrix)] <- 0
#change the row names so they make sence
rownames(allmatrix)<-c("Pre", "Post", "1910s-1920s","1930s-1980s", "1990s-2000s", "Rainier Pre", "Rainier Post", "Shasta 1910s-1920s","Shasta 1930s-1980s", "Shasta 1990s-2000s")

#chord dist
allvare.dist <- vegdist(decostand(allmatrix, "norm"), "euclidean")
allvare.dist

#NMDS for the 4 sites together
allexample_NMDS=metaMDS(allmatrix,k=4,trymax=100)

stressplot(allexample_NMDS)
plot(allexample_NMDS)
ordiplot(allexample_NMDS,type="n")
orditorp(allexample_NMDS,display="species",col="red",air=0.01)
orditorp(allexample_NMDS,display="sites",cex=1.25,air=0.01)
ordicluster(allexample_NMDS,hclust(vegdist(allmatrix,"bray")))
######################################################################
allmatrix2<-rbind.fill(prehelrichT, posthelrichT, lasrich1020T, lasrich3080T,lasrich9000T, prerainrichT, postrainrichT, shasrich1020T, shasrich3080T)
#get rid of the NA's and replace them with 0
allmatrix2[is.na(allmatrix2)] <- 0
#change the row names so they make sence
rownames(allmatrix2)<-c("Pre Helens", "Post Helens", "Lassen 1910s-1920s","Lassen 1930s-1980s", "Lassen 1990s-2000s", "Rainier Pre", "Rainier Post", "Shasta 1910s-1920s","Shasta 1930s-1980s")

#chord dist
allvare.dist2 <- vegdist(decostand(allmatrix2, "norm"), "euclidean")
allvare.dist2

#NMDS for the 4 sites together
allexample_NMDS2=metaMDS(allmatrix2,k=4,trymax=100)

stressplot(allexample_NMDS2)
plot(allexample_NMDS2)
```

```
ordiplot(allexample_NMDS2,type="n")
orditorp(allexample_NMDS2,display="species",col="red",air=0.01)
orditorp(allexample_NMDS2,display="sites",cex=1.25,air=0.01)
ordicluster(allexample_NMDS2,hclust(vegdist(allmatrix2,"bray")))

allvare.dist2test<-as.matrix(allvare.dist2)
write.csv(allvare.dist2test, file = "all_variables_7_bins.csv")

allvare.disttest<-as.matrix(allvare.dist)
write.csv(allvare.disttest, file = "all_variables_8_bins.csv")




#Do the other ecological metrics for shasta and rainier

#Shasta first

#Shannon index (evenness)
diversity(shasrich1020T)
diversity(shasrich3080T)
diversity(shasrich9000T)


#Hurlbert Index for evenness, or unbiased Simpson (Hurlbert 1971)
#saw this at http://www.inside-r.org/packages/cran/vegan/docs/diversity
rarefy(shasrich1020T, 2) - 1
rarefy(shasrich3080T, 2) - 1
rarefy(shasrich9000T, 2) - 1

#create matrix for just imediately after and 100 years later
shastamatrix<-rbind.fill(shasrich1020T,shasrich3080T,shasrich9000T)
#get rid of the NA's and replace them with 0
shastamatrix[is.na(shastamatrix)] <- 0
#change the row names so they make sence
rownames(shastamatrix)<-c("1910s-1920s","1930s-1980s", "1990s-2000s")


#i want to find chao
estimateR(shastamatrix)


#returns sample size for each bin
sum(shastamatrix[1,])
```

```
sum(shastamatrix[2,])
sum(shastamatrix[3,])

#Now Rainier

#Shannon index (evenness)
diversity(prerainrichT)
diversity(postrainrichT)


#Hurlbert Index for evenness, or unbiased Simpson (Hurlbert 1971)
#saw this at http://www.inside-r.org/packages/cran/vegan/docs/diversity
rarefy(prerainrichT, 2) - 1
rarefy(postrainrichT, 2) - 1

#create matrix for just imediately after and 100 years later
rainieramatrix<-rbind.fill(prerainrichT,postrainrichT)
#get rid of the NA's and replace them with 0
rainieramatrix[is.na(rainieramatrix)] <- 0
#change the row names so they make sence
rownames(rainieramatrix)<-c("pre","post")


#i want to find chao
estimateR(rainieramatrix)


#returns sample size for each bin
sum(rainieramatrix[1,])
sum(rainieramatrix[2,])



#Rainier post-eruption
rainbinpost80<-rainnowhale[rainnowhale$year==1980,]
postrainrich80<-count(rainbinpost80, 'scientificname')
rownames(postrainrich80)<-postrainrich80$scientificname
postrainrich80$scientificname<-NULL
colnames(postrainrich80)<-NULL
postrainrichT80<-t(postrainrich80)
postrainrichT80<-data.frame(postrainrichT80)

rainbinpost81<-rainnowhale[rainnowhale$year==1981,]
postrainrich81<-count(rainbinpost81, 'scientificname')
rownames(postrainrich81)<-postrainrich81$scientificname
postrainrich81$scientificname<-NULL
```

```
colnames(postrainrich81)<-NULL
postrainrichT81<-t(postrainrich81)
postrainrichT81<-data.frame(postrainrichT81)

rainbinpost82<-rainnowhale[rainnowhale$year==1982,]
postrainrich82<-count(rainbinpost82, 'scientificname')
rownames(postrainrich82)<-postrainrich82$scientificname
postrainrich82$scientificname<-NULL
colnames(postrainrich82)<-NULL
postrainrichT82<-t(postrainrich82)
postrainrichT82<-data.frame(postrainrichT82)

rainbinpost83<-rainnowhale[rainnowhale$year==1983,]
postrainrich83<-count(rainbinpost83, 'scientificname')
rownames(postrainrich83)<-postrainrich83$scientificname
postrainrich83$scientificname<-NULL
colnames(postrainrich83)<-NULL
postrainrichT83<-t(postrainrich83)
postrainrichT83<-data.frame(postrainrichT83)

rainbinpost84<-rainnowhale[rainnowhale$year==1984,]
postrainrich84<-count(rainbinpost84, 'scientificname')
rownames(postrainrich84)<-postrainrich84$scientificname
postrainrich84$scientificname<-NULL
colnames(postrainrich84)<-NULL
postrainrichT84<-t(postrainrich84)
postrainrichT84<-data.frame(postrainrichT84)

rainbinpost85<-rainnowhale[rainnowhale$year==1985,]
postrainrich85<-count(rainbinpost85, 'scientificname')
rownames(postrainrich85)<-postrainrich85$scientificname
postrainrich85$scientificname<-NULL
colnames(postrainrich85)<-NULL
postrainrichT85<-t(postrainrich85)
postrainrichT85<-data.frame(postrainrichT85)

rainbinpost99<-rainnowhale[rainnowhale$year==1999,]
postrainrich99<-count(rainbinpost99, 'scientificname')
rownames(postrainrich99)<-postrainrich99$scientificname
postrainrich99$scientificname<-NULL
colnames(postrainrich99)<-NULL
postrainrichT99<-t(postrainrich99)
postrainrichT99<-data.frame(postrainrichT99)

#Shannon index (evenness)
diversity(postrainrichT80)
```

```
diversity(postrainrichT81)
diversity(postrainrichT82)
diversity(postrainrichT83)
diversity(postrainrichT84)
diversity(postrainrichT85)


#Hurlbert Index for evenness, or unbiased Simpson (Hurlbert 1971)
rarefy(postrainrichT80, 2) - 1
rarefy(postrainrichT81, 2) - 1
rarefy(postrainrichT82, 2) - 1
rarefy(postrainrichT83, 2) - 1
rarefy(postrainrichT84, 2) - 1
rarefy(postrainrichT85, 2) - 1

#create matrix for just imediately after and 100 years later
rainieramatrixyr<-
rbind.fill(postrainrichT80,postrainrichT81,postrainrichT82,postrainrichT83,postrainrichT84,post
rainrichT85)
#get rid of the NA's and replace them with 0
rainieramatrixyr[is.na(rainieramatrixyr)] <- 0
#change the row names so they make sence
rownames(rainieramatrixyr)<-c("80","81","82","83","84","85")


#i want to find chao
estimateR(rainieramatrixyr)


#returns sample size for each bin
sum(rainieramatrixyr[1,])
sum(rainieramatrixyr[2,])
sum(rainieramatrixyr[3,])
sum(rainieramatrixyr[4,])
sum(rainieramatrixyr[5,])
sum(rainieramatrixyr[6,])

#St Helens post-eruption
postheldata80<-postheldata[postheldata$year==1980,]
posthelrich80<-count(postheldata80, 'scientificname')
rownames(posthelrich80)<-posthelrich80$scientificname
posthelrich80$scientificname<-NULL
colnames(posthelrich80)<-NULL
posthelrichT80<-t(posthelrich80)
posthelrichT80<-data.frame(posthelrichT80)
```

```
postheldata81<-postheldata[postheldata$year==1981,]
posthelrich81<-count(postheldata81, 'scientificname')
rownames(posthelrich81)<-posthelrich81$scientificname
posthelrich81$scientificname<-NULL
colnames(posthelrich81)<-NULL
posthelrichT81<-t(posthelrich81)
posthelrichT81<-data.frame(posthelrichT81)

postheldata82<-postheldata[postheldata$year==1982,]
posthelrich82<-count(postheldata82, 'scientificname')
rownames(posthelrich82)<-posthelrich82$scientificname
posthelrich82$scientificname<-NULL
colnames(posthelrich82)<-NULL
posthelrichT82<-t(posthelrich82)
posthelrichT82<-data.frame(posthelrichT82)

postheldata83<-postheldata[postheldata$year==1983,]
posthelrich83<-count(postheldata83, 'scientificname')
rownames(posthelrich83)<-posthelrich83$scientificname
posthelrich83$scientificname<-NULL
colnames(posthelrich83)<-NULL
posthelrichT83<-t(posthelrich83)
posthelrichT83<-data.frame(posthelrichT83)

postheldata84<-postheldata[postheldata$year==1984,]
posthelrich84<-count(postheldata84, 'scientificname')
rownames(posthelrich84)<-posthelrich84$scientificname
posthelrich84$scientificname<-NULL
colnames(posthelrich84)<-NULL
posthelrichT84<-t(posthelrich84)
posthelrichT84<-data.frame(posthelrichT84)

postheldata85<-postheldata[postheldata$year==1985,]
posthelrich85<-count(postheldata85, 'scientificname')
rownames(posthelrich85)<-posthelrich85$scientificname
posthelrich85$scientificname<-NULL
colnames(posthelrich85)<-NULL
posthelrichT85<-t(posthelrich85)
posthelrichT85<-data.frame(posthelrichT85)

postheldata99<-postheldata[postheldata$year==1999,]
posthelrich99<-count(postheldata99, 'scientificname')
rownames(posthelrich99)<-posthelrich99$scientificname
posthelrich99$scientificname<-NULL
colnames(posthelrich99)<-NULL
posthelrichT99<-t(posthelrich99)
```

```
posthelrichT99<-data.frame(posthelrichT99)

#Shannon index (evenness)
diversity(posthelrichT80)
diversity(posthelrichT81)
diversity(posthelrichT82)
diversity(posthelrichT83)
diversity(posthelrichT84)
diversity(posthelrichT85)
diversity(posthelrichT99)


#Hurlbert Index for evenness, or unbiased Simpson (Hurlbert 1971)
rarefy(posthelrichT80, 2) - 1
rarefy(posthelrichT81, 2) - 1
rarefy(posthelrichT82, 2) - 1
rarefy(posthelrichT83, 2) - 1
rarefy(posthelrichT84, 2) - 1
rarefy(posthelrichT85, 2) - 1
rarefy(posthelrichT99, 2) - 1
```

APPENDIX D

RAW DATA FOR CHAPTER IV

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				lower	premolar	p2
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				lower	premolar	p3
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				lower	premolar	p4
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				lower	molar	m1
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				lower	molar	m2
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				lower	molar	m3
JODA 10226	Deer Gulch South	Equidae	*Miohippus*	sp.	John Day	Big Basin			lower		
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	premolar	p1
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	premolar	p2
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	premolar	p3
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	premolar	p4
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	molar	m1

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	molar	m2
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	molar	m3
JODA 1196	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	A	lower		
JODA 1233	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	D	lower	premolar	p2
JODA 1233	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	D	lower		
JODA 12340	JDNM–52, Logan Butte	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		lower		
JODA 13004	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	lower	molar	m3
JODA 13244	JDNM–7 Foree	Equidae			John Day	Turtle Cove	Lower	E	lower		
JODA 13244	JDNM–7 Foree	Equidae			John Day	Turtle Cove	Lower	E	lower		
JODA 14952	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	lower	molar	m1
JODA 14952	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	lower	molar	m2
JODA 14952	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	lower	molar	m3
JODA 15390	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	D	lower	molar	m2
JODA 15390	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	D	lower	molar	m3

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
JODA 15427	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		lower	premolar	p4
JODA 15427	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		lower	molar	m1
JODA 15427	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		lower	molar	m2
JODA 16189	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	premolar	p4
JODA 1751	JDNM–41 Artman Basin (Picture Gorge 25)	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	premolar	p2
JODA 1863	826A	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	lower	molar	m1
JODA 1863	826A	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	lower	molar	m2
JODA 1863	826A	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	lower	molar	M3
JODA 1902	JDNM–8 Sheep Rock	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			lower	molar	m1
JODA 1902	JDNM–8 Sheep Rock	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			lower	molar	m2
JODA 1902	JDNM–8 Sheep Rock	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			lower	molar	m3
JODA 1908	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		lower	molar	m2
JODA 2835	JDNM–55 Lawson Ranch (Haystack 29)	Equidae	*Miohippus*	sp.	John Day	Haystack Valley			lower		
JODA 2897	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	molar	m2

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
JODA 2897	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	molar	m3
JODA 3052	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	lower	molar	m2
JODA 3382	JDNM–35 Roundup Flat	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	A	lower		
JODA 3428	JDNM–	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			lower		
JODA 3670	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	lower	molar	m3
JODA 4405	JDNM– Sutton Mountain	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		lower	molar	m1
JODA 4405	JDNM– Sutton Mountain	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		lower	molar	m2
JODA 4405	JDNM– Sutton Mountain	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		lower	molar	m3
JODA 4408	JDNM–26 Sutton Mountain, Slater's Site	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Upper		lower	molar	m3
JODA 4789	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	lower		
JODA 4793	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	lower	premolar	p2
JODA 4853	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	D	lower		
JODA 4895	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	B	lower	molar	m3
JODA 5788	JDNM–64 Sorefoot Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		lower		

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
JODA 6156	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			lower	premolar	p2
JODA 6156	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			lower	premolar	p3
JODA 6156	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			lower	molar	m1
JODA 6156	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			lower	molar	m2
JODA 6156	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			lower	molar	m3
JODA 6215	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			lower	premolar	p3
JODA 6234	BLM Land Exchange Tract 58	Equidae	*Miohippus*	sp.	John Day				lower	molar	m3
JODA 7072	JDNM–8 Sheep Rock	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Upper	K2	lower		
JODA 7227	JDNM–171, Leonard	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	B	lower	molar	m1
JODA 7227	JDNM–171, Leonard	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	B	lower	molar	m2
JODA 7551	JDNM–171, Leonard	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	B	lower		
JODA 768	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	lower		
JODA 8256	JDNM–36 Upper Deep Creek (Picture Gorge 15)	Equidae	*Mesohippus*	sp.	John Day	Turtle Cove	Upper	H	lower		
JODA 8266	JDNM–49 Bone Creek (upper)	Equidae	*Miohippus*	sp.	John Day	Kimberly		M	lower	molar	m3

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
JODA 8288	Badlands north of section high above Longview Ranch	Equidae	*Mesohippus*	sp.	John Day	Turtle Cove	Upper	H?	lower		
JODA 8323	JDNM–36 Upper Deep Creek (Picture Gorge 15)	Equidae	*Mesohippus*	sp.	John Day	Turtle Cove	Upper	J	lower		
JODA 917	JDNM–24 Lower Carroll Rim West	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		lower	molar	m3
JODA 969	JDNM–8 Sheep Rock	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			lower	premolar	p2
UOMNH F-30304	UO 2705–E. Side of the cove, Clarno, OR	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			lower	molar	m1
UOMNH F-30304	UO 2705–E. Side of the cove, Clarno, OR	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			lower	molar	m2
UOMNH F-4013	UO 2275–Spray	Equidae	*Miohippus*	sp.	John Day				lower	premolar	p4
UOMNH F-4013	UO 2275–Spray	Equidae	*Miohippus*	sp.	John Day				lower	molar	m1
UOMNH F-4013	UO 2275–Spray	Equidae	*Miohippus*	sp.	John Day				lower	molar	m3
UOMNH F-4610	UO 2676–Clarno, OR	Equidae	*Miohippus*	sp.	John Day				lower		
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				lower	premolar	p2
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				lower	premolar	p3

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				lower	premolar	p4
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				lower	molar	m1
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				lower	molar	m2
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				lower	molar	m3
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				upper	premolar	P2
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				upper	premolar	P3
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				upper	premolar	P4
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				upper	molar	M1
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				upper	molar	M2
AMNH FM 7261	John Day Basin	Equidae	*Miohippus*	*equiceps*	John Day				upper	molar	M3
AMNH FM 7291	John Day Basin	Equidae	*Miohippus*	*primus*	John Day				upper	premolar	P4
AMNH FM 7291	John Day Basin	Equidae	*Miohippus*	*primus*	John Day				upper	molar	M1
AMNH FM 7291	John Day Basin	Equidae	*Miohippus*	*primus*	John Day				upper	molar	M2
AMNH FM 7291	John Day Basin	Equidae	*Miohippus*	*primus*	John Day				upper	molar	M3
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper	premolar	P2

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper	premolar	P3
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper	premolar	P4
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper	molar	M1
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper	molar	M2
JODA 1086	JDNM–3 John Day General, Branson Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper	molar	M3
JODA 11975	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	upper	premolar	P4
JODA 11975	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	upper	molar	M1
JODA 11975	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	upper	molar	M2
JODA 11975	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	upper	molar	M3
JODA 12035	JDNM–227, Spring Canyon	Equidae	*Miohippus*	sp.	John Day	Haystack Valley?			upper		
JODA 1256	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper		
JODA 13014	JDNM–171, Leonard	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	B	upper		
JODA 14172	JDNM–7B Foree North	Equidae	*Mesohippus*	sp.	John Day	Turtle Cove	Lower	E	upper	molar	M3

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
JODA 14221	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	B	upper	premolar	P2
JODA 14235	JDNM–9 Blue Basin	Equidae	*Mesohippus*	sp.	John Day	Turtle Cove	Lower	C	upper	molar	M1
JODA 14890	East of field across from Cant Ranch	Equidae	*Miohippus*	sp.	John Day	Big Basin			upper		
JODA 15427	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	molar	M2
JODA 15427	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	molar	M3
JODA 15966	JDNM–7A Foree South	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper		
JODA 16396	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	upper	premolar	P4
JODA 1863	826A	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	upper	premolar	P4
JODA 1863	826A	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	upper	molar	M1
JODA 1863	826A	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	upper	molar	M2
JODA 1863	826A	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	F	upper	molar	M3
JODA 3085	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper		
JODA 310	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper		

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
JODA 328	JDNM–3 John Day General, Drainage of Deep Creek (Sambar Ranch)	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			upper		
JODA 3314	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper	molar	M3
JODA 3317	JDNM–67 Deer Gulch	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper		
JODA 3536	JDNM– Rudio Creek	Equidae	*Miohippus*	sp.	John Day				upper		
JODA 366	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper	molar	M2
JODA 378	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper		
JODA 378	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper		
JODA 378	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper		
JODA 4644	JDNM–64 Sorefoot Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper		
JODA 4811	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	B	upper		
JODA 4890	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	upper		
JODA 4918	JDNM–9 Blue Basin	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	upper		
JODA 4970	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	B	upper		
JODA 5787	JDNM–64 Sorefoot Creek	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper		

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
JODA 5903	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			upper	molar	M1
JODA 5903	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			upper	molar	M2
JODA 5903	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			upper	molar	M3
JODA 6175	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			upper	molar	M3
JODA 6175	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			upper		
JODA 6175	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			upper		
JODA 6175	JDNM–140 Lonerock	Equidae	*Miohippus*	sp.	John Day	Kimberly			upper		
JODA 6363	JDNM–7 Foree	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	upper	molar	M
JODA 6753	JDNM–8 Sheep Rock	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	upper	molar	M3
JODA 7105	JDNM–52, Logan Butte	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	molar	M2
JODA 7294	JDNM–52, Logan Butte	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper		
JODA 7369	JDNM–140 Lonerock	Equidae	*Archaeohippus*	sp.	John Day	Kimberly			upper	premolar	P2
JODA 7369	JDNM–140 Lonerock	Equidae	*Archaeohippus*	sp.	John Day	Kimberly			upper	premolar	P3
JODA 7369	JDNM–140 Lonerock	Equidae	*Archaeohippus*	sp.	John Day	Kimberly			upper	premolar	P4
JODA 7369	JDNM–140 Lonerock	Equidae	*Archaeohippus*	sp.	John Day	Kimberly			upper	molar	M1
JODA 7369	JDNM–140 Lonerock	Equidae	*Archaeohippus*	sp.	John Day	Kimberly			upper	molar	M2

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
JODA 7369	JDNM–140 Lonerock	Equidae	*Archaeohippus*	sp.	John Day	Kimberly			upper	molar	M3
JODA 7740	JDNM–7B Foree North	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	E	upper	molar	M
JODA 8578	JDNM–7B Foree North	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower	C	upper	molar	M1
UCMP 1162	–870, Rudio 2	Equidae	*Miohippus*	*longiceps*	John Day	Kimberly			upper	premolar	P2
UCMP 1162	–870, Rudio 2	Equidae	*Miohippus*	*longiceps*	John Day	Kimberly			upper	premolar	P3
UCMP 1162	–870, Rudio 2	Equidae	*Miohippus*	*longiceps*	John Day	Kimberly			upper	premolar	P4
UCMP 1162	–870, Rudio 2	Equidae	*Miohippus*	*longiceps*	John Day	Kimberly			upper	molar	M1
UCMP 1162	–870, Rudio 2	Equidae	*Miohippus*	*longiceps*	John Day	Kimberly			upper	molar	M2
UCMP 1162	–870, Rudio 2	Equidae	*Miohippus*	*longiceps*	John Day	Kimberly			upper	molar	M3
UCMP 376	V67101–Middle Fork, horse beds of cotton wood creek	Equidae	*Miohippus*	*acutidens*	John Day	Turtle Cove	Lower		upper	premolar	P2
UCMP 376	V67101–Middle Fork, horse beds of cotton wood creek	Equidae	*Miohippus*	*acutidens*	John Day	Turtle Cove	Lower		upper	premolar	P3
UCMP 376	V67101–Middle Fork, horse beds of cotton wood creek	Equidae	*Miohippus*	*acutidens*	John Day	Turtle Cove	Lower		upper	premolar	P4
UCMP 376	V67101–Middle Fork, horse beds of cotton wood creek	Equidae	*Miohippus*	*acutidens*	John Day	Turtle Cove	Lower		upper	molar	M1

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
UCMP 376	V67101–Middle Fork, horse beds of cotton wood creek	Equidae	*Miohippus*	*acutidens*	John Day	Turtle Cove	Lower		upper	molar	M2
UCMP 376	V67101–Middle Fork, horse beds of cotton wood creek	Equidae	*Miohippus*	*acutidens*	John Day	Turtle Cove	Lower		upper	molar	M3
UCMP 75279	V6630–Logan Butte, South Canyon 2	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	premolar	P2
UCMP 75279	V6630–Logan Butte, South Canyon 2	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	premolar	P3
UCMP 75279	V6630–Logan Butte, South Canyon 2	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	premolar	P4
UCMP 75279	V6630–Logan Butte, South Canyon 2	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	molar	M1
UCMP 75279	V6630–Logan Butte, South Canyon 2	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	molar	M2
UCMP 75279	V6630–Logan Butte, South Canyon 2	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	molar	M3
UOMNH F-35197	UO 12985–Longview Ranch of Condon	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			upper		
UOMNH F-35197	UO 12985–Longview Ranch of Condon	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			upper		

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
UOMNH F-4609	UO 12985–	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			upper	molar	M2
UOMNH F-4609	UO 12985–	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			upper	molar	M3
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				upper	premolar	P2
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				upper	premolar	P3
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				upper	premolar	P4
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				upper	molar	M1
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				upper	molar	M2
UOMNH F-58207	John Day Basin	Equidae	*Miohippus*	sp.	John Day				upper	molar	M3
UOMNH F-775	UO 12985–	Equidae	*Miohippus*	sp.	John Day	Turtle Cove			upper	molar	M3
UWBM 53305	UWBM C0095, Picture Gorge 16	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Upper		upper	premolar	P2
UWBM 53305	UWBM C0095, Picture Gorge 16	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Upper		upper	premolar	P3
UWBM 53305	UWBM C0095, Picture Gorge 16	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Upper		upper	premolar	P4
UWBM 53305	UWBM C0095, Picture Gorge 16	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Upper		upper	molar	M1

Specimen #	Locality	Family	Genus	species	Formation	Member	Upper or Lower Turtle Cove Member	geologic subunit	upper or lower	Premolar or Molar	Tooth
UWBM 53305	UWBM C0095, Picture Gorge 16	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Upper		upper	molar	M2
UWBM 53305	UWBM C0095, Picture Gorge 16	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Upper		upper	molar	M3
UWBM 53424	Picture Gorge 20 (Foree Beds)	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	premolar	P2
UWBM 53424	Picture Gorge 20 (Foree Beds)	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	premolar	P3
UWBM 53424	Picture Gorge 20 (Foree Beds)	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	premolar	P4
UWBM 53424	Picture Gorge 20 (Foree Beds)	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	molar	M1
UWBM 53424	Picture Gorge 20 (Foree Beds)	Equidae	*Miohippus*	sp.	John Day	Turtle Cove	Lower		upper	molar	M2
YPM VP 011275	John Day River	Equidae	*Miohippus*	*annectens*	John Day				upper	premolar	P2
YPM VP 011275	John Day River	Equidae	*Miohippus*	*annectens*	John Day				upper	premolar	P3
YPM VP 012230	John Day River	Equidae	*Miohippus*	*annectens*	John Day				upper	premolar	P2
YPM VP 012230	John Day River	Equidae	*Miohippus*	*annectens*	John Day				upper	premolar	P3
YPM VP 012230	John Day River	Equidae	*Miohippus*	*annectens*	John Day				upper	premolar	P4
YPM VP 012230	John Day River	Equidae	*Miohippus*	*annectens*	John Day				upper	molar	M1
YPM VP 012230	John Day River	Equidae	*Miohippus*	*annectens*	John Day				upper	molar	M2
YPM VP 012230	John Day River	Equidae	*Miohippus*	*annectens*	John Day				upper	molar	M3

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
AMNH FM 7261	15.07	7.89				cast
AMNH FM 7261	13.20	9.35				cast
AMNH FM 7261	13.36	9.92				cast
AMNH FM 7261	12.75	9.16				cast
AMNH FM 7261	13.56	8.91				cast
AMNH FM 7261	17.45	8.59				cast
JODA 10226		8.40				broken tooth, labeled as Mesohippus
JODA 1086	8.24	4.28				
JODA 1086	14.66	9.30				
JODA 1086	13.34	10.48				
JODA 1086	14.82	11.68				
JODA 1086	13.22	10.12				
JODA 1086	13.93	10.14				

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
JODA 1086	18.32	9.33				
JODA 1196	11.29	7.46				
JODA 1233	13.88	10.08				
JODA 1233		10.66				broken tooth
JODA 12340	14.21	11.07				
JODA 13004	17.04	9.23				
JODA 13244	13.07					broken tooth
JODA 13244	12.84	8.69				
JODA 14952	13.00	8.53				
JODA 14952	12.39	9.10				
JODA 14952	19.26	9.69				
JODA 15390	14.22	9.50				
JODA 15390	18.24	8.88				
JODA 15427	14.62	10.73				
JODA 15427		11.96				broken Tooth

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
JODA 15427	14.08	10.72				
JODA 16189	13.78	10.47				
JODA 1751	15.87	9.95				
JODA 1863	14.96					closed skull and jaw
JODA 1863	15.82					closed skull and jaw
JODA 1863	17.09					closed skull and jaw
JODA 1902	14.01	9.98				
JODA 1902	14.40	10.10				
JODA 1902	17.92	9.07				
JODA 1908	14.01	9.76				
JODA 2835	16.58	10.61				
JODA 2897		9.20				broken Tooth
JODA 2897	17.51	8.93				
JODA 3052	14.73	8.85				
JODA 3382		11.24				broken tooth

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
JODA 3428	13.81	10.67				
JODA 3670	16.61	8.37				
JODA 4405	12.72	8.26				
JODA 4405	12.27	7.79				
JODA 4405	15.68	7.39				
JODA 4408	16.54	7.93				
JODA 4789	13.41	10.52				
JODA 4793	12.40	6.89				
JODA 4853	11.55	8.77				
JODA 4895	15.61	7.55				
JODA 5788	12.72	9.08				
JODA 6156	13.04	7.95				
JODA 6156	13.02	9.95				
JODA 6156	12.37	9.66				
JODA 6156	12.78	9.47				
JODA 6156	16.98	8.19				
JODA 6215	12.86	10.11				
JODA 6234	17.19	8.55				

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
JODA 7072		8.69				broken tooth
JODA 7227	13.67	10.92				
JODA 7227	12.92	9.64				
JODA 7551	13.07	8.93				
JODA 768	14.12	9.71				
JODA 8256	12.73	9.98				
JODA 8266	17.49	9.19				
JODA 8288		10.98				broken tooth
JODA 8323	12.30	12.23				
JODA 917	18.12	8.82				
JODA 969	15.13	7.96				
UOMNH F-30304	12.93	8.94				
UOMNH F-30304	12.98	9.06				
UOMNH F-4013	11.92	10.25				
UOMNH F-4013	12.26	9.26				

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
UOMNH F-4013	14.46	7.52				
UOMNH F-4610	13.33	9.36				
UOMNH F-58207	11.22	7.06				
UOMNH F-58207	11.69	8.91				
UOMNH F-58207	11.04	8.35				
UOMNH F-58207	10.53	7.96				
UOMNH F-58207	11.52	7.94				
UOMNH F-58207	14.99	6.86				
AMNH FM 7261	16.01	14.30	4.32	0.27	none	cast
AMNH FM 7261	15.49	15.29	3.51	0.23	none	cast
AMNH FM 7261	14.28	15.91	3.03	0.21	none	cast
AMNH FM 7261	14.46	15.79	3.34	0.23	none	cast
AMNH FM 7261	13.96	16.39	4.19	0.30	3	cast
AMNH FM 7261	14.77	17.06	4.58	0.31	3	cast
AMNH FM 7291	14.54	17.53	7.60	0.52	2	cast
AMNH FM 7291	14.37	16.83	8.62	0.60	2	cast
AMNH FM 7291	15.40	16.96	7.90	0.51	2	cast
AMNH FM 7291	14.91	17.58	8.06	0.54	2	cast
JODA 1086	16.99	16.01	5.20	0.31	none	
JODA 1086	16.05	17.67	4.64	0.29	none	
JODA 1086	15.83	19.09	4.34	0.27	2	
JODA 1086	14.17	17.43	4.04	0.29	none	

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
JODA 1086	14.61	19.00	4.64	0.32	3	
JODA 1086	13.84	17.36	5.06	0.37	2	
JODA 11975	13.65					in matrix
JODA 11975	13.26					in matrix
JODA 11975	13.68	13.11	3.84	0.28	none	
JODA 11975	14.73	14.84	3.36	0.23	none	obscured
JODA 12035	12.89	14.75	5.83	0.45	3	
JODA 1256	13.53	16.52	3.60	0.27	none	
JODA 13014	12.45				2	broken tooth
JODA 14172	13.38	14.88	5.81	0.43	1	no roots
JODA 14221	13.48	12.45	4.50	0.33	3	
JODA 14235	10.70	13.88	5.17	0.48	1	
JODA 14890					1	boken tooth
JODA 15427	13.96	16.76			3	broken tooth

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
JODA 15427	14.81	17.33	5.96	0.40	2	
JODA 15966	12.28					broken tooth
JODA 16396	13.01	16.08	3.94	0.30	2	labeled as Mesohippus
JODA 1863	15.63		7.11	0.45		closed skull and jaw
JODA 1863	15.82		8.10	0.51		closed skull and jaw
JODA 1863	16.53		8.42	0.51		closed skull and jaw
JODA 1863	15.25		7.28	0.48		closed skull and jaw
JODA 3085	12.98	15.06			3	broken tooth
JODA 310	13.46	16.15	4.56	0.34	3	
JODA 328	14.40	19.01	7.19	0.50	2	
JODA 3314		8.29				
JODA 3317	12.40	15.86			2	broken tooth
JODA 3536	14.16	16.45	4.30	0.30	3	in red matrix
JODA 366	13.77	14.35	3.76	0.27	none	
JODA 378	14.10	16.62	5.39	0.38	3	

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
JODA 378	13.86	17.16	4.90	0.35	3	
JODA 378	13.79	16.11	5.55	0.40	3	
JODA 4644	13.99	16.79	4.27	0.31	none	
JODA 4811	12.38				3	broken tooth
JODA 4890	13.65		5.65	0.41	3	
JODA 4918	12.81					broken tooth
JODA 4970	13.54	17.57	7.26	0.54	2	
JODA 5787	13.38	16.20	3.46	0.26	3	
JODA 5903	10.92	13.99	3.55	0.33	none	
JODA 5903	11.10	14.47	3.00	0.27	3	
JODA 5903	11.76	13.35	3.56	0.30	3	
JODA 6175	11.79	13.31			3	obsured by matrix
JODA 6175	12.11	14.97	5.23	0.43	3	
JODA 6175	13.01	15.55	5.52	0.42	3	
JODA 6175	11.99	14.70	4.29	0.36	3	
JODA 6363	12.70					broken tooth
JODA 6753	12.28	13.72	4.72	0.38	2	
JODA 7105	15.57	16.55	3.88	0.25	3	
JODA 7294	13.92	16.52	6.70	0.48	2	no roots

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
JODA 7369		12.76	4.97		3	Broken tooth
JODA 7369	11.99	15.46	5.12	0.43	3	
JODA 7369					3	broken tooth
JODA 7369	11.44	14.80	4.12	0.36	3	
JODA 7369	11.75	14.63	4.89	0.42	3	
JODA 7369	11.37	14.63	5.40	0.47	3	
JODA 7740	13.08	14.61	4.97	0.38	2	
JODA 8578	15.21	16.39	6.75	0.44		juvinal w/ milk teeth, tooth obsured
UCMP 1162	15.68	16.22			none	cast, tooth broken
UCMP 1162	15.32	17.91	5.82	0.38	none	cast
UCMP 1162	14.43	16.99	5.17	0.36	3	cast
UCMP 1162	15.28	18.36	4.51	0.30	none	cast
UCMP 1162	16.40	18.69	5.43	0.33	3	cast
UCMP 1162	13.43	17.41	5.09	0.38	3	cast
UCMP 376	14.39	14.02	3.71	0.26	none	cast
UCMP 376	12.83	15.51	3.55	0.28	3	cast
UCMP 376	13.14	16.36	3.78	0.29	2	cast
UCMP 376	12.46	16.04	3.19	0.26	3	cast

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
UCMP 376	13.62	15.95	4.02	0.30	2	cast
UCMP 376	13.14	15.42	4.89	0.37	1	cast
UCMP 75279	15.54	15.06	4.81	0.31	none	cast
UCMP 75279	13.75	16.23	4.24	0.31	none	cast
UCMP 75279	14.53	17.20	4.32	0.30	none	cast
UCMP 75279	14.04	17.79	5.20	0.37	none	cast
UCMP 75279	13.98	17.15	4.96	0.35	3	cast
UCMP 75279	14.66	17.18	5.21	0.36	3	cast
UOMNH F-35197	13.94	12.70	3.99	0.29	3	OMSI
UOMNH F-35197	14.03	13.33	4.25	0.30	2	OMSI
UOMNH F-4609	14.03	16.76	5.87	0.42	3	
UOMNH F-4609	11.96	15.63	4.69	0.39	3	
UOMNH F-58207	12.75	12.24	5.15	0.40	2	
UOMNH F-58207	11.42	13.74	5.60	0.49	2	
UOMNH F-58207	11.73	14.06	5.91	0.50	2	
UOMNH F-58207	11.34	14.02	5.59	0.49	2	
UOMNH F-58207	11.94	14.64	6.30	0.53	1	

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
UOMNH F-58207	12.04	12.15	5.56	0.46	1	
UOMNH F-775	13.07	16.56	6.11	0.47	2	
UWBM 53305	14.76	13.67	4.94	0.33	none	cast
UWBM 53305	12.30	16.66	4.96	0.40	none	cast
UWBM 53305	13.99	16.95	4.82	0.34	3	cast
UWBM 53305	14.21	16.57	4.16	0.29	3	cast
UWBM 53305	14.24	18.21	4.95	0.35	3	cast
UWBM 53305	14.42	16.73	5.85	0.41	3	cast
UWBM 53424	15.18		5.54	0.36		closed skull and jaw, cast
UWBM 53424	14.54		7.12	0.49		closed skull and jaw, cast
UWBM 53424	14.58		7.35	0.50		closed skull and jaw, cast
UWBM 53424	13.48		7.42	0.55		closed skull and jaw, cast
UWBM 53424	14.03		7.92	0.56		closed skull and jaw, cast
YPM VP 011275	16.16	16.06	6.458	0.40	2	
YPM VP 011275	17.01	19.55	6.562	0.39	2	
YPM VP 012230	14.77	14.44	5.481	0.37	3	Type
YPM VP 012230	13.51	16.3	5.638	0.42	3	Type
YPM VP 012230	15.34	16.7	6.57	0.43	3	Type
YPM VP 012230	14.53	15.94	6.223	0.43	3	Type

Specimen #	APL (mm)	TW (mm)	Mesostyle Crown Height (mm)	HI	Hypostyle condition	notes
YPM VP 012230	14.92	16.79	6.91	0.46	3	Type
YPM VP 012230	12.77	14.53	6.496	0.51	3	Type

APPENDIX E

R CODE FOR CHAPTER IV

```
#This is code written by Nick Famoso to calculate an ordered logistic regression
#on data collected for Miohippus wear stages and Hypostyle condition
#Date: December 2014

#clear the memory
rm(list=ls())

#load the library
library(ordinal)
library(MASS)

data<-read.csv("Miohippus_Hypostyle.csv")

Hypostyle<-data$Hypostyle_condition
Hypostyle1<-data$Hypostyle_conditionA
Wear<-data$HI

#perform ordinal logistic regression
z<-polr(Hypostyle1~Wear, data = data, Hess=TRUE, method="logistic")
summary(z)

#present results with no p-value
(ctable <- coef(summary(z)))
#Get p-values
p<-pnorm(abs(ctable[,"t value"]), lower.tail=FALSE)*2
(ctable<-cbind(ctable, "pvalue" = p))


#run is without the M3
noM3<-data[ which(data$tooth!='M3'), ]

M3Hypostyle<-noM3$Hypostyle_condition
M3Hypostyle1<-noM3$Hypostyle_conditionA
M3Wear<-noM3$HI

#perform ordinal logistic regression
M3z<-polr(M3Hypostyle1~M3Wear, data = data, Hess=TRUE, method="logistic")
summary(M3z)

#present results with no p-value
(M3ctable <- coef(summary(M3z)))
#Get p-values
M3p<-pnorm(abs(M3ctable[,"t value"]), lower.tail=FALSE)*2
(M3ctable<-cbind(M3ctable, "pvalue" = M3p))
```

```
#plot the data
ordinal.regression<-function(y,x) {
  xp<-seq(min(x),max(x), length=100)
  yi<-matrix(nc=length(levels(y)), nr=length(y))
  ri<-list();
  ypi<-matrix(nc=length(levels(y)),nr=100)
  for (i in 1:length(levels(y))){
    yi[,i]<-as.numeric(y)>=i
    ri[[i]]<-glm(yi[,i]~x,family=binomial)
    ypi[,i]<-predict(ri[[i]], data.frame(x=xp),type='response')
  }
  plot(as.numeric(y)~x, xlab='Wear', ylab='Hypostyle')
  lines(xp, apply(ypi,1,sum),col='red',lwd=3)
}

ordinal.regression(Hypostyle1,Wear)

#plot without the M3s
ordinal.regression(M3Hypostyle1,M3Wear)

#another way to plot the data
ordinal.regression.two <- function (y,x) {
  xp <- seq(min(x),max(x), length=100)
  yi <- list();
  ri <- list();
  ypi <- matrix(nc=length(levels(y)), nr=100)
  for (i in 1:length(levels(y))) {
    ya <- as.numeric(y)
    o <- ya >= i
    ya <- ya[o]
    xa <- x[o]
    yi[[i]] <- ya == i
    ri[[i]] <- glm(yi[[i]] ~ xa, family=binomial)
    ypi[,i] <- predict(ri[[i]], data.frame(xa=xp), type='response')
  }

  # The plot is trickier to draw than earlier
  plot(as.numeric(y) ~ x)
  p <- matrix(0, nc=length(levels(y)), nr=100)
  for (i in 1:length(levels(y))) {
    p[,i] = ypi[,i] * (1 - apply(p,1,sum))
  }
  for (i in 1:length(levels(y))) {
    p[,i] = p[,i]*i
  }
  lines(xp, apply(p,1,sum), col='red', lwd=3)
```

```
}
ordinal.regression.two(Hypostyle1,Wear)
```

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