TROPHIC STRUCTURE EVOLUTION IN OREGON OLIGO-MIOCENE TERRESTRIAL COMMUNITIES

by

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A DISSERTATION

Presented to the Department of Earth Sciences
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in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy

December 2021

DISSERTATION APPROVAL PAGE

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Title: Trophic Structure Evolution In Oregon Oligo-Miocene Terrestrial Communities

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DISSERTATION ABSTRACT

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Title: Trophic structure evolution in Oregon Oligo-Miocene terrestrial communities

The goal of my dissertation is to expand our knowledge of how mammalian diets are affected by and affect other ecological and evolutionary processes. I did this by evaluating how diet is related to mammalian diversity, body mass, and evolution. I also evaluated and how environmental change affects mammalian functional diversity and community structure. I first, investigated whether tooth-size variation is driven by functional demands. I found that tooth-size variation is not determined by developmental controls or functional demands alone, but a combination of factors influence carnivoran tooth-size variation, such as differences in ontogeny, diet, sexual dimorphism, and evolutionary history. Next, I evaluated how type of omnivory is related to mammalian diversity, body mass, and evolution. Complete generalists are rare and most omnivorous mammals consume only invertebrate prey and non-fibrous plants. Omnivores that only consume invertebrate prey are on average smaller than omnivores that incorporate vertebrate prey. Transition rate models show that there are high transition rates from insectivorous omnivory to herbivory, and from vertebrate predation to prey mixing and ultimately insectivory. This work highlights that prey type is an important aspect of omnivore macroevolution and macroecology, as it is correlated with body mass and diet-related evolutionary transition rates. Next, I evaluated how past environmental change affected mammalian functional diversity and community structure in Oregon. Using the combined functional diversity and food web results, my work emphasizes that as the landscape changes, certain mammalian functional groups are lost. I show that these extinct communities are characterized by a decline in browsing species and mid-sized omnivores being replaced by more specialized hypercarnivores. Finally, using stable carbon isotope values I found that Oligo-Miocene ungulates were partitioning C_3 plant-

food resources. My work shows that a more homogeneous ungulate community arose as global temperatures decreased, and grasslands expanded.

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I am incredibly surprised I became a scientist. My entire life, my time in school was both incredibly overwhelming and enjoyable, and graduate school was much of the same. I went from being a very curious person to someone who could wield that curiosity to add knowledge to the world. I am incredibly fortunate that so many people took the time to help me become the scientist I am today.

I owe a huge debt of gratitude to my advisor Sam Hopkins for guiding me in my journey toward scientific progress. She was always there to provide the safety net or push I needed to navigate the many challenges of graduate school. I also am grateful to Edward Davis for being incredibly compassionate and answering my many questions about the world of stats. I am grateful to Scott Blumenthal for allowing me to perform analyses in his lab while he was training his graduate students and when a pandemic created unforeseen challenges. I am grateful to Rebecca Terry who provided numerous insights not just about science but also about life. Other members of the U.O. faculty such as, Ray Weldon, Matthew Polizzotto and Josh Roering, helped me with extensive advice, support, and knowledge. There are many other scientists who helped me with this work. They were very kind when I pestered them with questions at conferences or over email. There are too many of them to list, but they kindly provided me with coding advice or references that only improved my work.

I am also extremely grateful to the entire U.O. Department of Earth Sciences for having such a welcoming and supportive community. I was taught more than just science but how to collaborate, be a supportive colleague, teach, learn, and grow as a person. They did everything in their power to support me even when my dreams were a bit too ambitious. I can only hope I can be part of a similarly amazing community in the future.

I also would not be where I am today without my friends and family. Many friends excitedly helped me figure out complex problems or gave me advice when I felt directionless. My family similarly were unwavering fountains of support. Both my friends and family were there for me when I needed a shoulder to rest on or a person to celebrate with. Even after a pandemic made life harder, they were sparks of joy in an uncertain time. Finally, the largest thanks go to my lifelong partner and best friend Mitchell Hilbert. He somehow has an endless amount of patience, support, and joy.

Often, he singlehandedly kept my boat afloat when I felt like sinking. He did this all while making it look effortless, pursuing his own passions, and creating a wonderful life for the both of us. There is no question that I could not have written this dissertation without him.

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For the animals and the people who grow coffee

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CHAPTER I

INTRODUCTION

An organism's diet is how an animal meets its energetic needs. It is therefore no surprise that the diet of an animal is related to almost every other aspect of an animal's ecology and evolution. Most notably, diet and body size are intertwined because the size of an animal determines how much energy it needs to sustain itself. Many studies have shown that in mammals, body mass correlates with diet and various food materials consumed, such as prey size and type of plant material. As the environment shifts, the food materials on the landscape change in abundance causing differences in access and availability. The type of environment, therefore, plays a role in determining the body mass and trophic diversity of the mammals that live there by determining which food sources are available. A growing body of work has shown that extant ecosystems differ in their community composition especially with body mass and diet. However, how communities are composed today only gives us part of the picture. Understanding the composition of past ecosystems, and how past ecosystems experienced change, can give us a better grasp on the governing rules for how climate change affects mammalian functional diversity and community structure. Studying how past climate change affects mammal diet and body mass diversity is then imperative for mitigating current ecological change.

With the wealth of data available today about extant and extinct terrestrial communities it is now possible to ask detailed questions about how the diet of mammals relates these other ecological and evolutionary processes such as body mass, community composition, community structure, and extinction. Utilizing many types of data sources and methodologies this dissertation aims to bring a better understanding of 1) *How diet is related to mammalian diversity, body mass, and evolution.* 2) *How environmental change affects mammalian functional diversity and community structure*.

To begin addressing these knowledge gaps, I investigate whether tooth-size variation is driven by functional demands (Chapter II), how type of omnivory is related to mammalian diversity, body mass, and evolution (Chapter II) and how past environmental

change affected mammalian functional diversity and community structure in Oregon (Chapters IV, V).

Chapter II evaluates whether developmental controls or occlusion driven functional demands influence carnivoran tooth-size variation. It was published in the Journal of Mammalogy in 2021 and was co-authored with Samantha Hopkins and Edward Davis (University of Oregon). Developing morphological diagnoses for fossil mammals requires an understanding of intraspecific variation in the anatomical elements under study. Dental traits along with tooth size can be informative of taxonomic identity and body mass for extinct species. However, it was unclear what selective or developmental processes are responsible for documented patterns in tooth-size variation making application to the fossil record difficult. I assess combined species tooth-type variation and intraspecific tooth-size variation for 19 species. I also estimate phylogenetic signal for the coefficient of variation. Combined species tooth-size variation separated by tooth type shows that canines are more variable than molars and lower premolars. I find intraspecific tooth-size variation patterns differ between species. Comparisons of the coefficients of variation (CV) did not support the hypotheses that developmental controls or functional demands of occlusion constrain size variation in mammal teeth. My results suggest that a combination of factors influence carnivoran tooth-size variation, such as differences in ontogeny, diet, sexual dimorphism, and evolutionary history.

Chapter III addresses the issue that mammalian omnivores are a diverse group that are often lumped together in studies resulting in a lack of knowledge of their ecology and evolution. In this study I investigate the frequency at which vertebrate protein, invertebrate protein, fibrous plant material, and non-fibrous plant material are eaten together by mammalian omnivores. I quantify the body size distributions and phylogenetic signal of terrestrial mammals that consume different omnivorous diets and using multistate reversible jump MCMC, I assess the transition rates between diet strategies on the mammalian phylogenetic tree. I find that complete generalists are rare and most omnivorous mammals consume only invertebrate prey and non-fibrous plants. I also show that omnivores that only consume invertebrate prey are on average smaller than omnivores that incorporate vertebrate prey. My transition rate models show that there are high transition rates from insectivorous omnivory to herbivory, and from

vertebrate predation to prey mixing and ultimately insectivory. My results reveal that prey type is an important aspect of omnivore macroevolution and macroecology, as it is correlated with body mass and diet-related evolutionary transition rates. Chapter III is co-authored with Samantha Hopkins and Samantha Price and is under review at *Proceedings B*.

Chapter IV investigates how the environment determines what types of organisms exist on the landscape. Specifically, it explored how mammalian functional diversity and food web structure changed in the Oregon fossil record as global temperatures fluctuated and grasslands became more prevalent. Using body mass and diet data I evaluate trophic functional diversity and community structure for six fossil assemblages. Proposed food webs are reconstructed for each assemblage using modern documented predator-prey ecological trends. These food webs are used to calculate community structure metrics such as number of unique trophic nodes, link density, and overall connectance. Using the combined functional diversity and food web results, my work emphasizes that as the landscape changes certain functional groups are lost. I am able to show that these extinct communities are characterized by a decline in browsing species and mid-sized omnivores being replaced by more specialized hypercarnivores.

Building on Chapter IV, Chapter V further investigates how ungulates partitioned food resources during the change that was show in Chapter IV. By using stable carbon isotope analysis, I am able to show that certain ungulate species have statistically different mean carbon isotope values indicating niche partitioning of the C_3 plant food resources. My work shows that a more homogeneous herbivore community arose as global temperatures decreased, and grasslands expanded.

CHAPTER II

CARNIVORAN INTRASPECIFIC TOOTH-SIZE VARIATION SHOWS HETEROGENEITY ALONG THE TOOTH ROW AND AMONG SPECIES

Reuter, D.M., Hopkins, S.S. and Davis, E.B., 2021. Carnivoran intraspecific tooth-size variation shows heterogeneity along the tooth row and among species. Journal of Mammalogy, 102(1), pp.236-249.

1. Introduction

Quantification of variation is an integral step in the identification of species, and determination of population boundaries, and sex of individuals in fossil mammals (Cope and Lacy 1992; Plavcan and Cope 2001; Van Valkenburgh and Sacco 2002; Rodriguez et al. 2016). An assessment of intraspecific tooth-size variation is especially significant because teeth often are used to test evolutionary hypotheses with the fossil record. Teeth are durable and taxonomically distinct, making them valuable for identification of extinct species. Importantly, teeth provide data about an extinct animal's diet (Van Valkenburgh 1989; Friscia et al 2007; Evans and Pineda-Munoz 2018) and body mass (Legendre 1986; Van Valkenburgh 1990; Gordon 2003; Hopkins 2008). However, many extinct mammals are known only from isolated teeth. Furthermore, when studying closely-related organisms, the degree of size variation found within a sample of anatomical elements often has been used to determine the number of species present in a fossil assemblage (Simpson and Roe 1939; Gingerich 1974; Cope and Lacy 1992; Plavcan and Cope 2001; Davis and Calède 2012). Simpson and Roe (1939) observed that most values for a coefficient of variation (CV) calculated from anatomical elements of a mammalian species fall between 4% and 10%, and that most mixed samples have CV values that are higher. However, this suggested range for determining a taxonomically mixed sample is not always consistent along the tooth row, and some teeth have been observed to be more variable than others (Pengilly 1984; Meiri et al. 2005; Wolsan et al. 2015). Many problems can arise from interpreting ecological or taxonomic data from a population of isolated, highly variable elements without a comparative sample of extant organisms

(Emery-Wetherell and Davis 2018).

To adequately test evolutionary hypotheses with the teeth of extinct mammals an effort must be made to understand what selective or developmental processes are responsible for the differing amounts of size variation along the tooth row. Tooth development studies have found patterns of gene expression that form distinct developmental fields in the development of the tooth types: incisors, canines, premolars, and molars (Butler 1939, 1967; Colbourne and Sharpe 2003). Developmental fields have been suggested to cause differences in the magnitude of size variation among the teeth (Van Valen 1970). Research has not supported consistent patterns in size variation within tooth types, as were predicted by hypotheses of developmental fields. Instead, anterior to posterior tooth position (Gingerich 1974), tooth size (Pengilly 1984), and degree of occlusion (Gingerich and Winkler 1979), have been proposed as factors influencing intraspecific variation in tooth dimensions. Research results have been inconsistent in supporting or rejecting these hypotheses. For instance, tooth development studies suggest anterior to posterior tooth position is an important factor in determining tooth-size variation. Studies on extant mammals show that molar size is controlled largely by a balance among signaling molecules along the tooth row, producing molars that increase or decrease in size linearly in a successive manner (Kavanagh et al. 2007). It has been hypothesized that because size of the first molar influences size of subsequently initiated molars, intraspecific molar size variation would be higher in M3 compared with M1 (Kavanagh et al. 2007). Elevated size variation of M3 compared with M1 has been found in Vulpes vulpes (Gingerich and Winkler 1979; Pengilly 1984; Szuma 2000). However, this pattern does not appear to be consistent and was not found in black bears (Miller et al. 2009). In addition to these process-based hypotheses for differences in the magnitude of tooth-size variation, Polly (1998) showed that small teeth can look more variable than large teeth because constant measurement error inflates the sample standard deviation for measurements of small teeth. Other studies have suggested that this size-related bias is not large enough to obscure variation in the tooth row that can be explained by biological processes such as functional integration and selection on degree of occlusion (Dayan et al. 2002; Meiri et al. 2005). The degree of occlusion or functional integration across the dentition should influence the effectiveness of selection on size variation because teeth

with precisely occluding cusps should be under more stabilizing selection than teeth with less complex occlusion (Gingerich and Winkler 1979). This idea is supported by studies on *Ursus americanus*, *Felis silvestris*, *Pusa hispida*, *Pagophilus groenlandicus*, and numerous canids (Szuma 2000; Dayan et al. 2002; Meiri et al. 2005; Miller et al. 2007, Miller et al. 2009). Relaxation of functional constraints related to a lack of precise occlusion also has been used to explain the greater size variability in carnivoran canines (Meiri et al. 2005). In contrast, pinniped intraspecific tooth-size variation differs both along the tooth row of individual species and between species more than expected for a group with such poorly occluding teeth (Wolsan et al. 2015). The differing patterns among species does not support the functional constraint-occlusion hypothesis in pinnipeds but does lend support to hypotheses of developmental controls on the magnitude of variation in dental dimensions (Wolsan et al. 2019). There is no clear pattern of occlusion or developmental controls driving patterns of variation in the size of mammalian teeth.

In this study, we assess differences in magnitude of intraspecific size variation along the carnivoran tooth row, looking both within tooth position across species and among tooth positions, normalized among all species. We address the following questions: 1) Are magnitudes of intraspecific size variation different among tooth types? 2) Do teeth with a high degree of functional integration and occlusion, such as the carnassial pair, have a lower magnitude of size variation compared to other teeth in the tooth row? 3) Does the magnitude of intraspecific tooth-size variation relate to tooth position within the tooth row? 4) Are patterns of differences in the magnitude of intraspecific tooth-size variation consistent among species in ways that support the tooth development or functional constraint-occlusion hypotheses?

2. Methods

Length and width were measured for the permanent canines, premolars, and molars, of 193 specimens representing 19 carnivoran species (Supplementary Data S1, see Appendix A for all supplemental data). Families sampled were: Canidae, Mustelidae, Mephitidae, Ursidae, Felidae, Hyaenidae, and Herpestidae (Table 1). Tooth lengths were measured as the maximum mesiodistal crown length, and tooth widths were measured as

the maximum buccolingual crown width. Measurements were taken with digital calipers (Mitutoyo Absolute Digimatic Caliper Series 500) with a precision of 0.01mm and accuracy of ±0.0254mm. We did not use specimens with excessively worn or damaged teeth. A minimum of eight specimens were measured for each species sampled (Table 1). All specimens used in the study were from the University of Washington Burke Museum of Natural History and Culture (UWBM), Harvard University Museum of Comparative Zoology (MCZ), and the University of Oregon Museum of Natural and Cultural History (UOMNH; Supplementary Data S1). All measurements were taken by D.M. Reuter to minimize inter-operator error and recorded to 0.01 mm. All analyses were performed using Rstudio (R version 3.5.2; R Core Team, 2019).

First, we tested the hypothesis that tooth types (canine, premolar, or molar) have different levels of size variation, by converting each individual observation into a percentage of the intraspecific sample mean for the species to which it belongs. For example, specimen MCZ23098 had an upper canine length of 17.07 mm, and its species, *Crocuta crocuta*, had a mean length of 15.91 mm, so the re-scaled percentage of the intraspecific sample mean for this specimen would be 107.29. By re-scaling the values, we have a set of dimensionless observations that reference the same mean, 100, allowing us to compare all observations to one another, regardless of species or tooth position. In this way, we combined all observations for each tooth type, creating distributions for all canines, all premolars, and all molars, to allow fair comparisons of size variation among tooth types. We compared upper and lower tooth-type size variation using Levene tests on the mean-percent distributions (Levene 1960). To protect against an inflated type 1 error rate, we carried out a Bonferroni correction on our resulting p values using the p.adjust function in R stats package (R Core Team, 2019; Bonferroni 1936). We then undertook Levene tests comparing molar, premolar, and canine, mean-percent distributions to one another. Because the upper and lower premolars presented different levels of size variation, they were considered separately when compared to the molars and canines. The resulting p values were adjusted using a Bonferroni correction.

To test the hypothesis that precisely occluding teeth have lower amounts of intraspecific size variation we then compared individual tooth coefficients of variation (CV) to the CV values of the carnassial pair, which previously has been shown to be less

variable (Meiri et al. 2005). We compared the upper teeth to the upper fourth premolar (P4) and the lower teeth to the lower first molar (M1). This was done using the asymptotic test for equality of coefficients of variation (Feltz and Miller 1996) and the modified signed-likelihood ratio test (Krishnamoorthy and Lee 2014) implemented in the R package cvequality (Version 0.2.0; Marwick and Krishnamoorthy 2019). Because we were testing for higher levels of size variation, we compared the CV value for a tooth to the carnassial pair only if the CV value was larger than that of the carnassial pair. If variation in tooth dimensions is related to occlusion, we expect the CV values for occluding molars to be similar to the carnassial pair CV values. We also expect the CV for the premolars and canines to be significantly greater than for the carnassial pair if occlusion was a determining factor for reduced size variation. In addition, this method also allows us to test the assumption that developmental pathways influence tooth-size variation as M3 should be more variable than M1. The resulting p values were then adjusted using a Bonferroni correction.

Because of our broad taxonomic scope, we might see some family-related patterns in CV values. For example, felids are hypercarnivores that rely heavily on their carnassials to slice meat, and many have small vestigial upper molars that we expect will have elevated levels of size variation compared to the tightly-occluding carnassial pair. In contrast, ursids have large post-carnassial molars and modified P4 and M1and are expected to show the opposite pattern. We therefore estimated phylogenetic signal (Pagel's λ) of our CV values by using the phylosig function in the phytools package (Pagel 1999; Revell 2012). The phylogeny used was a carnivoran supertree based on molecular data that was pruned but original branch lengths maintained (Nyakatura and Bininda-Emonds 2012). This tree is widely used because of its high resolution and taxonomic coverage (Böhmer et al. 2019; Saladin et al. 2019; Parsons et al. 2020). The resulting p values were adjusted using a Bonferroni correction.

Table 1.—Coefficient of Variation values and number of specimens measured for each trait.

Measurement	*Canis latrans*	*Urocyon cinereoargenteus*	*Vulpes lagopus*	*Mephitis mephitis*	*Gulo gulo*	*Lontra canadensis*	*Martes americana*	*Taxidea taxus*	*Ursus americanus*	*Ursus arctos*	*Ursus maritimus*	*Acinonyx jubatus*	*Leopardus pardalis*	*Lynx rufus*	*Panthera leo*	*Puma concolor*	*Ichneumia albicauda*	*Suricata suricatta*	*Crocuta crocuta*
C^1L	6.75 11	10.39 10	7.46 10	12.14 11	7.03 10	10.04 7	9.50 11	4.93 8	10.84 9	17.25 9	18.69 5	6.74 8	8.65 10	8.80 10	12.60 10	7.13 9	6.79 10	8.73 10	5.89 9
P^1L	10.3 9 11	9.25 10	5.12 10		9.02 10	16.37 12	8.67 11		28.41 9	9.11 7	11.37 6						7.76 10		9.23 9
P^2L	6.80 11	6.80 10	6.26 10	8.84 11	5.88 10	7.23 12	5.17 11	7.96 8				9.18 8	14.87 10		6.31 11	29.80 9	8.32 10	5.90 10	6.91 9
P^3L	6.31 11	6.33 10	6.10 10	7.17 11	6.24 10	4.54 12	4.28 11	5.25 8	22.61 8	26.48 11	13.42 5	5.87 8	3.94 10	6.09 10	6.33 11	4.83 9	5.83 10	5.13 10	4.28 9
P^4L	6.25 11	4.31 10	5.00 10	5.42 11	5.16 10	4.82 12	5.57 11	4.46 8	6.97 9	7.63 11	7.15 7	4.33 8	3.61 10	5.61 10	6.11 11	3.83 9	5.26 10	4.94 10	2.37 9
M^1L	6.03 11	5.58 10	4.99 10	5.20 11	9.22 10	4.48 12	7.74 11	6.01 8	4.63 9	5.73 11	8.41 7	11.69 8	6.89 10	6.64 10	21.45 11	13.27 9	4.79 10	7.12 10	
M^2L	5.79 11	4.49 10	4.44 10						6.07 9	11.10 11	14.30 7						4.55 10	8.27 10	
C_1L	8.97 8	9.41 10	9.25 10	13.65 10	8.60 8	7.55 11	9.06 11	4.25 8	12.78 8	17.01 8	11.19 5	6.66 8	9.94 10	8.57 10	13.43 11	7.15 9	5.78 10	9.94 9	6.79 9

Table 1. (continued).

Measurement	*Canis latrans*	*Urocyon cinereoargenteus*	*Vulpes lagopus*	*Mephitis mephitis*	*Gulo gulo*	*Lontra canadensis*	*Martes americana*	*Taxidea taxus*	*Ursus americanus*	*Ursus arctos*	*Ursus maritimus*	*Acinonyx jubatus*	*Leopardus pardalis*	*Lynx rufus*	*Panthera leo*	*Puma concolor*	*Ichneumia albicauda*	*Suricata suricatta*	*Crocuta crocuta*
P_1L	8.45 10	9.72 10	7.57 9		8.34 8		8.68 11		6.35 8	11.10 8	23.43 5						7.86 10		
P_2L	13.26 10	6.24 10	7.18 10	9.70 10	7.32 7	4.26 11	3.00 11	5.30 7									6.30 10	5.14 9	5.39 9
P_3L	8.74 10	7.04 10	4.86 10	6.18 10	5.85 8	6.61 11	3.66 11	5.31 8	22.33 5			4.26 8	4.13 10	7.55 10	6.16 11	4.46 9	3.70 10	5.71 9	5.70 9
P_4L	6.72 10	5.71 10	5.38 10	5.52 10	5.44 8	5.15 11	3.62 11	3.85 8	5.55 8	12.59 9	7.00 5	5.05 8	4.60 10	5.36 10	7.12 11	4.76 9	6.28 10	6.37 9	4.93 9
M_1L	8.45 10	4.52 10	3.77 10	5.90 10	6.07 8	4.56 11	5.30 11	2.12 8	4.73 8	5.82 10	6.49 5	3.65 8	11.05 10	6.78 10	6.72 11	4.01 9	4.85 10	6.12 9	3.87 9
M_2L	10.28 10	10.39 10	7.60 10	13.97 10	7.26 8	5.73 11	11.23 11	11.54 8	3.38 8	7.41 10	7.19 5						2.86 10	3.78 9	
M_3L	13.44 9	10.82 10	12.51 9						6.50 8	7.39 10	16.38 5								
C^1W	7.99 11	8.50 10	5.84 10	17.30 11	8.16 10	6.41 7	8.96 11	7.23 8	16.39 9	14.82 9		7.04 8	8.69 10	10.48 10	11.48 10	6.95 9	8.04 10	8.04 10	4.26 9

Table 1. (continued).

Measurement	*Canis latrans*	*Urocyon cinereoargenteus*	*Vulpes lagopus*	*Mephitis mephitis*	*Gulo gulo*	*Lontra canadensis*	*Martes americana*	*Taxidea taxus*	*Ursus americanus*	*Ursus arctos*	*Ursus maritimus*	*Acinonyx jubatus*	*Leopardus pardalis*	*Lynx rufus*	*Panthera leo*	*Puma concolor*	*Ichneumia albicauda*	*Suricata suricatta*	*Crocuta crocuta*
P^1W	13.83 11	5.94 10	7.40 10		8.75 10	20.67 12	10.57 11		23.08 9	13.82 7	13.97 6						9.32 10		6.66 9
P^2W	10.78 11	8.24 10	9.56 10	14.19 11	8.43 10	7.22 12	6.84 11	3.08 8				14.26 8	12.70 10		9.35 11	23.12 9	14.66 10	8.42 10	8.11 9
P^3W	8.35 11	5.95 10	8.12 10	8.63 11	7.95 10	5.95 12	7.08 11	6.64 8	19.81 8	18.64 11	9.39 5	5.02 8	6.60 10	9.11 10	8.87 11	7.54 9	7.15 10	8.97 10	4.94 9
P^4W	7.21 11	6.41 10	8.57 10	6.98 11	6.71 10	8.75 12	7.27 11	4.07 8	10.23 9	9.33 11	17.12 6	7.30 8	8.08 10	8.52 10	9.71 11	3.92 9	6.69 10	4.42 10	4.78 8
M^1W	6.88 11	7.63 10	4.08 10	8.62 11	3.68 10	6.35 12	5.29 11	4.63 8	4.04 9	7.02 11	9.15 7	10.98 8	13.02 10	9.89 10	7.64 11	13.04 9	4.63 10	3.81 10	
M^2W	6.70 11	10.64 10	6.11 10						5.18 9	5.94 11	7.79 7						5.40 10	7.55 10	
C_1W	10.10 8	8.57 10	5.52 10	16.54 10	9.82 8	6.27 11	7.22 11	4.82 8	9.44 8	14.48 8	17.88 5	6.31 8	7.63 10	9.23 10	11.24 11	8.03 9	8.05 10	6.52 9	2.89 9
P_1W	10.13 10	6.36 10	8.51 9		9.64 8		5.55 11		12.20 8	14.58 8	17.13 5						7.70 10		

Table 1. (continued).

Measurement	*Canis latrans*	*Urocyon cinereoargenteus*	*Vulpes lagopus*	*Mephitis mephitis*	*Gulo gulo*	*Lontra canadensis*	*Martes americana*	*Taxidea taxus*	*Ursus americanus*	*Ursus arctos*	*Ursus maritimus*	*Acinonyx jubatus*	*Leopardus pardalis*	*Lynx rufus*	*Panthera leo*	*Puma concolor*	*Ichneumia albicauda*	*Suricata suricatta*	*Crocuta crocuta*
P_2W	9.92 10	5.41 10	6.51 10	6.72 10	5.36 7	6.02 11	4.67 11	5.00 8									10.47 10	5.10 9	4.48 9
P_3W	10.83 10	5.88 10	8.04 10	5.70 10	6.95 8	5.83 11	7.91 11	4.02 8	16.20 5			5.36 8	5.97 10	7.33 10	9.49 11	7.21 9	8.93 10	5.95 9	4.77 9
P_4W	7.06 10	6.70 10	5.34 10	6.72 10	8.86 8	6.35 11	5.97 11	4.82 8	5.05 8	10.01 9	9.13 5	8.88 8	5.55 10	6.64 10	9.10 11	4.51 9	6.12 10	5.66 9	4.79 9
M_1W	8.24 10	8.29 10	5.14 10	8.82 10	5.69 8	4.74 11	7.20 11	7.66 8	5.85 8	8.03 10	9.45 5	5.92 8	7.51 10	8.59 10	6.70 11	5.07 9	2.01 10	3.89 9	5.50 9
M_2W	10.31 10	8.82 10	6.53 10	9.09 10	6.62 8	3.00 10	4.93 11	9.16 8	6.53 8	9.36 10	9.88 5						4.60 10	5.40 9	
M_3W	8.48 9	11.30 10	8.84 9						6.04 8	8.69 10	12.47 5								

Table 2.—Summary statistics for tooth-type mean percent values. IQR: inter quartile range. Upper premolars are represented with an uppercase initial letter and lower premolars with a lowercase initial letter.

Measurement	n	Median	IQR	Standard Deviation
CL	350	99.93	12.01	9.30
PL	631	99.95	8.70	9.27
pL	519	100.11	8.38	6.87
ML	606	99.81	8.73	7.69
CW	349	100.33	11.42	9.36
PW	629	99.81	11.45	10.05
pW	520	100.03	8.50	7.18
MW	605	100.03	8.97	7.07

4. Results

When comparing size variation between upper and lower tooth-types, only the premolars differed with upper premolars significantly more variable than lower premolars in both length ($p < 0.05$) and width ($p < 0.0001$) after Bonferroni correction (Supplementary Data S2). We therefore considered premolars separately in the subsequent Levene tests. Our results showed that canines were significantly more variable than both molars and lower premolars in length and width (Table 2, Table 3, Figure 1). Upper premolars were not significantly more variable than the canines in both length and width. Upper premolar length was not significantly more variable than molar length. However, upper premolar width variation was significantly greater than molar width variation ($p < 0.0001$).

Our CV values differed considerably along the tooth row, among species, and among families (Figs. 2, 3). Overall, the carnassial pair exhibited small CV values (Figs. 2, 3). In many species the anterior and posterior teeth showed elevated CV values compared with the carnassial pair. Some of the largest CV values were found in *Puma concolor* for P2 (length, 29.80; width, 23.12) and *Ursus americanus* for P1 (length, 28.41; width, 23.08). Smallest CV values were obtained for *Ichneumia albicauda* M1 width at 2.01 and *Crocuta crocuta* P4 length at 2.37. Both ursids and felids had high CV

values for anterior and posterior teeth, while canids and non-felid feliforms tended to have lower values. Among the Musteloidea, *Mephitis mephitis* and *Lontra canadensis* exhibited larger CV values toward the front of the tooth row.

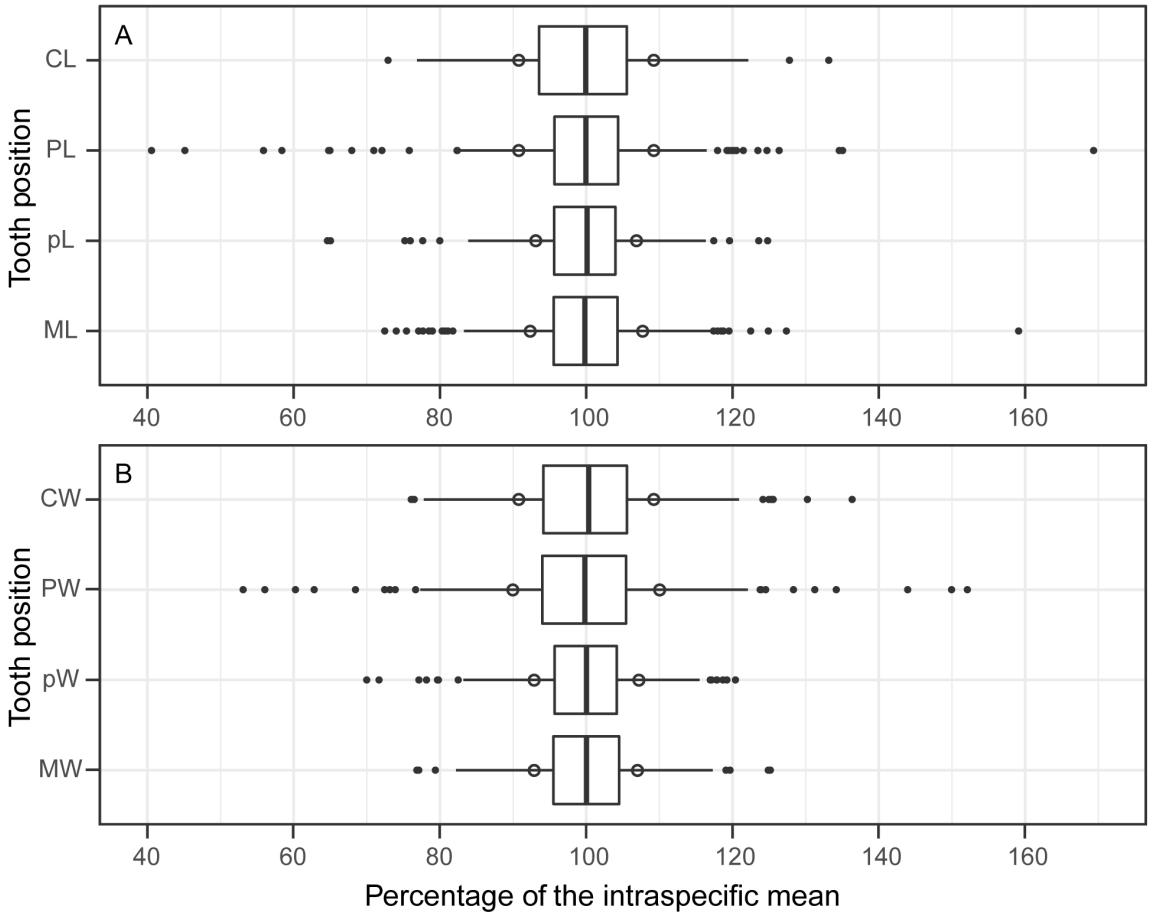


Figure. 1.—Distributions of tooth-type observations converted into a percentage of the intraspecific sample mean for each tooth. Line inside box represents the median, lower and upper box boundaries represent the first and third quartiles, and lower and upper whisker lines represent 1.5 interquartile range. Standard deviation is represented by open circles. (A) represents the length measurements for each tooth type and (B) represents the width measurements for each tooth type. Tooth types compared: C, canines; P, upper premolars; p, lower premolars; M, molars.

Roughly 20% of our CV equality tests showed significant differences between the carnassial pair and the other teeth (Tables 4, 5). However, Bonferroni correction on both tests for the large number of comparisons produced only four p values below 0.05. These include *Puma concolor* P2 length ($p < 0.01$) and width ($p < 0.05$), and *Ichneumia albicauda* P2 width ($p < 0.05$) and P3 width ($p < 0.05$). *Taxidea taxus* M2 length also was significant after Bonferroni correction ($p < 0.05$) but only for the modified signed-likelihood ratio test. Phylogenetic signal estimates per tooth were low and after adjusting the p values for multiple comparisons, only P3 length had a p value less than $p = 0.05$ (Table 6).

Table 3.—Levene test results to comparing tooth types mean-percent values with upper and lower premolars considered separately. *represent $p < 0.05$. Upper premolars are represented with an uppercase initial letter and lower premolars with a lowercase initial letter.

Comparison	F	*p*.unadj	*p*.adj
CL-PL	6.9373	0.0086	0.1029
CL-pL	38.4269	<0.0001	<0.0001*
CL-ML	20.1926	<0.0001	<0.0001*
PL-pL	8.5474	0.0035	0.0423*
PL-ML	1.9394	0.1640	1.0000
ML-pL	3.4830	0.0623	0.7471
CW-PW	0.0005	0.9830	1.0000
CW-pW	23.6369	<0.0001	<0.0001*
CW-MW	26.4961	<0.0001	<0.0001*
PW-pW	24.0949	<0.0001	<0.0001*
PW-MW	27.4234	<0.0001	<0.0001*
MW-pW	0.0001	0.9938	1.0000

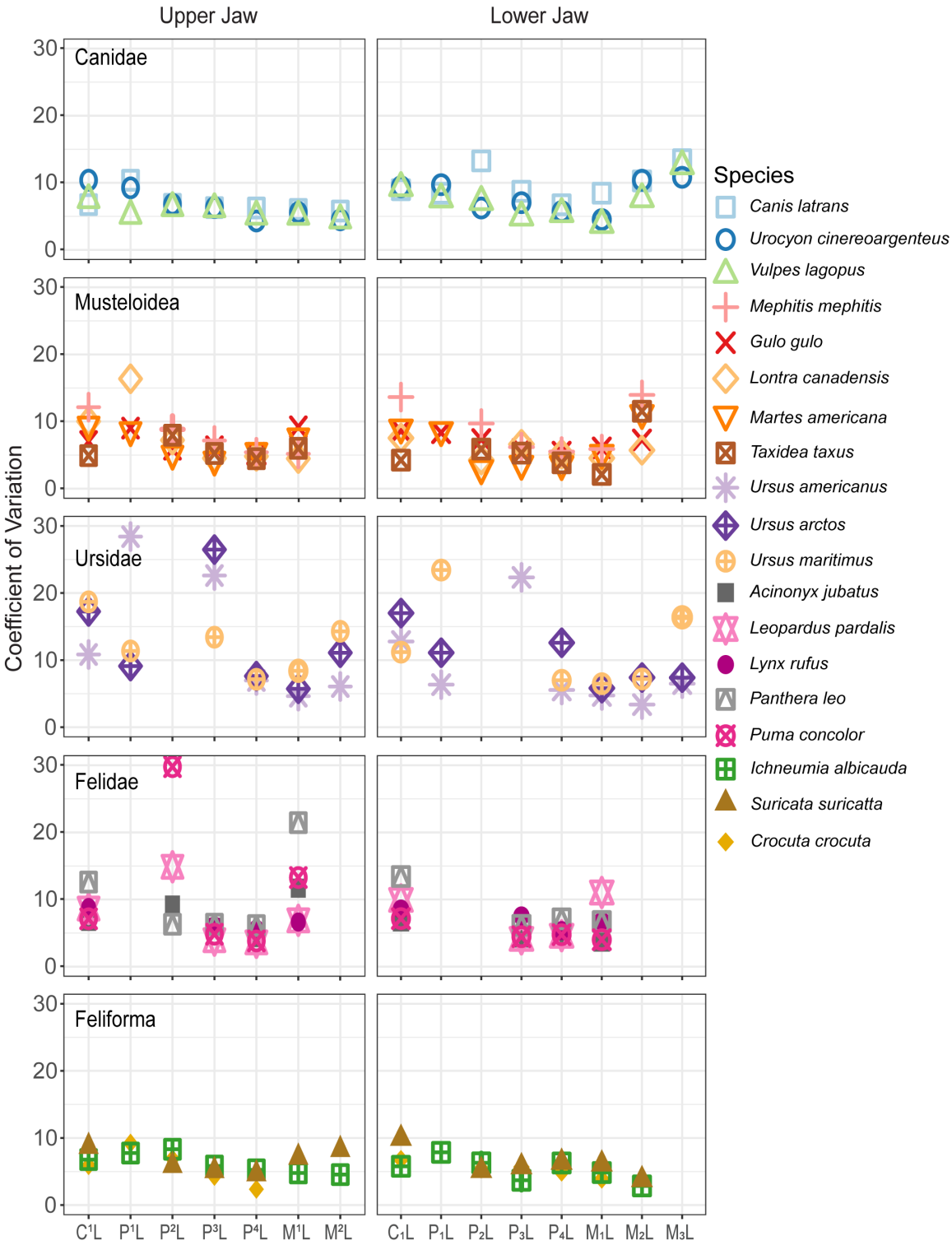


Figure 2.—Coefficient of Variation of length measurements for all 19 species included in this study. Species are represented by symbols and color. Upper jaw measurements are in the left column and lower jaw measurements are in the right column.

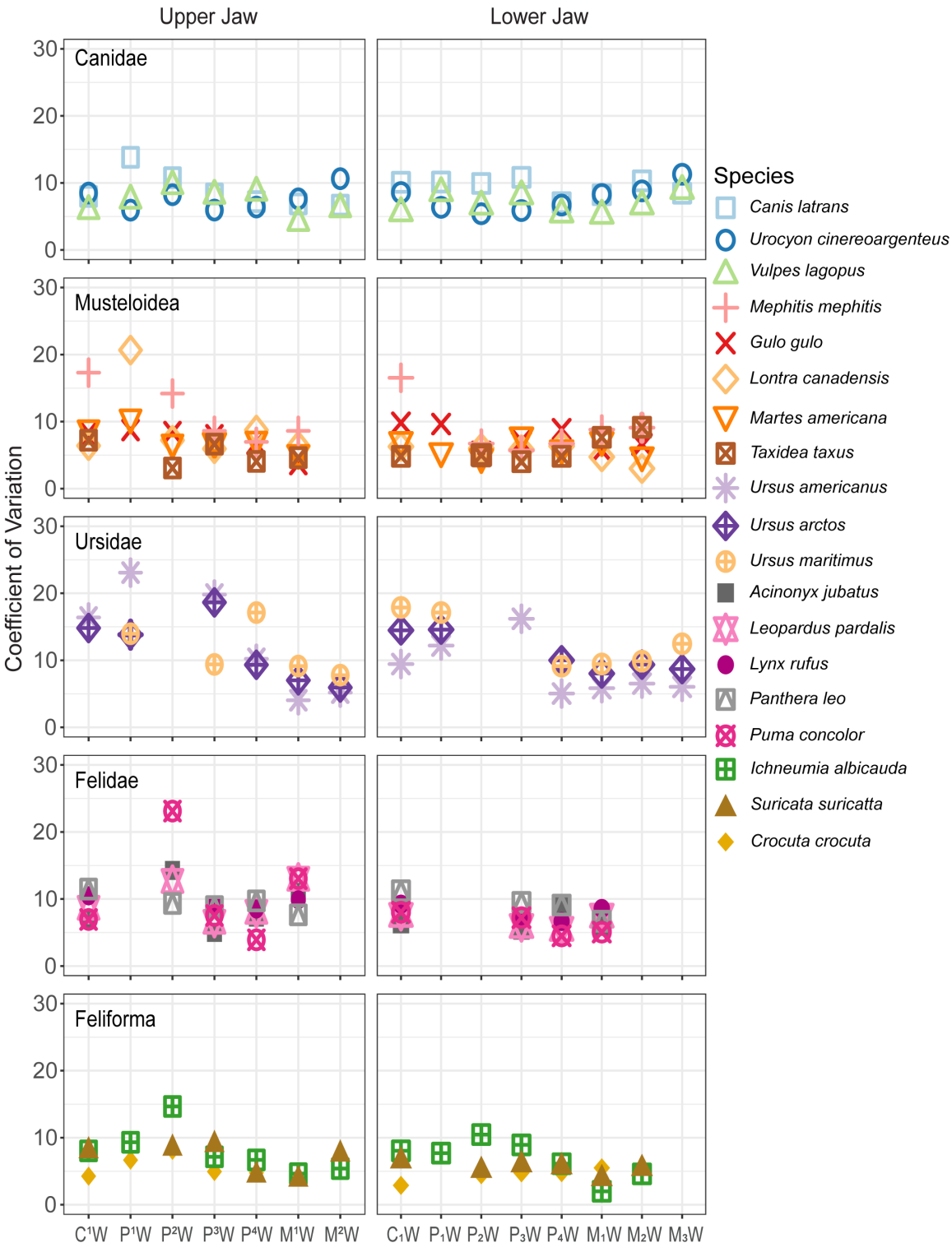


Fig. 3.—Coefficient of Variation of width measurements for all 19 species included in this study. Species are represented by symbols and color. Upper jaw measurements are in the left column and lower jaw measurements are in the right column.

5. Discussion

Our results suggest that many factors govern tooth-size variation in carnivorans. Among tooth-types, canines are the most variable teeth in the tooth row; they varied more in both length and width compared with molars and lower premolars. This finding is consistent with intraspecific variation patterns found in other taxa (Szuma 2000; Dayan et al. 2002; Meiri et al 2005; Wolsan et al. 2015). While this result fits with the occlusion-driven hypothesis, we did not control for sex in our study and cannot say whether elevated sexual dimorphism in the canines resulted in greater canine intraspecific size variation. Sexual dimorphism in the canines compared to the carnassial pair has been found in many carnivorans (Szuma 2000; Van Valkenburgh and Sacco 2002). Nevertheless, researchers who controlled for sex in their studies disagree whether canine intraspecific size variation is governed by natural selection, developmental differences, sexual dimorphism, or a combination of these factors (Szuma 2000; Meiri et al. 2005; Wolsan et al. 2015, 2019). Our results when comparing upper and lower tooth-type size variation show a similarly unclear pattern. We found that upper premolars are significantly more variable than lower premolars: upper premolars are similar to canines, with greater size variation, and lower premolars are similar to molars, with less size variation. P4 is a precisely occluding tooth with presumed constraints on its size variability and therefore should reduce overall variability in upper premolar dimensions. However, the distributions for CV values for P4 (median length, 5.16; median width, 7.27) and P4 (median length, 5.43; median width, 6.35) are not significantly different (Mann-Whitney-Wilcoxon test, length, $W = 215$ $p = 0.32$; width, $W = 142$, $p = 0.27$). The differences between the upper and lower premolar intraspecific size variation do not suggest that occlusion is the driving factor behind tooth-type differences in intraspecific tooth-size variation. It is unclear whether this pattern of higher intraspecific size variation in the canines and upper premolars is caused by natural selection, developmental processes, or the interaction between the two.

The CV values we obtained also show differences along the tooth row and indicate that tooth position is an important influence on intraspecific tooth-size variation. The magnitude of these tooth-row CV patterns differs among the families. For instance, felids and ursids have a strong pattern of higher CV values at the anterior and posterior

ends of the tooth row. Although intraspecific tooth-size variation along the tooth row seems to follow general patterns within carnivoran families, our phylogenetic signal estimates for most measurements are low and not significant, suggesting that levels of size variation are not structured phylogenetically. Importantly, phylogenetic signal estimates for many of the anterior and posterior cheek teeth, which have different levels of occlusion between the carnivoran families are low. However, length variation associated with P3 has a significant phylogenetic signal, even after adjusting for multiple comparisons. This result suggests that evolutionary history in part plays a role in determining intraspecific tooth-size variation for the lower third premolar, but this idea should be tested further with a larger number of species. The lack of high phylogenetic signal estimates show that our CV values are more varied than expected given the phylogenetic relationship of the taxa included in this study.

For many species, our CV values show greater size variation for the canines, anterior premolars, and posterior molars, agreeing with previous findings (Gingerich and Winkler 1979; Pengilly 1984; Szuma 2000; Dayan et al. 2002; Meiri et al. 2005). Many of our tooth-row CV patterns agree with the hypothesis that M3, which develops later ontogenetically, should have higher amounts of size variation than M1 (Kavanagh et al. 2007). Furthermore, the patterns of high CV values for the canines, anterior premolars, and posterior molars present in our CV values agree with the hypothesis that precisely occluding teeth should be under stronger selection and should therefore vary less than teeth with less precise occlusion (Gingerich and Winkler 1979; Dayan et al. 2002; Meiri et al. 2005). An extreme example of this can be found in CV values of the felid P2 and M1, especially in *Puma concolor*. These teeth often were observed to never have erupted in many adult museum specimens that were not included in this study. These elevated levels of size variation agree with past work that found P2 and M1 in *Felis silvestris* were vestigial, with greater levels of intraspecific size variation than expected given the size of the teeth (Dayan et al. 2002).

In contrast with CV values, our results from equality of coefficients of variation tests evidence no obvious pattern to support the hypothesis that poorly-occluding teeth are more variable than precisely occluding carnassials. In addition, our results do not support the hypothesis that M3 is consistently more variable in size than M1. We also

found no consistent pattern associated with family. For instance, the felids *Puma concolor*, *Panthera leo*, and *Acinonyx jubatus*, have CVs for M1 length that were significantly greater those for P4 length, but *Lynx rufus* and *Leopardus pardalis* did not. Similarly, lower canine length CVs are greater than M1 length CVs for the two fox species but not for *Canis latrans*. Overall, our CV equality results suggest that there is more diversity in magnitudes of intraspecific size variation in the tooth row than expected given the occlusion or developmental hypotheses. Our findings support results of other studies that have found intraspecific size variation patterns differ among species (Miller et al 2009; Meiri et al. 2005, 2015).

It is important to note that our tooth-type size variation results are not reflected in our CV equality comparisons. It is tempting to argue small sample size effects ($n < 15$ for most species) on power for our inability to detect patterns of increased canine size variability at the species level. After all, we were able to detect such a signal when we pooled our observations into a single canine sample. However, the modified signed-likelihood ratio test and the asymptotic test for equality of coefficients of variation have satisfactory type I error rates at low sample sizes (Feltz and Miller 1996; Krishnamoorthy and Lee 2014), it thus is reasonable to expect that increased tooth-size variation could be detected with our sample sizes. Indeed, the lack of agreement between our tests focused at different levels suggests that intraspecific variation in tooth size is governed by multiple interacting factors. Differences in evolutionary history, diet, ontogeny, and degree of sexual dimorphism could have combined effects that result in differing intraspecific variation patterns within the same family. This idea is supported by previous studies that found diet and phylogeny correlate with tooth integration (Meiri et al. 2005) and that tooth variation heterogeneity in pinnipeds is related to reduced modularity, high integration, and functional requirements (Wolsan et al. 2015; Wolsan et al. 2019).

We suggest that many interacting factors, such as diet, ontogeny, sexual dimorphism, and evolutionary history, influence carnivoran intraspecific tooth-size variation more than solely occlusion-driven functional demands or developmental influences. In many species, these interacting influences mask the overall combined tooth-type variation pattern where canines have the most size variation, followed by upper premolars. Our results point to a greater need to document patterns of variation in

tooth size of extant species because there is a great deal of heterogeneity among species. Studies also should prioritize detailed specimen data instead of summary statistics, to allow for a better understanding of the nuances of a group's intraspecific variation patterns. Importantly, detailed published records of intraspecific variation patterns will allow for better applications to the fossil record. This work has shown that the quantification of variation is a critical initial step in comparative analyses because intraspecific tooth-size variation patterns differ substantially along the tooth row and among species in ways that cannot be explained by one governing rule.

CHAPTER III

WHAT IS A MAMMALIAN OMNIVORE? INSIGHTS INTO MAMMALIAN DIET DIVERSITY, BODY MASS, AND EVOLUTION.

1. Introduction

Using three simple trophic levels: omnivory, carnivory, and herbivory, dietary type in mammals has been found to correlate with body-size differences [1], life-history traits [2], tooth morphology [3], digestive-tract morphology [4], diversification rates [5], and geographical distribution [6]. From these studies, we have learned that omnivores have intermediate tooth morphology [3] and intermediate body sizes [1] between herbivores and carnivores. We have also learned that mammalian omnivores have lower diversification rates than herbivores and carnivores [5]. Omnivory is often an "evolutionary sink" with most of omnivore diversity coming from transitions into omnivory from other specialist dietary groups instead of within guild speciation [5]. This pattern has been found in birds as well as in mammals [7]. While our understanding of how diet influences mammalian evolution and ecology has improved, we still have limited knowledge of what constitutes a mammalian omnivore and how differences in omnivore ecology influence these macroevolutionary findings.

Omnivores are considered generalists in terms of being able to gain substantial energy and nutrition from both plant and animal sources; however, they can vary in their degree of dietary specialization and food mixing. It has been observed that most mammals are not complete generalists and only combine certain food materials, such as fruit and animal material or fruit and foliage, because it would be difficult physiologically to digest all three [4]. Many taxon-specific studies have also shown omnivores specialize in eating specific food items, sometimes for particular times of the year [e.g. 8-12]. These differences in specialization and food mixing among omnivores have been understudied in macroevolutionary studies, which leaves open questions for evolutionary biologists. We know from previous studies that differences within diet type below the three basic trophic levels cause important variation among macroevolutionary trends [7]. For instance, when body mass trends are investigated in carnivorous mammals, insectivorous

mammals are smaller than vertebrate predators [13-14]. In addition, studying diversification rates among diet categories of ruminants, which are all herbivores, found that mixed-feeding ruminants had higher diversification rates than browsing ruminants [15]. Despite these successes in unpacking other diet categories, omnivory has been left mostly untouched even though dietary variation is well documented among many mammalian omnivores [8-12]. Important information from ecological and phylogenetic comparative studies can be gained when omnivory is broken down into more detailed dietary categorizations [16].

In this study we further investigate the evolution of mammalian omnivory by quantifying: 1) which food materials are most often eaten together among mammals, 2) how mammalian omnivorous dietary strategies are distributed on the tree of life, 3) the transition rates into and out of mammalian omnivore dietary states, and 4) the correlation between omnivorous diet type and patterns in mammalian body mass. These objectives are crucial for building our basic knowledge of omnivore macroecology and macroevolution. Understanding the patterns in combinations of foods mammalian omnivores consume will expand our understanding of the macroevolutionary limitations of mixing food materials. Knowing how omnivorous strategies are distributed across the mammalian tree of life will help us to understand how omnivory evolves through time across different lineages. Including more detailed diet information when estimating the dietary transitions that have occurred over the tree of life will allow us to identify which diets are acting as long-term strategies, temporary states, or evolutionary sinks. Finally, a deeper look at the relationship between body size and type of omnivory will let us test whether the body mass patterns we see in specialist groups occur in food mixing lineages.

2. Methods

2.1 Dataset and phylogenetic tree

Using previously published datasets, we compiled diet data and body masses for 1437 terrestrial mammals. Aquatic mammals, dependent on a food web with a dramatically different structure, are expected to experience different ecological and evolutionary dynamics than terrestrial mammals [17] and have been excluded from this analysis. Diet data were taken from a previously published diet dataset [5]. Although the data in Price *et*

al. 2012 were analyzed using the three basic trophic categories, they were originally collected using more detailed categories and dietary descriptions. Food types consumed were split into four food categories: invertebrate protein, vertebrate protein, fibrous plant parts (mature leaves, stems, wood, and bark), and nonfibrous plant parts (any other parts of plants). We used these four food types to assign each species to one of fifteen diet guilds (Table 1). Body masses for omnivorous species were gathered from the PanTHERIA database [18]. For all phylogenetically-informed analyses, we used a fully resolved set of phylogenetic trees from Faurby and Svenning [19].

Table 1 – Number of species found in each diet category. Four food categories were used to determine diet type: invertebrate protein, vertebrate protein, and fibrous or non-fibrous plant parts

Diet Guilds	Broad Guild	Number of Species
Nonfibrous/Fibrous	Herbivore	316
Invert	Insectivore	263
Fibrous	Herbivore	160
Nonfibrous	Herbivore	158
Invert/Nonfibrous/Fibrous	Omnivore	144
Invert/Nonfibrous	Omnivore	136
Vert/Invert	Carnivore	86
Vert/Invert/Nonfibrous	Omnivore	69
Vert/Invert/Nonfibrous/Fibrous	Omnivore	41
Vert	Carnivore	36
Invert/Fibrous	Omnivore	8
Vert/Invert/Fibrous	Omnivore	7
Vert/Nonfibrous	Omnivore	7
Vert/Nonfibrous/Fibrous	Omnivore	5
Vert/Fibrous	Omnivore	1

2.2 Omnivore body mass

To understand the relationship between body size and diet in omnivorous mammals (n=418) we ran a phylogenetic ANOVA comparing the natural logged body masses using the phylANOVA function (phytools package,) [20] in the statistical program R [21]. We also checked for equality of variance between groups using the leveneTest function from the car package in R (Supplemental data 1, see Appendix B for

all supplemental data) [22]. We performed the ANOVA with 10000 simulations and post hoc comparisons adjusting the p-values using the Holm-Bonferroni method. We then used the results of the ANOVA to simplify the dietary guilds to represent only differences in prey type (Table 2). We used these revised diet categories for further analyses to increase our statistical power and decrease our computational time.

2.3 Phylogenetic signal

We calculated the phylogenetic signal of each simplified diet category treating each diet category as a binary trait [23] over ten randomly selected trees with the phylo.d function in the caper package in R [24]. This method calculates a D statistic which is close to 1 if the observed trait has a phylogenetically random distribution or 0 if the observed trait is dispersed on the tree in a way that is consistent with a threshold model of Brownian motion evolution [23]. The trait distribution for the Brownian motion model is calculated by simulating a continuous trait along the phylogeny, defining a threshold value that ensures that the number of tips with each character state remains the same as in the original dataset, then defining the character state at each tip using the threshold value of the continuous trait. Values lower than 0 indicate phylogenetic clustering beyond what is expected by the Brownian motion threshold model. The phylo.d function also tests for significant departure from both a phylogenetically random distribution and the phylogenetic distribution generated under the threshold model.

2.4 Transition rates

We calculated transition rates between dietary guilds using Bayesian Markov Chain Monte Carlo (MCMC) methods in the program BayesTraits [25]. Specifically, a multistate reversible jump MCMC was used to estimate transition rates without assuming a single model of trait evolution [26]. Reversible jump MCMC explores all possible models and generates a posterior distribution of models and parameter estimates by setting each transition rate parameter to either a unique value, equal to one or more of the other transition rates, or zero. This process allows for the exploration of loglikelihood especially when there are many possible models. Because this is computationally

intensive, all BayesTraits analyses were run on the University of Oregon Talapas High Performance Computing cluster.

To consider variability in tree topology we ran independent chains on 100 randomly selected fully resolved trees [19]. We used hyperpriors to seed the exponential prior on the parameters using a uniform distribution on the interval 0 - 10 and 0 - 2 on all 100 trees. To ensure stationarity was reached each chain was run for 1 billion iterations with a sampling interval of 300,000 and a burn-in of 100,000 iterations. We examined the effective sample sizes, autocorrelation, and convergence using packages coda and btw in R (Supplemental data 2) [27-28]. We also checked the autotuning mechanism by examining schedule files to make sure the chains were mixing appropriately. The medians and interquartile ranges were then calculated for each transition rate along with the frequency with which a transition rate was reconstructed as zero (% Z).

To investigate the significance of differences in transition rates, we ran the same analyses on a tree with randomly reassigned dietary categories. We produced our random dataset in R using the sample function on our existing data to guarantee the same number of individuals in each dietary guild. We then used the same reversible jump MCMC procedure in BayesTraits to calculate median transition rates, % Z, and model posterior distribution. This allowed us to determine whether our observed results differed from those expected when there is no phylogenetic signal in dietary guilds.

3. Results

3.1 Diversity

There are large differences in species richness among mammalian diet types (Table 1). Herbivores that eat both non-fibrous and fibrous plant material are the most diverse (n=316, 22% of dataset) followed by insectivores (n=263, 18% of dataset). The omnivorous diet strategy with the highest species richness is consuming invertebrate prey and both non-fibrous and fibrous plant material (n=144, 10% of dataset) closely followed by consuming invertebrate prey and non-fibrous plant material (n=136, 9% of dataset). Predators that eat both vertebrate and invertebrate prey are more diverse (n=86, 6% of dataset) than any omnivorous strategy that incorporates vertebrate prey. Mixing all four food types (n=41, 3% of dataset) only has slightly higher species richness than

specializing on vertebrate prey (n=36, 3% of dataset). Five dietary categories have fewer than 10 species making these rare diets in Mammalia. These categories mix fibrous plant material with either invertebrate or vertebrate prey, or vertebrate prey with either fibrous or non-fibrous plant material. The least occupied dietary guild is eating vertebrate prey and fibrous plants. The panda, *Ailuropoda melanoleuca*, is the sole member of this guild. Pandas eat mostly fibrous plants (bamboo leaves and shoots) but also consume vertebrate prey in the form of rodents and other small vertebrates [29].

When our dataset is sorted into groups separated by animal prey type (Table 2), diversity patterns among omnivorous strategies still exist. Invertebrate omnivory is the second most diverse diet type (n=288, 20% of dataset) on the mammalian tree after herbivory (n=634, 44% of dataset). The diet strategy with the lowest species richness is mixing vertebrate prey with plant material (n=13, 1% of dataset). Examples of species with these unique diets are: *Chrysocyon brachyurus*, *Ailuropoda melanoleuca*, and *Ailurus fulgens* [8, 29, 30].

Table 2 – BayesTraits categories and phylogenetic signal results *=different from random, ′= different from both a random distribution and Brownian motion

Simplified Diet Guilds	BayesTraits categories	Number of Species	Phylogenetic signal- mean D + mean SD
Herbivore	A	634	0.030 ± 0.005 *
Invert omnivore	C	288	0.461 ± 0.003 ′
Invert	B	263	-0.072 ± 0.007 *
Vert/Invert Omnivore	G	117	0.505 ± 0.004 ′
Vert/Invert	F	86	0.440 ± 0.004 ′
Vert	D	36	0.096 ± 0.014 *
Vert Omnivore	E	13	0.813 ± 0.026 ′

3.2 Omnivore body mass

When we compared body mass distributions among the different omnivorous strategies, we found that the lower ranges are similar among all groups, but omnivores that eat all food materials have a larger upper body mass limit. The largest omnivore is *Ursus arctos* (Vert/Invert Omnivore 172 kg) and the smallest is *Sorex trowbridgii* (Invert Omnivore 3.8 g). Although these diet groups have similar body mass ranges, they have very different distributions (see Figure 1). For instance, although there are a few large

omnivores that specialize on insects, such as the sloth bear *Melursus ursinus* [11], most insectivorous omnivores are small (mean= 1.51kg, Table 3). In fact, most insectivorous omnivores are much smaller than the omnivores in the two other dietary groups, with generalist omnivores having intermediate body masses (mean= 10.17kg) and omnivores that only consume vertebrate prey having the largest mean body mass (mean= 23.09kg). Table 3 and Figure 1 also show that when omnivores are grouped by plant material consumed the groups have similar body mass ranges and distributions to each other.

Our phylogenetic ANOVA results confirm that when omnivores are grouped by prey type there are significant differences between their means but there is not a significant difference when omnivores are grouped by plant material consumed (Table 3). Pairwise comparisons with adjusted p-values reveal omnivores that consume only invertebrate prey have a significantly lower average body mass than both groups of omnivores that consume vertebrate material (Table 4). There was not a significant difference between omnivores that eat both prey types and omnivores that only eat vertebrate material. The pairwise tests combined with the body mass distributions in Figure 1 suggest that most insectivorous omnivores are much smaller than omnivores that include vertebrate material in their diets despite the body mass ranges being similar. When we compared omnivore body mass grouped by plant material consumed, there is no significant difference between the average body mass of the omnivores that consume fibrous plant material and nonfibrous plant material. This result agrees with the initial observation that the body mass distributions are similar between these two groups.

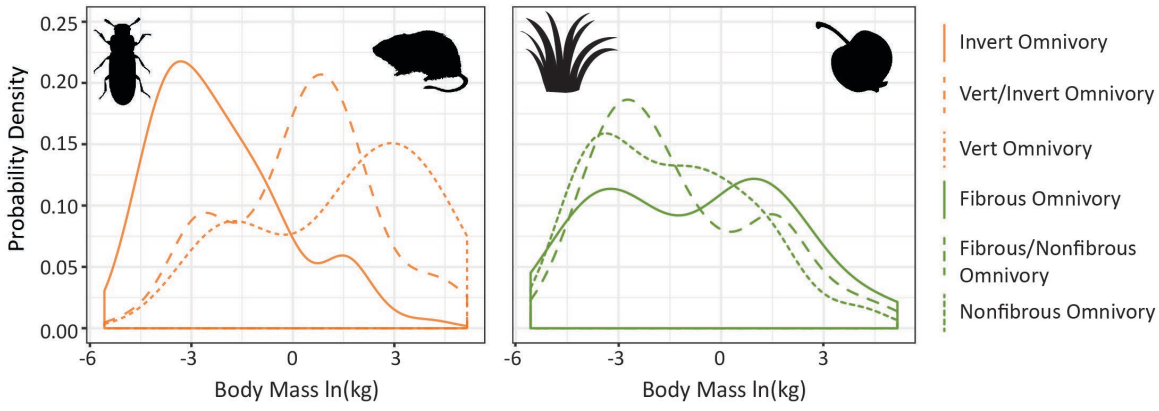


Figure 1 Omnivore body mass distributions separated by diet type.

Table 3 – Omnivore body mass distributions

Omnivore Diet Category	**Body Mass in Kilograms mean (range)**	**Body Mass in ln(Kilograms) mean (range)**
Grouped by Plant material		
Fibrous Omnivore	8.65 (0.012-108.4)	-0.72 (-4.40-4.69)
Fibrous/Nonfibrous Omnivore	5.82 (0.004-172.7)	-1.22 (-5.43-5.15)
Nonfibrous Omnivore	3.21 (0.003-99.9)	-1.47 (-5.57-4.60)
Grouped by prey type		
Invert Omnivore	1.51 (0.004-93.1)	-2.10 (-5.57-4.53)
Vert Omnivore	23.09 (0.073-108.4)	1.45 (-2.62-4.69)
Vert/Invert Omnivore	10.17 (0.007-172.7)	0.28 (-5.01-5.15)

Table 4 - Phylogenetic ANOVA results

	F value	P value
Grouped by vegetation type	1.08	0.86
Grouped by prey type	66.89	0.0016

3.3 Phylogenetic signal

We found that herbivores, insectivores, and hypercarnivores have phylogenetic signal consistent with a Brownian Motion threshold model of evolution (Table 2). We also found that omnivores and mixed feeding dietary guilds, such as mammals that consume both invertebrate and vertebrate prey, have a phylogenetic distribution that is more dispersed than the Brownian motion threshold model but are clustered more than expected under the random model. These intermediate phylogenetic signal values were also found for mixed feeders (e.g. mammals that consume both fibrous and nonfibrous plant material) and omnivores when guilds were defined by plant material consumed (Supplemental data 3). These phylogenetic signal values suggest that mixed feeders have

multiple origins on the mammalian tree and are not as phylogenetically clustered as herbivores, insectivores, and hypercarnivores that specialize on vertebrate prey (Figure 2). Omnivores that only eat vertebrate prey had the highest D estimate (D = 0.813 ± 0.026) showing that they are the most dispersed on the tree while insectivores were the most phylogenetically clustered with the lowest estimate of D (D = -0.072 ± 0.007). It is worth noting that D is most powerful with samples sizes 50 and above [23]. However, our standard deviation values for both hypercarnivores and omnivores that only eat vertebrate prey, which have sample sizes below 50, were low (Table 2), suggesting the low sample sizes are unlikely to be influencing estimates of the evolutionary mode.

Table 5- Phylogenetic ANOVA Pairwise posthoc test using method = "holm" results

	Fibrous Omnivore	Fibrous/Nonfibrous Omnivore	Nonfibrous Omnivore
Fibrous Omnivore		t= 0.80 p= 1	t= 1.20 p= 1
Fibrous/Nonfibrous Omnivore	t= -0.80 p= 1		t= 1.05 p= 1
Nonfibrous Omnivore	t= -1.20 p= 1	t= 1.05 p= 1	

	Invert Omnivore	Vert Omnivore	Vert/Invert Omnivore
Invert Omnivore		t= -6.04 p= 0.0009	t= -10.48 p= 0.0072
Vert Omnivore	t= 6.03 p= 0.0009		t= 1.93 p= 0.11
Vert/Invert Omnivore	t= 10.48 p= 0.0072	t= -1.93 p= 0.11	

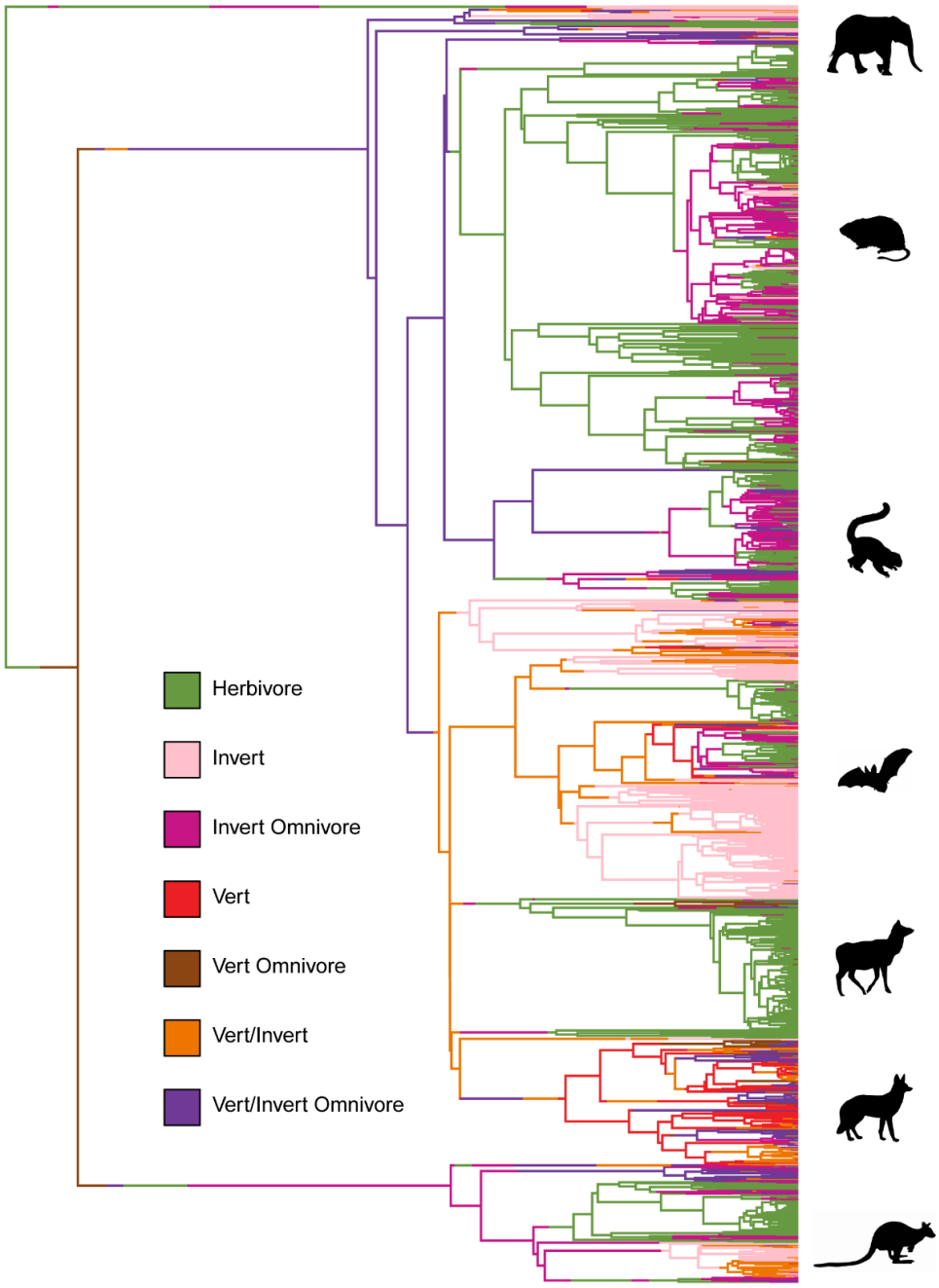


Figure 2 Diet distributions on the mammalian phylogeny. Created using make.simmap function from phytools package.

3.3 Transition rates

We confirmed that constraining the hyperprior interval made little difference to the transition rate estimates, as both hyperprior intervals (0-10 and 0-2) converged on similar average rates (Supplemental data 4). Our randomized dataset produced overall higher transition rates and converged on lower likelihood values (Supplemental data 5) than the empirical data, which is consistent with the phylogenetic signal within our dataset having a substantial impact. Our analysis shows low to nonexistent transition rates between specialized dietary guilds (Table 6). For example, there are low transition rates out of herbivory and insectivory and many of these rates are estimated as zero in 90% of the models (Table 7). Our model results also indicate transitions to a new food type have intermediate steps through omnivory or mixed feeding (Figure 3). We also found that the invertebrate omnivore guild has high transition rates into herbivory, while other guilds do not (Figure 4). Transition rates out of vertebrate prey specialists were also high for transitions into Vert/Invert carnivory and Vert/Invert omnivory. Some high median transition rates between omnivorous and mixed feeding guilds have high IQRs (and hence are poorly constrained), such as the transition between Vert/Invert mixed feeding and Vert/Invert omnivory. There are also quite a few intermediate transition rates that are well constrained, such as the transition from invertebrate omnivory to insectivory.

4. Discussion

Our findings reveal that although macroevolutionary differences exist among the three trophic groups (herbivory, omnivory, and carnivory), there are macroecological and macroevolutionary patterns within omnivory that have been previously overlooked. Within omnivory, diet type is reflected in patterns of diversity, body mass, phylogenetic signal, and evolutionary transition rates. Specifically, our results show that prey type plays a large role in omnivore macroevolution and ecology.

Table 6- Median Transition Rates ± IQR hyperprior exp 0,2

	Herbivore	Invert	Invert Omn	Vert	Vert Omn	Vert/Invert	Vert/Invert Omn
Herbivore	NA	0±0	**0.7166±0.1338**	0±0	0.0790±0.0571	0±0	0±0
Invert	0±0	NA	0.0793±0.0623	0±0	0±0	**0.6945±0.1361**	0±0
Invert Omn	**2.3193±0.3704**	**0.6792±0.1534**	NA	0±0	0.0420±0.0720	0±0.0484	**0.7168±0.1340**
Vert	0±0.0595	0±0.0775	0±0.0790	NA	0.5506±0.6444	**2.2681±0.4289**	**2.1878±0.5934**
Vert Omn	0.0885±0.7246	0.0499±0.1468	0.0878±0.7775	**0.6409±0.8278**	NA	0.0664±0.6094	**2.2586±0.4514**
Vert/Invert	0±0.0430	**2.3009±0.3813**	**0.6961±0.1827**	**0.7409±0.1929**	0±0.0570	NA	**1.7794±1.5314**
Vert/Invert Omn	0.0867±0.1206	0.0411±0.0906	**2.1752±1.3540**	0.1326±0.5881	0.0550±0.1500	**0.7420±0.1909**	NA

Table 7- %Z= percent of models hyperprior exp 0,2 that estimated the transition rate as zero

	Herbivore	Invert	Invert Omn	Vert	Vert Omn	Vert/Invert	Vert/Invert Omn
Herbivore	NA	96.76	0	97.79	0.09	97.61	91.09
Invert	93.64	NA	5.35	90.50	92.55	0	77.27
Invert Omn	0	0	NA	86.89	40.13	65.99	0
Vert	61.89	53.46	53.06	NA	18.11	0.21	0.10
Vert Omn	30.36	42.04	30.36	20.53	NA	36.26	0.81
Vert/Invert	69.18	0	6.20	0.07	62.97	NA	0
Vert/Invert Omn	14.32	44.37	0	9.67	39.68	0.01	NA

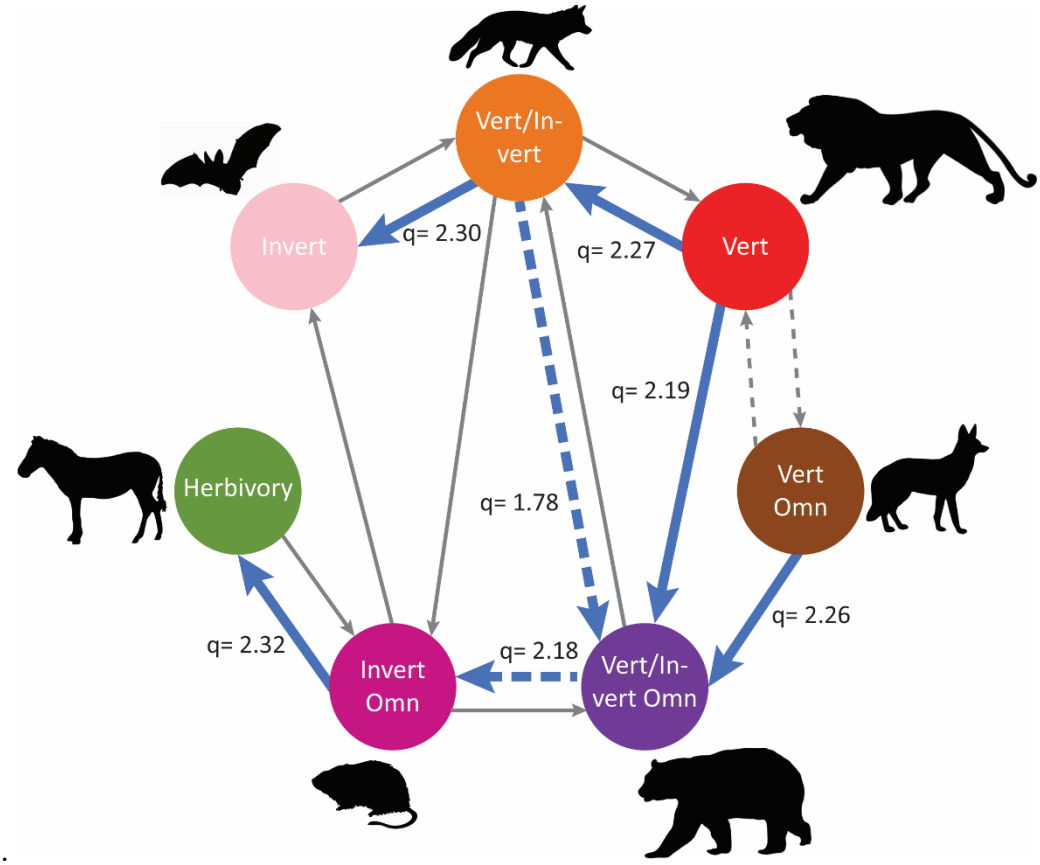


Figure 3 - Summary of transition rates among dietary groups estimated using reversible jump MCMC. Thick dark blue arrows represent high transition rates. Smaller gray arrows represent lower transition rates. Dashed arrows represent high interquartile ranges around the median. q represents the median transition rate estimated from the posterior distribution of models.

In addition to prey type correlating with diversity, our results show that there is a relationship between omnivore prey selection and body mass. We found that omnivores specializing on invertebrate prey are on average smaller (mean body mass of 1.51 kg) than omnivores that incorporate vertebrate prey into their diet (mean body mass of 10.17 kg for Vert/Invert omnivory and 23.09 for Vert omnivory). Carbone *et al.* [13] estimated that the maximum sustainable mass for insectivores is around 21.5 kg and that the transition from small to large prey occurs around this mass as well. For our data set 21.5 kg is around the mean body mass for omnivores that only incorporate vertebrate prey and most omnivores that incorporate invertebrate prey are below this mass. Omnivores should be less energetically constrained by their prey because they are also relying on plant food sources for their energetic needs. However, our findings highlight that the overall trend

found in the order Carnivora [13] and nonvolant terrestrial mammals [14] is still detectable when examining the body masses of mammalian omnivores. It is evident that most insectivorous omnivores are smaller than omnivores that incorporate vertebrate prey and most are below the maximum sustainable body mass of 21.5 kg for specialist insectivores. Additionally, our phylogenetic ANOVA results indicate that omnivores that only eat invertebrate prey are smaller than both mixed-prey-feeding omnivores and omnivores that only eat vertebrate prey. This result further confirms that incorporating vertebrate prey as an omnivore requires a larger body mass just as it does for purely carnivorous mammals.

In contrast with the prey type correlations, we did not find a difference between incorporating fibrous plant material versus non-fibrous plant material. We did find some variation in phylogenetic signal (Supplemental data 3) related to plant material consumed, but these differences were neither as large nor as significant as the differences related to prey type. We also found that body mass was not different between omnivores that eat fibrous plants and non-fibrous plants suggesting that plant material consumed does not constrain body mass in the same way that prey selection does. Morphological differences based on amount of plant material [3] and diversification differences related to type of plant material consumed [15] have been found in groups of mammals highlighting the importance of plant material for mammalian ecology. However, the nature of the relationship between body mass and fibrous plant material utilization is less clear. Originally, fiber content was thought to scale with body mass because of decreasing digestibility [33]. Other studies have highlighted small mammal capacities to digest fibrous material [34] and that there are inconsistencies with the proposed body mass pattern [35]. Our dataset contains many small mammals that combine fibrous plant material with other food sources and our results show that a wide variety of omnivores in both phylogeny and body mass utilize fibrous and non-fibrous plant material. We suggest that omnivore body mass does not reflect the earlier proposed energetic and physiological constraints of consuming fibrous material [33] and instead agrees with work suggesting that it might be more a question of access and abundance rather than digestibility [34,35]. Nevertheless, it seems that omnivores are released from some of the proposed body size constraints of consuming fibrous material, possibly because it is not always the main food

source. Potentially, a more detailed dataset that focuses not only on plant food material properties but also amounts may reveal more subtle relationships between plant material and body size within mammalian omnivores and could yield similar relationships to those we found in prey selection.

Our study establishes a clear association between prey type and mammalian macroevolutionary rates. We found that herbivory, insectivory, and carnivory are phylogenetically clustered. This pattern combined with high diversity suggests that dietary specialization on either insects or plant material is highly successful but evolutionarily constrained. This result is expected given the morphological and physiological adaptations necessary for successful dietary specialization. Additionally, our reversible jump MCMC model results show that transition events out of herbivory and insectivory occur at low rates and only to particular mixed feeding strategies, supporting the idea that there is low dietary flexibility in herbivores and insectivores. Despite also being clustered on the mammalian tree of life, carnivores that specialize on vertebrate prey have higher transition rates into mixed feeding strategies and omnivory. This result should come as no surprise as the order Carnivora is known for its diversity of diets [36]. The phylogenetic signal found in omnivores suggests that omnivorous strategies are dispersed over the tree of life and are the result of transitions from these specialist groups as opposed to diversification within omnivorous lineages; which agrees with past work on both mammals [5] and birds [7]. Specifically, our results show that the transitions into omnivory and prey mixing occur at higher rates from carnivores that specialize on vertebrate prey and at lower rates from herbivores and insectivores.

The existence of high transition rates into diets that incorporate insects and low transition rates into vertebrate prey specialists is probably influenced by the ease of developing physiological and morphological traits that are needed to integrate different prey types. The rarity of transitioning to vertebrate prey might be related to the need for certain traits such as increased body size [13] and stronger jaws and teeth [37] in vertebrate predators. Higher transitions into insectivorous diets could also be because invertebrate prey is abundant and more easily obtained than vertebrate prey. It is also important to note that while we found high transition rates from specializing in vertebrate prey to incorporating more plant and insect material this trend does not appear to be a

common one in the fossil record. Hypercarnivory has been shown to act as an evolutionary ratchet causing hypercarnivores to further specialize on meat consumption [38]. Further hypercarnivory also puts species at greater risk for extinction. The phylogenetic clustering we found in vertebrate prey specialists is consistent with the idea of such an evolutionary ratchet. Our analysis does not include extinct lineages and so we might be missing many hypercarnivorous lineages that would lower the transition of this guild. However, another reason we find high transition rates might be related to differences in body mass, as the evolutionary rachet has mostly been found in large hypercarnivores [38]. The majority of mammals are small bodied, which implies that many of these transitions to insectivory and omnivory are happening in smaller carnivores. This hypothesis would align well with our body mass findings. An example of such a transition is in the termite specialist the aardwolf, *Proteles cristata*. It is small compared to other extant hyaenids and is thought to have evolved from more carnivorous lineages [39]. Our models show that when transitions happen out of hypercarnivory there is a strong tendency to incorporate invertebrates or invertebrates along with some plant material.

Our results also show that transitions out of mixed feeding strategies are fueled by prey type. Most omnivorous dietary guilds appear to have one major evolutionary pathway to a diet similar to their own (e.g. omnivores that specialize on vertebrate prey transitioning to eating both vertebrate and invertebrate prey). There are, however, higher interquartile ranges for some transition rates between mixed feeding groups indicating that these transitions are harder to estimate with the current dataset. Despite this uncertainty, our models had low rates of estimating these transition rates as zero. Our models show that there are higher rates toward increasing invertebrate specialization and eventually herbivory within omnivory. Herbivory involves many diametrically opposed adaptations to those for vertebrate prey (e.g. long vs short gut length, flat grinding teeth vs sharp slicing teeth) which would make this dietary transition difficult without intermediate steps utilizing less vertebrate material. For instance, the giant panda, which is estimated to have switched to a mostly bamboo diet ~2 million years ago [40] still retains the morphology and the gut microbiome similar to more omnivorous bear species and has evolved ways of dealing with fibrous material that are different than other

herbivores causing lower quality digestion [41-43]. This transition from large omnivore toward greater herbivory highlights the physiological difficulties of moving to drastically new food materials. Overall, our models show that going from one specialist group to another goes through an omnivorous or mixed feeding stage incorporating both food types. Transitions out of omnivory into a more specialist diet are probably key moments in evolutionary history and could lead to diversification events, which could explain the clustered phylogenetic signal found for specialist groups like insectivory and herbivory.

5. Conclusions

Scientists should consider whether lumping omnivores into a single diet category is ecologically meaningful for the questions being asked, as it may not encapsulate their diverse ecological strategies and evolutionary trends. Omnivory has different macroevolutionary trends hidden within it primarily driven by prey type. Despite eating both plants and animals, the body size of omnivores is primarily influenced by prey type. Similarly, two main evolutionary pathways dominate our transition rate models, one from vertebrate predation to increasingly insectivorous omnivory and ultimately herbivory, and one from vertebrate predation to prey mixing and ultimately insectivory. Therefore, prey type is an under-appreciated but important macroecological variable that future studies of mammalian omnivory should include.

CHAPTER IV

OREGON OLIGO-MIOCENE TROPHIC DIVERSITY AND COMMUNITY STRUCTURE

1. Introduction

An organism's diet and body mass determine energetic needs and interactions with the environment and are therefore important in determining community composition. There is growing evidence that animal community structure differs between environments resulting in different trophic and body size diversity depending on factors such as temperature and precipitation (Badgely and Fox 2000). This pattern has been shown in modern environments (Rodríguez et al. 2006) and when fossil localities are compared (Gunnell et al. 1995, Stegner and Holmes 2013). Furthermore, studies have shown that both modern (Davidson et al. 2009, Cooke et al. 2019) and past (Boyer 2010, Terry et al. 2011) ecological trait data, such as body size and diet, can be important for predicting modern extinctions in organisms sharing the same traits. Two of the most classic examples of diet and body mass acting as important traits, with respect to extinction and community composition, is the end Pleistocene extinction and the North American extinction of browsing ungulates during the Miocene. The end Pleistocene extinction is unique because of the dramatic size bias of the extinction (Koch and Barnosky 2006) and the Miocene decline of browsing ungulates highlights how changes in vegetation and climate can select against certain functional groups (Janis et al. 2000, 2002, 2004). Studies of these past functional diversity dynamics have provided important insights into how changes to our planet's climate/environment can restructure animal communities. Today, megaherbivores are still disappearing from the landscape and the past extinctions provide a forecast of what the consequences of those disappearances might be (Ripple et al. 2015). Understanding the composition of past ecosystems, and how past ecosystems experienced change, can give us a better grasp on the governing rules for how climate change affects mammalian functional diversity and community structure.

One key moment in Earth's history that saw dramatic shifts in community composition was the Oligo-Miocene interval. During this time interval the world saw a global expansion of grass-dominated habitats (Strömberg 2011) and mammalian communities started resembling the communities we have today. Region-specific studies have documented the variability in North American grassland expansion and the resulting community composition change over the last 20 million years. Most work has focused on the Great Plains (Stegner and Holmes 2013), the onset of C_4 grasses (Feranec and Pagnac 2013, Kita et al. 2014), or large herbivore ecology (Feranec and MacFadden 2006, Barry et al. 1995, Janis et al. 2000, 2002, 2004). During the Oligo-Miocene interval, Oregon was topographically complex and in a climatic zone that favored C_3 plants over C_4 plants (Ehleringer and Cerling 2002), making it substantially different from the other regions that have been previously studied. Substantial work on paleosols and faunal occurrences has been conducted to understand the paleoclimates of the fossil localities in Oregon. Paleosol work suggests that global cooling during the Oligocene led to sub-humid temperate conditions in Oregon (~30 Ma) (Bestland et al. 1997). Later in the Oligocene, it became cooler and drier, and woodland habitats began to give way to bunch grasses and shrubs (Retallack et al. 2000, Retallack, 2004, 2007). Warm-wet forests returned in the middle Miocene (~16 Ma) (Retallack 2009) as global temperatures rose during the mid-Miocene Climatic Optimum. The warm period was followed by cooling which resulted in the spread of sod grasslands (Retallack 2009). The Oregon Oligo-Miocene fossil record is, therefore, an ideal system to study functional diversity changes because it records nearly 40 million years, is well dated because of the prevalence of volcanic deposits, and has had hundreds of specimens collected over the last 100 years (Fremd 2010). The years of paleontological work now make it possible to assemble and assess how past climate and vegetation changes influenced mammalian functional diversity in the Oregon fossil record.

Additionally, the sheer amount of paleoecological data available today allow for a closer look at past community structure than ever before. The number of studies that reconstruct the diet of extinct species and the growing understanding of the relationship between diet and body mass (Reuter 2021 CHAPTER II, Carbone et al. 1999) allow for detailed estimates of past trophic connections. Through data synthesis ancient food webs

for extinct communities can be reconstructed (Dunne et al. 2008). These food webs can be a powerful tool for understanding past trophic relationships (Dunne et al. 2008, 2014) and how they respond to perturbations such as climate change (Roopnarine and Angielczyk 2015, Lozano et al. 2016). Using the amount of data available for Oregon's extinct communities to reconstruct food webs will provide new insights into how changing climate restructured Oregon's mammalian communities. In this study I aim to answer the following two questions: 1. How has Oregon mammalian community structure changed over the last 28Ma? 2. Are differences in community structure driven by particular trophic strategies? To accomplish this goal, I compiled trophic functional diversity of six fossil assemblages and reconstructed food webs for each fossil assemblage using modern predator-prey interactions and existing diet data. The results of this work add to our biogeographical knowledge of Cenozoic ecosystem change and help efforts to forecast future ecological dynamics by adding to our understanding of how animal diet and body mass interacts with the environment to structure mammalian communities.

2. Methods

This study focused on five well collected and dated Oregon fossiliferous formations: The John Day Formation Turtle Cove Member (~29 to 26 Ma) (Fisher and Rensberger 1972, Albright et al. 2008), the Mascall Formation (~16-13 Ma) (Maguire et al. 2018), the Juntura Formation (~12.5-9.5) (Camp et al. 2003, Hooper et al. 2002), the Rattlesnake Formation (~6.9–7.3 Ma) (Streck and Grunder 1995, Prothero et al. 2006) and the McKay Formation (~5.5-6 Ma) (Martin et al. 2018). The Turtle Cove member was split between above and below the Picture Gorge Ignimbrite which has been dated to 28.7 Ma (Albright et al. 2008). These formations document the environmental change that occurred in Oregon as global temperature fluctuated through the Oligo-Miocene (Figure 1).

Faunal occurrences for the formations were compiled from the Paleobiology Database (paleobiodb.org) with additional information from published descriptions (e.g., Maguire et al. 2018). Body mass was reconstructed for extinct species using m1 area and regressions from Legendre (1986). Data for m1 area were compiled from the Paleobiology Database with additional information from published descriptions (see

Appendix C for all for measurement references). If a species m1 was not available, comparisons with other members of the genus were used to make a decision about using another species measurement or a genus average. Some unique species have no other member of their genus and are missing an m1 measurement. The body mass of these species was assumed from descriptions or comparisons to living species (see *Watay tabutsigwii* and McLaughlin et al. 2016). Diet data for extinct species were collected from both the Paleobiology database and, when more detail was needed, primary literature reviews (see Appendix C for references). The literature reviews drew from studies that included dental morphology, microwear, and measowear. Species diets were categorized using seven dietary categories (carnivory, insectivory, omnivory, and herbivory: browser, grazer, mixed feeder). Extant mammal species occurrences were downloaded from the IUCN via a polygon centered on the John Day Basin. Bats and human commensals were removed from the extant mammal species as they are not comparable to the fossil assemblages. Body masses and diet categories for extant animals were compiled from the PanTHERIA Database (Jones et al. 2009) and primary literature sources such as species accounts when data was not available through PanTHERIA, or when further description was needed to determine the herbivorous diet type.

The modern assemblage had a large number of small omnivorous taxa when compared to the fossil localities. Capture studies make it possible to obtain detailed diet data for extant small mammal species, making it easier to detect omnivorous diets. For example, the Coast mole in the modern John Day dataset (*Scapanus orarius*) is classified as an omnivore based upon its stomach contents, which was noted by Whitaker et al. (1979) to have plant material. It is impossible to get the same diet resolution for extinct species. This inability to detect omnivorous diets in extinct species resulted in the modern dataset having a higher small omnivore richness than the fossil dataset. With this in mind and the work done by Reuter et al. 2021 (Chapter III), many extinct small mammals, such as squirrels and mice, were given two diet guilds, one herbivorous, which agrees with the Paleobiology database, one omnivorous, which aligns with extant family diet data. Both the omnivore heavy (OH, aligns with extant family diet data) and omnivore light (OL, agrees with the Paleobiology database) datasets were then used for functional diversity comparisons.

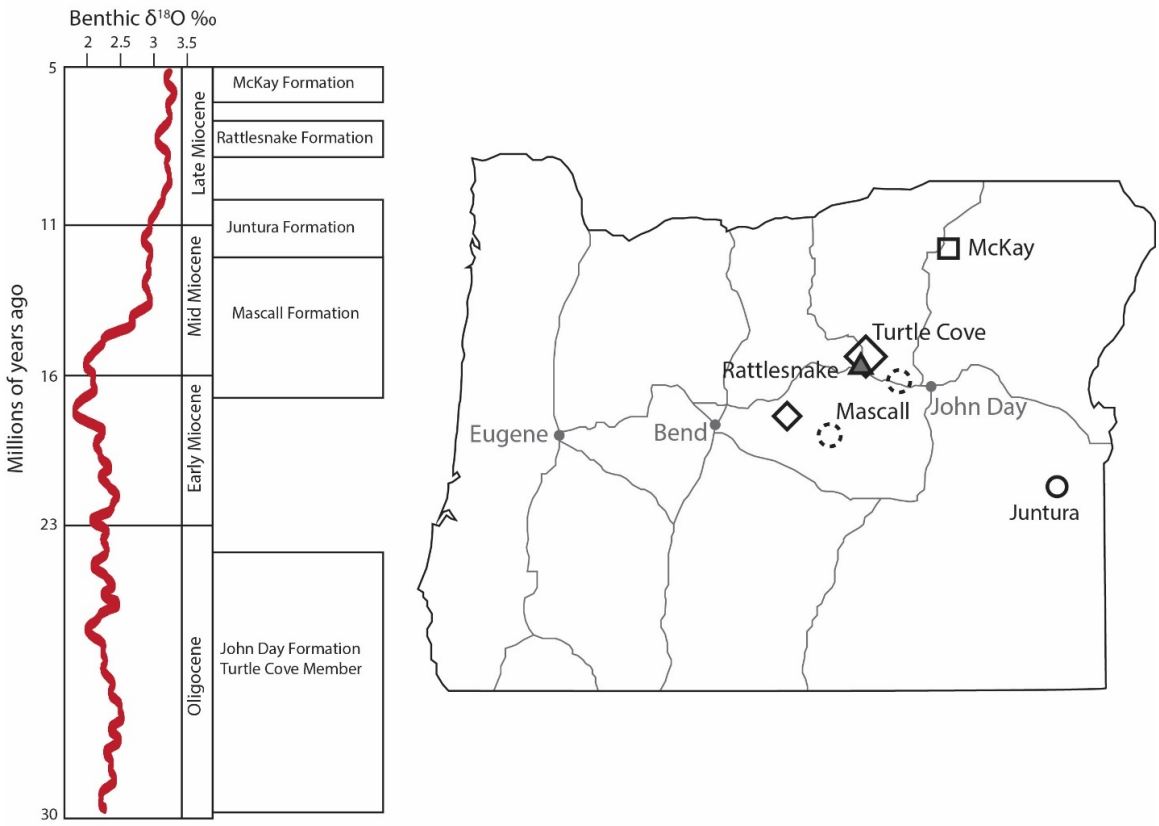


Figure 1 Stratigraphic and age context of formations included in this study. Red line represents the Benthic $\delta^{18}O$ from Westerhold et al. 2020, which documents changes in deep ocean temperature. Map of Oregon indicates the geographic area of the fossil localities included in this study.

Species were then summarized by genus and divided into body mass categories: XLH: >44 kg herbivores; LH: 8–44 kg herbivores; MH: 0.5–8 kg herbivores; SH: <0.5 kg herbivores; LC: >8 kg carnivores; MC: 0.5–8 kg carnivores; SC: <0.5 kg carnivores; LO: >8 kg omnivores; MO: 0.5–8 kg omnivores; SO: <0.5 kg omnivores; MI: 0.5–8 kg insectivores; SI: <0.5 kg insectivores. These categories have been shown in the past to differ between environments (Legendre 1986, Barnosky and Shabel 2005, Stegner and Holmes 2013).

Pairwise Fisher's exact tests with Monte Carlo p-value simulations (5000 replicates) were performed to compare community structure between assemblages. All p-values were then adjusted using Holm p-value adjustment for multiple comparisons. This method was used before by Stegner and Holmes (2013) to detect differences in Great Plains extinct communities.

2.1 Food Webs

To understand the structure of the relationships among species, food webs were reconstructed for each fossil assemblage. Links were reconstructed using the prey and predator body mass rules found in Table 1. These rules are based on modern body mass predator prey relationships outlined in previous studies (Carbon et al. 1999, Sinclair et al. 2003, Owen-Smith and Mills 2008). These studies have shown that predators of certain size classes specialize on prey of predictable mass because of their energetic needs (Carbon et al. 1999, Sinclair et al. 2003, Owen-Smith and Mills 2008). For instance, Carbone et al. 1999 found that predators weighing under 21.5kg tend to eat invertebrates and prey weighing 45% or less of their body mass, while predators weighing over 21.5kg eat prey 45% or more of their body mass. Predator behavioral details such as pack hunting were not incorporated into the food webs but would result in larger prey taken by species that pack hunt. Carnivores were also allowed to prey on other carnivorous species because is a common behavior to show aggression and kill smaller competitors. In many environments it is common for the larger predator to regulate the population sizes of smaller predators (Reomer et al. 2009).

Table 1 – Body mass rules used to reconstruct predator prey relationships

Predator size classes	**Example**	**Prey size classes consumed**	**Example**
<4.5kg	*Martes americana*	**<2**	*Neotoma cinerea*
4.5-10kg	*Taxidea taxus*	<4.5kg	*Lepus americanus*
10-21.5kg	*Canis latrans*	<9.5kg	*Erethizon dorsatum*
>21.5-45 kg	*Canis lupus*	9.5-120kg	*Odocoileus virginianus*
>45kg	*Puma concolor*	>9.5	*Cervus canadensis*

After links were reconstructed, the link and node data were then used to generate one food web per site. Food web metrics such as link density and overall connectance were calculated in R using the *cheddar* package (Hudson et al. 2013). Link density is calculated as L/S, or the average number of connections (L) per species (S) and connectance is calculated as L/S^2, or the total number of links divided by the number of links possible in the web. These two metrics are extremely useful for understanding the degree of specialization within a web.

Interpreting food web metrics such as connectance and can be difficult when taphonomic biases might exist (Shaw et al. 2021). Taphonomic bias can be partly accounted for by reconstructing "Trophic Species Webs" (Dunne et al. 2002, 2008) (see Appendix C for examples of original webs and "Trophic Species Webs"). These are calculated by collapsing all nodes that have identical relationships in the food web into a "trophic species" that represents a node in a new web. Doing so can tell you how much redundancy is in a community and can help when comparing between food webs that could be missing taxa. For instance, many of the small omnivores found in the modern assemblage have the same links in the food web and were collapsed into one node, making it more feasible to compare the modern web to the less species-rich fossil localities. These trophic species were then used to generate the Trophic Species Webs that were used to calculate link density and overall connectance.

3. Results

3.1 Functional Diversity

Using different definitions for omnivory resulted in a difference in mammal functional diversity, mostly in respect to the number of insectivores and herbivores in the assemblages. Using a more inclusive definition of omnivory (OH dataset) made all fossil localities align better with the modern data (Table 2). It increased the small omnivore count and decreased the small insectivore and small herbivore count. The Mascall formation has the largest number of genera classified as small omnivores (n=14), which is similar to the modern number (n=16). The Fisher's exact test results show that using the omnivore-light dataset, the Lower Turtle Cove and the Rattlesnake were significantly different than the modern John Day mammal community (Table 3). In the omnivore-

Table 2 – Number of genera by functional group; OL: omnivore light dataset, OH: omnivore heavy dataset. XLH: >44 kg herbivores; LH: 8–44 kg herbivores; MH: 0.5–8 kg herbivores; SH: <0.5 kg herbivores; LC: >8 kg carnivores; MC: 0.5–8 kg carnivores; SC: <0.5 kg carnivores; LO: >8 kg omnivores; MO: 0.5–8 kg omnivores; SO: <0.5 kg omnivores; MI: 0.5–8 kg insectivores; SI: <0.5 kg insectivores.

Locality	Age in millions of years	XLH	LH	MH	SH	LO	MO	SO	LC	MC	SC	MI	SI	Total richness
Modern John Day Basin		OL: 5 OH: 5	OL: 1 OH: 1	OL: 5 OH: 5	OL: 5 OH: 5	OL: 2 OH: 2	OL: 5 OH: 5	OL: 16 OH: 16	OL: 4 OH: 4	OL: 4 OH: 4	OL: 2 OH: 2	OL: 0 OH: 0	OL: 0 OH: 0	49
McKay Formation	~6-5	OL: 4 OH: 4	OL: 1 OH: 1	OL: 2 OH: 1	OL: 7 OH: 5	OL: 3 OH: 3	OL: 0 OH: 1	OL: 8 OH: 10	OL: 2 OH: 2	OL: 3 OH: 3	OL: 0 OH: 0	OL: 0 OH: 0	OL: 4 OH: 4	34
Rattlesnake Formation	~7-6.9	OL: 9 OH: 9	OL: 2 OH: 2	OL: 2 OH: 2	OL: 4 OH: 2	OL: 8 OH: 9	OL: 0 OH: 0	OL: 1 OH: 3	OL: 2 OH: 1	OL: 4 OH: 4	OL: 0 OH: 0	OL: 0 OH: 0	OL: 1 OH: 1	33
Juntura Formation	~13-10	OL: 7 OH: 7	OL: 2 OH: 2	OL: 1 OH: 1	OL: 8 OH: 5	OL: 4 OH: 4	OL: 0 OH: 0	OL: 4 OH: 10	OL: 2 OH: 2	OL: 2 OH: 2	OL: 0 OH: 0	OL: 0 OH: 0	OL: 6 OH: 3	36
Mascall Formation	~16-13	OL: 13 OH: 13	OL: 4 OH: 4	OL: 4 OH: 3	OL: 11 OH: 5	OL: 4 OH: 4	OL: 3 OH: 4	OL: 7 OH: 14	OL: 4 OH: 4	OL: 2 OH: 2	OL: 0 OH: 0	OL: 0 OH: 0	OL: 3 OH: 2	55
Upper Turtle Cove Member	~28.7-26	OL: 5 OH: 5	OL: 5 OH: 5	OL: 2 OH: 2	OL: 11 OH: 9	OL: 8 OH: 8	OL: 2 OH: 3	OL: 4 OH: 6	OL: 2 OH: 2	OL: 1 OH: 1	OL: 0 OH: 0	OL: 1 OH: 0	OL: 1 OH: 1	42
Lower Turtle Cove Member	~29-28.7	OL: 4 OH: 4	OL: 2 OH: 2	OL: 3 OH: 3	OL: 4 OH: 3	OL: 12 OH: 12	OL: 3 OH: 3	OL: 1 OH: 2	OL: 5 OH: 5	OL: 1 OH: 1	OL: 0 OH: 0	OL: 0 OH: 0	OL: 1 OH: 1	36

heavy dataset, only the Rattlesnake community is different from the modern assemblage. The pairwise tests probably have low power given the lower species counts and high categorical counts. However, the test was able to identify that the Rattlesnake and the modern assemblages have different community compositions. This result from the Fisher's exact test agrees with the raw functional diversity data that the Rattlesnake has higher numbers of large omnivores and very few small omnivores. The Lower Turtle Cove, which also has a higher number of large omnivores (n= 12) was not found to be different from the modern assemblage, suggesting that the Fisher's exact test is mainly being influenced by the number of small omnivores.

Figure 2 represents the reconstructed diet and body mass distributions for the OH dataset. The reconstructed diet and body mass distributions show that the fossil communities differ from each other in their community proportions. Herbivore functional diversity is very different among the formations (Figure 1). The modern Oregon assemblage mostly consists of mixed feeding taxa, while many of the fossil localities have a higher proportion of large browsing taxa. The Mascall fauna stands out for having the most size and diet categories filled and the largest proportion of extra-large browsers. The modern, Rattlesnake, and McKay communities have a lower proportion of browsers compared with the Mascall and Turtle Cove communities. When looking at the distribution of omnivores in the communities, the Lower Turtle cove fauna and the Rattlesnake fauna have distinctly different omnivore communities than the other assemblages. Specifically, they have more large omnivores than small omnivores which is not the case in the McKay, Juntura, Mascall, and modern communities. This pattern was apparent in both the OL and OH datasets. The Lower Turtle Cove has the highest number of large omnivores (n=12). These genera consist mainly of canids and tayassiuds which are in low numbers or non-existent in the modern John Day community. The McKay, Juntura, Mascall, and modern communities have high numbers of small omnivore genera and lower numbers of large and medium omnivores genera. As discussed in the methods the modern assemblage has the highest proportion of small omnivores (n=16) and these mostly consist of mice and squirrels. The proportion of carnivorous taxa also differ between assemblages but not as dramatically as the omnivores and herbivores. The Lower Turtle Cove has a large number of large carnivores

setting it apart from the other formations. The Rattlesnake and McKay communities have a higher proportion of medium carnivores than large carnivores which is not the case in the other communities. The Modern John Day community has a fairly even carnivore community with species in all size classes, which is not the case in the extinct communities.

Table 3 – P-values of pairwise Fisher's exact tests (Monte Carlo P-value simulation with Holm P-value adjustment) on functional group distributions. OL: omnivore light dataset, OH: omnivore heavy dataset.

	Modern John Day Basin	McKay Formation	Rattlesnake Formation	Juntura Formation	Mascall Formation	Upper Turtle Cove Member
Modern John Day Basin						
McKay Formation	OL: 1.00 OH: 1.00					
Rattlesnake Formation	OL: **0.02** OH: **0.04**	OL: 0.34 OH: 1.00				
Juntura Formation	OL: 0.06 OH: 1.00	OL: 1.00 OH: 1.00	OL: 1.00 OH: 1.00			
Mascall Formation	OL: 1.00 OH: 1.00	OL: 1.00 OH: 1.00	OL: 1.00 OH: 1.00	OL: 1.00 OH: 1.00		
Upper Turtle Cove Member	OL: 0.06 OH: 0.90	OL: 1.00 OH: 1.00	OL: 1.00 OH: 1.00	OL: 1.00 OH: 1.00	OL: 1.00 OH: 1.00	
Lower Turtle Cove Member	OL: **0.02** OH: 0.06	OL: **0.26** OH: 0.44	OL: 1.00 OH: 1.00	OL: 0.76 OH: 0.48	OL: 1.00 OH: 0.68	OL: 1.00 OH: 1.00

3.1 Food web structure

Reconstructed food webs allowed for more detailed community structure trends to be detected. The trophic species food webs plotted by prey-averaged trophic level and body mass show that the Mascall, Juntura, Rattlesnake and McKay are similar to one another when compared to the Upper and Lower Turtle Cove webs (Figure 3). In terms of body mass, the Turtle Cove webs and the modern webs do not have herbivores that are as large as the largest herbivores in the Mascall-McKay webs. Additionally, the modern food web is missing a large-bodied lower trophic level omnivore that is taken up by the Tayassiuds in the other webs. When comparing trophic positions, the McKay web shows that there are few omnivores that occupy high trophic levels like in the other webs.

The food web metrics show that although the Lower Turtle Cove has only 40 species it has 29 unique nodes which is the highest number of unique nodes in the dataset. Even the modern food web has fewer unique nodes (n=27). The Mascall formation, which has the highest species richness of the extinct communities, has a lower number of unique nodes than the Upper and Lower Turtle Cove communities (n=25). The Mascall Trophic Species Web shows that species occupy similar roles in the community bringing the number of unique nodes (trophic species) down. The McKay food webs have the lowest link density suggesting that there is a higher level of specialization in the McKay food webs. When food web connectance is compared among Trophic Species Webs the McKay and Mascall food webs have the lowest values and the Turtle Cove webs have the highest values.

Table 4 – Food web metrics for both the Species and Trophic species webs. Link density is calculated as L/S, or the average number of connections (L) per species (S) and connectance is calculated as L/S2, or the total number of links divided by the number of links possible.

Faunal Assemblage	Number of Nodes	Link density	Connectance	Trophic Species (number of unique nodes)	Trophic species web Link density	Trophic species web connectance
Modern Oregon	70	12.1	0.17	27	6.4	0.24
McKay Formation	38	4.0	0.11	19	3.2	0.17
Rattlesnake Formation	36	5.9	0.16	22	4.5	0.20
Juntura Formation	41	4.7	0.12	20	3.9	0.20
Mascall Formation	62	6.6	0.11	25	4.5	0.18
Upper Turtle Cove Member	48	7	0.15	26	6.4	0.25
Lower Turtle Cove Member	43	10	0.23	29	8.4	0.29

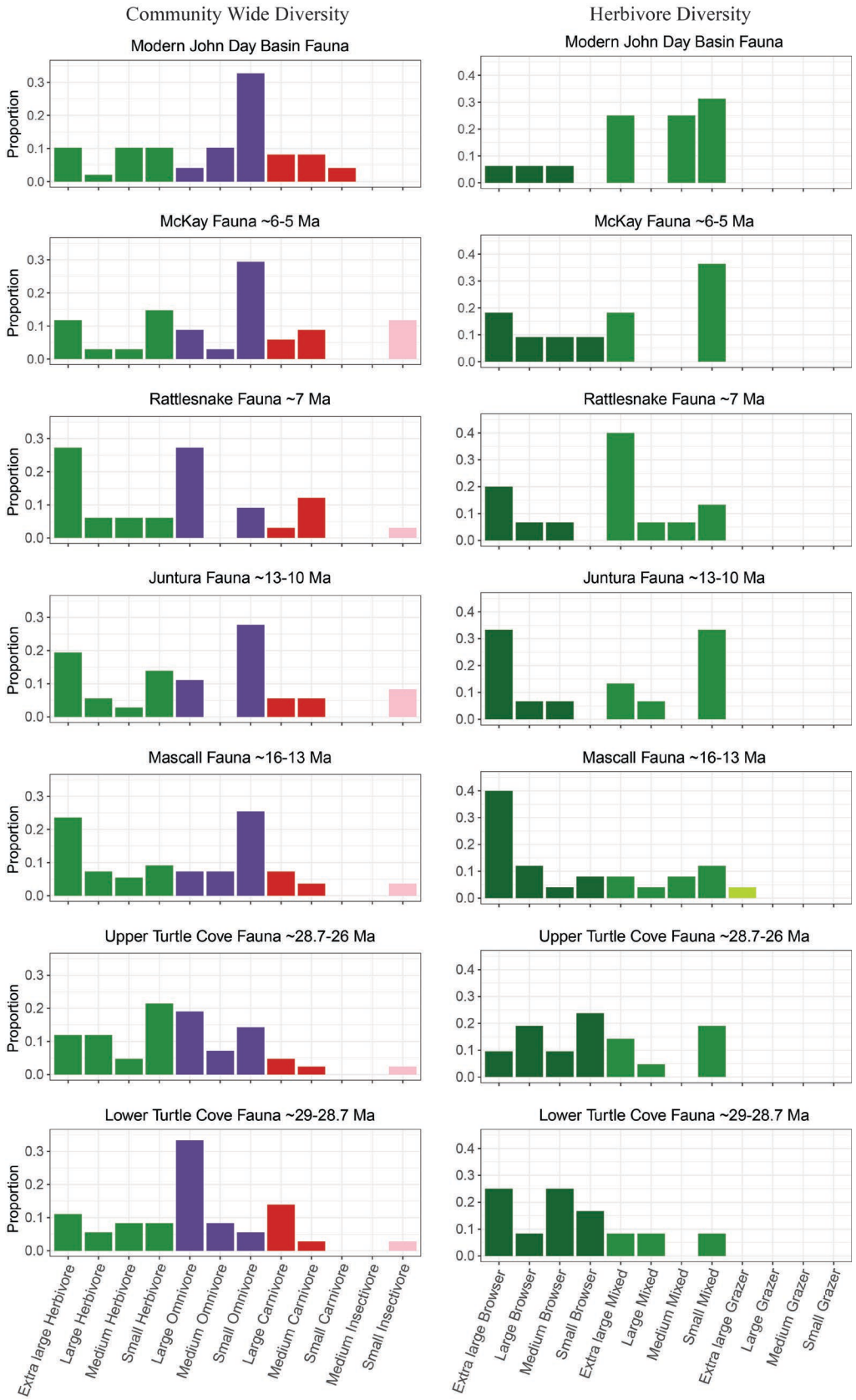


Figure 2 Proportion of genera in each functional group for the omnivore heavy (OH) dataset.

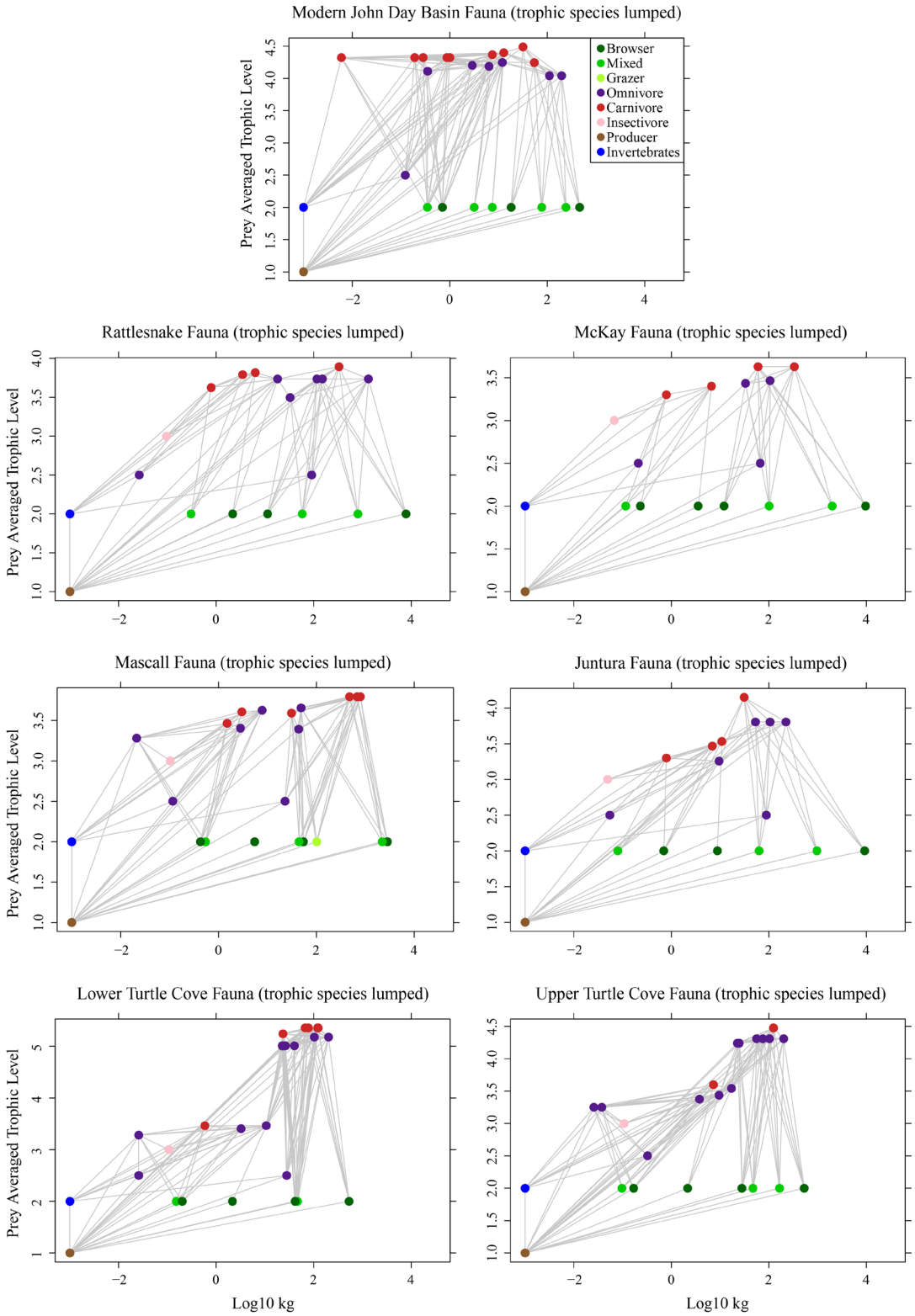


Figure 3 Reconstructed Trophic Species food webs for each community. Nodes are represented with circles and links between predators and prey are represented by grey lines. Nodes represent a "Tropic species" which was generated by lumping species together that have the same ecological links.

4. Discussion

The combined functional diversity and food web data document community shifts that occurred as Oregon experienced changes in climate and vegetation. Past paleosol and stable isotopic work has shown that Oregon experienced environmental changes that were similar to those happening on a global scale, with landscapes becoming drier (Drewicz and Kohn 2018) and more open (Retallack 2009) after the mid-Miocene Climatic Optimum. However, site specific work on faunal occurrences and community composition suggests variability in these general trends. Both open-habitat adapted taxa and arboreal species have been found in the Turtle Cove units, thus it has been suggested that the Turtle Cove had a mosaic open woodland environment (Samuels et al. 2015). The Rattlesnake Formation has evidence for grassland and semiarid wooded shrubland environments (Retallack et al. 2002), and boreal organisms, beavers, and petrified wood fragments suggest some forested areas (Samuels and Cavin 2013). Shotwell pointed out that the Juntura formation is a mixture between a pond bank and woodland community (Shotwell 1963) and the McKay fauna was from mostly a pond bank community with nearby woodlands and grasslands (Shotwell 1956).

Despite there being evidence of some wooded communities persisting in Oregon into the late Miocene, the shift from a more browsing herbivore community to a more mixed feeding herbivore community is still detectable in Oregon and mirrors the broader North American trend (Janis et al. 2000, 2002, 2004). My results show that the Upper and Lower Turtle Cove as well as the Mascall had higher proportions of browsing taxa than the later assemblages and the modern community. The Mascall fauna also has the largest diversity in herbivore body masses and diets which agrees with past work that has shown that the mid-Miocene Climatic Optimum was a period of high herbivore diversity (Janis et al. 2000, 2002, 2004). After the mid-Miocene Climatic Optimum, ungulate browser diversity fell. This pattern is also true for small mammals with the diet shift in small mammals happening earlier than the pattern detected in ungulates (Samuels and Hopkins 2017). Rodent and lagomorph brachydont and mesodont species declined in diversity but hypselodont species increased in diversity during the Miocene (Samuels and Hopkins 2017). The data in this study show that both these decreases in ungulate and small mammal browsing taxa hold true for Oregon. The data also indicate that herbivore body

mass diversity also changed between communities. Food webs plotted by body mass indicate that the Turtle Cove food webs and the modern food webs have a smaller maximum herbivore body mass than the other Oregon communities. The Turtle Cove member and modern communities lack Proboscideans which were important members of Miocene-Pleistocene North American communities and occupy a unique position in the Miocene webs.

The same Oligo-Miocene climate shifts that affected herbivore functional diversity also affected omnivore functional diversity. Modern omnivore diversity has been found to track temperature and precipitation patterns and to decrease as seasonality increases (Badgely and Fox 2000). In addition, frugivorous species are most diverse in tropical environments where fruit is available year-round (Badgely and Fox 2000). In the extinct Oregon communities, there is a decrease in the more plant-dependent omnivores, which agrees with the modern data that suggest that the number of omnivorous and frugivorous species should decline with seasonality. At the end of the Oligocene and into the Miocene, the frugivorous omnivore *Ekgmowechashala* goes extinct, marking the last record of a Primate in North America before humans arrive millions of years later (Samuels et al. 2015). This extinction was probably caused by the cooling and drying climate that was emerging in the time of the upper John Day Formation, eliminating the forested environments *Ekgmowechashala* occupied (Samuels et al. 2015). Coinciding with the Mid-Miocene climatic optimum, the Mascall formation was again wet and humid and supported a wide variety of forest dwelling omnivores such as *Cynarctoides*, which has curiously similar teeth to herbivores for a canid (Wang et al. 2004), and *Bassariscus antiquus*, which was likely a nocturnal omnivore much like the living member of the genus (Barrett et al. 2020). After the Mid-Miocene climatic optimum, the climate in Oregon cooled. The cooling is reflected in the Juntura, Rattlesnake, and McKay communities having a lower proportion of mid-sized omnivores, the category *Cynarctoides* and *Bassariscus* occupied in the Mascall community. Instead, the Juntura, Rattlesnake, and McKay communities have a higher proportion of mid-sized carnivores, such as mustelids, likely representing the reliance of small mammals on a more seasonal and open landscape. It should be noted that the functional diversity data also show the sudden influx of immigrant taxa during the Hemphillian (~7 MA). This immigration is

reflected in the Rattlesnake community having a greater proportion of large omnivores in the community than both the Juntura and McKay. A number of carnivorans found in the Rattlesnake deposits, such as the large bear *Indarctos* and the fisher *Pekania*, are thought to have immigrated from Asia to North America (Qiu Z.-X. 2003, Samuels and Cavin 2013), contributing to the higher proportions of large omnivores and mid-sized carnivores found in the Rattlesnake community. The modern John Day community has a more diverse mid-sized omnivore and carnivore community than the Juntura, Rattlesnake, and McKay communities, but it is unclear if the mid-sized omnivores have low populations and are rare in the John Day region landscape compared with the carnivores. If they are, this would make the Modern community and the McKay fairly similar in terms of functional diversity.

The food webs add to this picture of community change and show that the Upper and Lower Turtle Cove communities had more unique nodes and higher connectance suggesting that they had more robust and interconnected ecosystems than the other communities. This is probably being caused by the high diversity of omnivores, mainly composed of canids, which range in body mass and trophic level in the webs. Omnivores that do not share food resources with their animal prey tend to stabilize ecosystems, unlike omnivores that directly compete with their prey for food resources (McLeod and Leroux 2021) so these canids might have had a stabilizing effect on the ecosystem if they utilized a wide variety of food resources. The Mascall food webs are distinct from the upper and lower Turtle Cove communities by having fewer “trophic species” despite having a higher species richness. This shows that the Mascall species occupy similar roles in the community and the high herbivore diversity is fairly redundant. The high diversity of herbivores with fewer links in the Mascall also brings the connectance in the community down possibly resulting in a less stable ecosystem. The Juntura and Rattlesnake food webs are similar except the Rattlesnake has a higher link density, possibly reflecting the immigration of omnivores like bears. The McKay community has a lower proportion of omnivores over 0.5kg and is instead composed of small insectivorous omnivores like mice and squirrels. This difference in composition is reflected in the low link density and connectance in the McKay food web, a result of the high degree of specialization in higher trophic level species. Additionally, the modern

John Day omnivore community is characterized by having only a few large omnivores, such as Ursids, but has diverse community of small to mid-sized omnivores and carnivores that are more evenly spaced in terms of body mass. The high omnivore body mass diversity is most likely causing the high connectance found in the food web. The modern community, however, is missing tayassiuds, which occupy a unique position in most extinct food webs as a large-bodied, low trophic level omnivore. The last fossil evidence we have of tayassuids in Oregon is in the Late Pleistocene deposits of Fossil Lake (Elfman 1931). Their disappearance from Oregon resulted in a unique position in the food web being lost after it persisted for about 30 million years.

Taphonomic biases can make it difficult to detect faunal differences in the fossil record. The Oregon communities do show some potential taphonomic issues that make it difficult to completely compare their functional diversity. Specifically, the Rattlesnake formation has never been screen washed. As a result, the community looks depauperate of small mammals, as confirmed by the Fisher's exact test which found the Rattlesnake community significantly different from the modern community. However, the other patterns shown by the results, such as the shift from a more browsing herbivore community to a more mixed feeding herbivore community, should not be as heavily influenced by collection method. The larger mammals allow for conclusions to be made about environmental influence on community composition.

5. Conclusions

Overall, the combined functional diversity and food web data document three distinct community shifts. First, Oregon communities went from well-connected omnivore and browser-rich communities in the Oligocene to less connected more herbivore-rich communities in the Middle Miocene. Then, after the Mid-Miocene climatic optimum, browser and omnivore diversity fell and started to change to a state seen in the modern community, which is characterized by having a higher proportion of mixed feeders and a lower proportion of large omnivores. The final community shift was during the Pleistocene extinction, when Proboscideans and tayassiuds went extinct, resulting in unique positions in the food webs being lost after members of these groups had been in Oregon for tens of millions of years. I have shown that just like the Great

Plains, Oregon does see a shift from more large-bodied browsing taxa to a smaller, more mixed feeding herbivore community. Oregon also has had shifts in omnivore functional diversity as warm forests changed to more open habitats.

If we are to understand how our actions affect the ecosystems around us, then paleoecological studies are imperative for completing our picture of how our world functions. The results of this work contribute to the growing knowledge that as climate shifts cause landscape evolution, certain mammalian functional groups are more at risk of extinction. This study highlights that modern conservation efforts should not only investigate changes to herbivore populations but also omnivore populations. The changes in the extinct communities suggest that extant mid-sized omnivorous species might experience local extinction with the loss of forested habitats. Omnivores were lost in the past and could be impacted in the future.

CHAPTER V

OREGON OLIGO-MIOCENE HERBIVORE COMMUNITY NICHE PARTITIONING: INSIGHTS FROM STABLE ISOTOPE ANALYSIS

1. Introduction

During the Oligo-Miocene (~30 -5 Ma), the world saw a global expansion of grass-dominated habitats (Strömberg 2011) and dramatic changes in ungulate (hooved mammal) diversity (Janis et al. 2000). Fossil assemblages from this 20 million year window capture a key moment when ungulate diversity changes coincide with climate and vegetation changes. In North America, the Great Plains phytolith record indicates a mix of grassy and wooded patches in the middle Miocene and uniformly open grasslands during the latest Miocene (Strömberg 2011). North American ungulate diversity also changes during this time, with ungulate diversity being highest around 16 Ma, suggesting a degree of resource partitioning that was different from today's depauperate ecosystems (Janis et al. 2000). Then, as grasslands spread, ungulate diversity fell, declining as the Miocene progressed (Barry et al. 1995, Janis et al. 2000, 2002, 2004). By the late Miocene, global temperatures were decreasing and many browsing taxa were lost completely, such as the Oreodonts, a previously successful North American endemic group (Janis et al. 1998). These changes ultimately contributed to the formation of modern ungulate communities, characterized by low diversity and low abundance in browsing taxa. However, across North America there was a significant amount of heterogeneity in the timing of these vegetation changes (Strömberg 2011, Chen et al. 2015) and potentially in faunal adaptations to changing environments.

Previous work in Oregon has shown that the paleoecology follows many of the same trends in the environment and vegetation seen elsewhere in North America, with browsing genera being lost after the mid-Miocene Climatic Optimum (Reuter 2021 Chapter IV). Additionally, Maguire (2015) found that in Oregon *Archaeohippus* had a narrow diet and went extinct in the region shortly afterward the mid-Miocene Climatic Optimum. However, it is still unclear how the numerous ungulates partitioned available plant-food resrouces and if the conclusions of Maguire (2015) that narrow browsing

niche breadth led to local extinctions are true of other ungulates as well. Additionally, how the resulting mixed feeding ungulate communities partitioned food is not known. Stable isotopic work can give a more detailed picture of ungulate diet and how niche partitioning changed as browser diversity fell. Importantly, Oregon stayed in a climatic zone that favors C_3 plants over C_4 plants (Ehleringer and Cerling 2002) making it possible to make predictions of what the plant assemblage could have looked like.

To better understand ungulate communities during this period of immense change, I use stable carbon isotope analyses of tooth enamel from three Oregon fossil assemblages, to reconstruct resource partitioning and niche breadth. This study expands on previous isotopic work on Oregon fossil mammals (Maguire 2015, Drewicz and Kohn 2018), which mostly focused on equids or poorly identified specimens. The results of this project will broaden our knowledge of Oligo-Miocene changes in ungulate ecological diversity, resource partitioning, and niche breadth. Specifically, I am interested in answering the following questions: 1. Is there isotopic evidence that Oregon Oligo-Miocene ungulate species partitioned available plant-food resources in a purely C_3 environment? 2. Did niche partitioning change with habitat change?

2. Materials and methods

Stable carbon isotope composition in plants depends upon the photosynthetic pathway used by specific plant species. C_3 plants, which photosynthesize using the Calvin Cycle, have a mean δ13C value of ~-28.5‰ and include many trees, herbs, and cool-growing-season grasses (Ehleringer et al. 1991, Kohn 2010). C_4 plants, which include warm-growing-season grasses and sedges, photosynthesize carbon using the Hatch-Slack cycle and have a mean δ13C value of ~−13‰ (Ehleringer et al. 1991, Cerling et al. 1997). Among plants using the C_3 photosynthetic pathway, stable isotope variation is influenced by differences in light intensity, temperature, and water stress, resulting in a wide range in carbon isotope values ($\delta^{13}C$) from −20‰ to −37‰ in plant tissues (Farquhar et al. 1989, Kohn 2010). Studies have shown that C_3 plants can have lower $\delta^{13}C$ values in closed habitats and higher values in more dry and open habitats (Farquhar et al. 1989, Kohn 2010).

The variation in $\delta^{13}C$ values of C_3 plants makes it possible to reconstruct aspects of the diet of organisms that fed on these plants because the isotopic signals are reliably recorded in the body tissues of consumers (Cerling et al. 1997, Feranec 2007). The tooth enamel of medium to large-bodied mammal herbivores has been shown to be consistently enriched by ~14.1±0.5‰ compared with the plant-food resource the animal was eating while the tooth was developing (Cerling and Harris 1999). Previous stable carbon isotope analyses of extant ungulate tooth enamel have successfully detected diet variations among species in purely C_3 systems (Feranec 2007), which is promising because Oregon has long been in a climatic zone that favors C_3 plants over C_4 plants (Ehleringer and Cerling 2002). Specifically, this method allows for an evaluation of an extinct animal's place within closed forested vs. open C_3 grassland ecosystems.

This study focuses on fossil material housed in both the Museum of Natural and Cultural History and the John Day Fossil Beds National Monument, including specimens collected from the John Day Formation Turtle Cove Member (~29 to 26 Ma) (Fisher and Rensberger 1972, Albright et al. 2008), the Mascall Formation (~16-13 Ma) (Maguire et al. 2018), and the Rattlesnake Formation (~6.9–7.3 Ma) (Streck and Grunder 1995, Prothero et al. 2006) (Table 1). Enamel samples were collected from fossil teeth for stable carbon and oxygen isotope analyses. The fossil teeth were sampled using a rotary hand drill with a diamond bit, removing ~3-4 mg of powdered enamel from a previously damaged or non-diagnostic region of the tooth. Broken teeth provide the added benefit of more easily distinguishing enamel from dentin, or matrix. Enamel samples were pretreated using 0.1 M buffered acetic acid to remove any secondary carbonate. ~600 µg of dry sample were weighed and then analyzed by phosphoric acid digestion at 70ºC using a Thermo Gas Bench II. Liberated CO2 was analyzed on a Thermo MAT 253 isotope ratio mass spectrometer in the University of Oregon Stable Isotope Lab. Measured isotope ratios were normalized to the VPDB scale using calcite and tooth enamel reference materials that were analyzed alongside the samples for each run.

3. Results

Results for measurements taken in this study can be found in Table 1. Combined data from this study, Magiure 2015, and Drewicz and Kohn 2018 can be found in Table 2 and 3.

Table 1 – Mean δ13C (‰), S.D. δ13C (‰), and number of specimens measured for this study

Formation	Group	n	Mean δ13C (‰)	S.D. δ13C (‰)
Rattlesnake	Antilocapridae	6	-10.25	1.17
Rattlesnake	*Hipparion*	4	-10.45	0.86
Rattlesnake	*Neohipparion*	1	-9.9	
Rattlesnake	*Platygonus oregonensis*	2	-10.35	1.20
Rattlesnake	*Pliohippus*	3	-10.8	0.56
Rattlesnake	*Prosthennops*	2	-10.75	0.49
Rattlesnake	Rhinocerotidae	2	-11	0.42
Rattlesnake	Tayassuidae	3	-11.33	0.51
Mascall	*Archaeohippus*	2	-8.5	1.98
Mascall	*Blastomeryx*	1	-9.5	
Mascall	*Desmatippus*	1	-10.4	
Mascall	*Dromomeryx*	5	-10.68	0.84
Mascall	Rhinocerotidae	6	-10.05	0.88
Mascall	Tayassuidae	1	-8.3	
Mascall	*Ticholeptus*	5	-11.62	1.65
John Day	*Agriochoerus antiquus*	5	-10.68	0.59
John Day	*Archaeotherium*	8	-11.38	1.28
John Day	*Diceratherium*	5	-10.36	0.79
John Day	*Diceratherium armatum*	3	-10.03	0.96
John Day	*Eporeodon*	3	-13	0.46
John Day	*Hypertragulus*	2	-10.7	0.71
John Day	*Mesohippus*	3	-10.83	0.61
John Day	*Miohippus*	7	-9.89	1.01
John Day	*Nanotragulus planiceps*	3	-10.87	0.32
John Day	*Paroreodon*	2	-11.2	0.99
John Day	*Perchoerus probus*	3	-9.33	0.96
John Day	Tayassuidae	2	-9.95	1.77
John Day	*Thinohyus*	1	-10	

Table 2 – Mean δ13C (‰), S.D. δ13C (‰), and number of specimens measured for this study, Maguire 2015, and and Drewicz and Kohn 2018

Formation	Group	n	Mean δ13C (‰)	S.D. δ13C (‰)
Rattlesnake	Antilocapridae	6	-10.25	1.17
Rattlesnake	*Hipparion*	4	-10.45	0.86
Rattlesnake	*Neohipparion*	1	-9.90	
Rattlesnake	*Platygonus oregonensis*	2	-10.35	1.20
Rattlesnake	*Pliohippus*	3	-10.80	0.56
Rattlesnake	*Prosthennops*	2	-10.75	0.49
Rattlesnake	Rhinocerotidae	2	-11.00	0.42
Rattlesnake	Tayassuidae	3	-11.33	0.51
Mascall	*Acritohippus*	6	-10.92	0.90
Mascall	*Archaeohippus*	9	-8.87	0.77
Mascall	*Blastomeryx*	1	-9.50	
Mascall	*Desmatippus*	3	-10.32	0.29
Mascall	*Dromomeryx*	5	-10.68	0.84
Mascall	*Merychippus*	44	-10.60	0.85
Mascall	*Parahippus*	4	-10.74	1.16
Mascall	Rhinocerotidae	6	-10.05	0.88
Mascall	Tayassuidae	1	-8.30	NA
Mascall	*Ticholeptus*	5	-11.62	1.65
John Day	*Agriochoerus antiquus*	5	-10.68	0.59
John Day	*Archaeotherium*	8	-11.38	1.28
John Day	*Diceratherium*	8	-10.58	0.72
John Day	*Diceratherium armatum*	3	-10.03	0.96
John Day	*Eporeodon*	6	-12.60	0.63
John Day	*Hypertragulus*	2	-10.70	0.71
John Day	*Mesohippus*	3	-10.83	0.61
John Day	*Miohippus*	7	-9.89	1.01
John Day	*Nanotragulus planiceps*	3	-10.87	0.32
John Day	*Parahippus*	2	-10.45	0.07
John Day	*Paroreodon*	2	-11.20	0.99
John Day	*Perchoerus probus*	3	-9.33	0.96
John Day	Tayassuidae	2	-9.95	1.77
John Day	*Thinohyus*	1	-10.00	

Table 3 – Mean, Median, standard deviation of δ13C (‰), and number of specimens measured for each formation. These values are based on measurements taken for this study, Maguire 2015, and Drewicz and Kohn 2018

Formation	n	Median $\delta^{13}C$ (‰)	Mean $\delta^{13}C$ (‰)	S.D. (‰)
Rattlesnake	23	-10.9	-10.6	0.84
Mascall	21	-10.39	-10.42	1.10
John Day Turtle Cove member	47	-10.5	-10.76	1.16

Individual carbon isotopic ratios show a range of -13.4‰ to -8.3‰ for the John Day, -13.10‰ to -7.10‰ for Mascall, and -11.9‰ to -8.9‰ for the Rattlesnake. The Rattlesnake formation has the narrowest range of values but has a similar median (-10.9‰) and mean (-10.6‰) $\delta^{13}C$ to the other assemblages. An ANOVA found no difference between the mean carbon isotopic values for these communities (*p*-value= 0.201). These values are within the bounds that were estimated for a purely C_3 vegetation environment.

Tukey's test results comparing mean $\delta^{13}C$ can be found in Table 4. ANOVA and Tukey test results show that there are five group pairs in the John Day formation that have significantly different mean carbon isotopic values. All of these pairs include *Eporeodon* which was found to have the lowest mean $\delta^{13}C$ (-12.60‰) in the community. *Eporeodon* was found to be significantly different than both groups of *Diceratherium*, *Miohippus*, *Perchoerus probus*, and the lumped unidentified Tayassuidae specimens. *Perchoerus probus* had the highest mean carbon isotopic value (-9.33‰) and the highest individual $\delta^{13}C$ (-8.3‰). *Archaeotherium* has the largest variability in values and some of them are also quite low and are similar to measurements from *Eporeodon* specimens (Figure 1).

In the Mascall community only three group pairs were found to be significantly different from one another. These include *Archaeohippus* (mean -8.87‰ $\delta^{13}C$) and *Acritohippus* (mean -10.92‰ $\delta^{13}C$) which were previously found to differ from one another by Maguire (2015). *Ticholeptus* and *Archaeohippus* were also found to differ significantly (*p*-value= 0.000). Additionally, *Ticholeptus* and the unidentified Tayassuidae were also found to be significantly different (*p*-value= 0.042), however, the

Tayassuidae only has a sample size of one so this difference should be noted with caution. *Ticholeptus* also differs from the other species by having a wide range of values even though it has a low mean $\delta^{13}C$ (-11.62‰) (Figure 2).

ANOVA results indicated that the Rattlesnake fauna do not have significantly different mean carbon isotopic values (*p*-value= 0.728). Figure 3 and Table 1 also show that many taxonomic groups have similar distributions and standard deviations. The Antilocapridae samples have the highest amount of variation compared with the other taxon sampled form the Rattlesnake Formation, but it also has the highest sample size. Certain taxonomic groups are quite different in the Rattlesnake Formation compared to the other fossil collections included in this study. For instance, the enamel from Tayassuids had fairly enriched $\delta^{13}C$ values in both the Turtle Cove Formation and the Mascall Formation. In the Rattlesnake formation many of them have lower $\delta^{13}C$ values than the other organisms sampled.

4. Discussion

The results of this study show that ungulates in both the John Day formation and the Mascall formation partitioned niche space by consuming isotopically different plant-food resources. Either they consumed plants from slightly different parts of their habitat or different parts of the C_3 plants present on the landscape. Both the John Day Formation and the Mascall Formation have been reconstructed as a mosaic open woodland landscape (Samuels et al. 2015, Maguire 2015) which would have allowed for some organisms to consume plants from a combination of wooded patches and more open patches. In the John Day Formation, our results show that compared to other ungulates in the community, especially the rhinos and *Miohippus*, *Eporeodon* was probably eating foods in a more closed part of the habitat. Previous studies have suggested that *Eporeodon* has mesowear patterns consistent with mixed feeders or browsers that consumed a fair amount of grit (Mihlbachler and Solounias 2006). The work done here has provided more detail to the diet of *Eporeodon* in the John Day formation and suggests that it was browsing in more densely vegetated areas than *Diceratherium* and *Miohippus.*

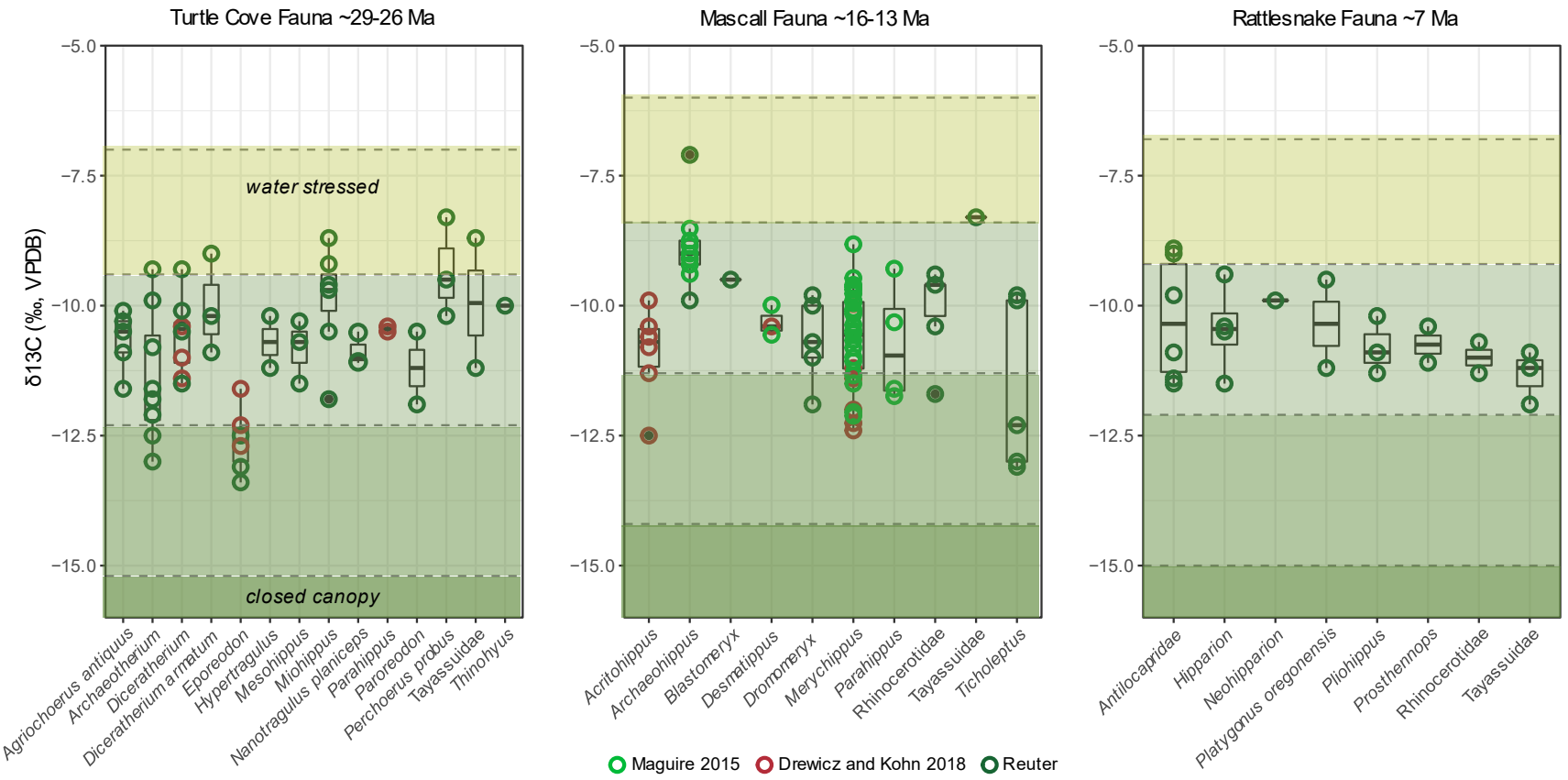


Figure 1 –$\delta^{13}C$ values for each taxon at different stratigraphic ranges. Line inside box plots represents the median, lower and upper box boundaries represent the first and third quartiles, and lower and upper whisker lines represent 1.5 interquartile range. Gray dashed lines represent boundaries between predicted diets. Predictions are based on $\delta^{13}C$ values from modern C_3 floras from Kohn 2010 that were adjusted for diet-enamel enrichment and change in atmospheric $\delta^{13}C$ values through time (see supplemental for enrichment values).

Table 4 – Tukey test p-values on combined data from this study, Maguire 2015, and Drewicz and Kohn 2018. Top row represents the species pairwise comparisons.

Mascall	1	2	3	4	5	6	7	8	9
1. Acritohippus									
2. Archaeohippus	**0.002**								
3. Blastomeryx	0.910	1.000							
4. Desmatippus	0.995	0.349	0.999						
5. Dromomeryx	1.000	0.021	0.973	1.000					
6. Merychippus	0.998	0.000	0.971	1.000	1.000				
7. Parahippus	1.000	0.033	0.967	1.000	1.000	1.000			
8. Rhinocerotidae	0.819	0.306	1.000	1.000	0.978	0.929	0.975		
9. Tayassuidae	0.209	1.000	0.995	0.656	0.348	0.287	0.344	0.745	
10. Ticholeptus	0.956	**0.000**	0.515	0.628	0.828	0.353	0.908	0.140	**0.042**

John Day	1	2	3	4	5	6	7	8	9	10	11	12	13
1. Agriochoerus antiquus													
2. Archaeotherium	0.983												
3. Diceratherium	1.000	0.880											
4. Diceratherium armatum	0.999	0.644	1.000										
5. Eporeodon	0.060	0.435	**0.011**	**0.016**									
6. Hypertragulus	1.000	0.999	1.000	1.000	0.394								
7. Mesohippus	1.000	1.000	1.000	0.998	0.289	1.000							
8. Miohippus	0.961	0.126	0.966	1.000	**0.000**	0.997	0.958						
9. Nanotragulus planiceps	1.000	1.000	1.000	0.997	0.316	1.000	1.000	0.945					
10. Parahippus	1.000	0.988	1.000	1.000	0.220	1.000	1.000	1.000	1.000				
11. Paroreodon	1.000	1.000	1.000	0.976	0.821	1.000	1.000	0.862	1.000	1.000			
12. Perchoerus probus	0.741	0.090	0.748	0.999	**0.001**	0.922	0.745	1.000	0.718	0.983	0.597		
13. Tayassuidae	0.999	0.768	1.000	1.000	**0.049**	1.000	0.998	1.000	0.997	1.000	0.980	1.000	
14. Thinohyus	1.000	0.973	1.000	1.000	0.343	1.000	1.000	1.000	1.000	1.000	0.998	1.000	1.000

Similar patterns were found in the Mascall as the only Oreodont *Ticholeptus* was found to have the lowest $\delta^{13}C$ in the community. The low mean $\delta^{13}C$ of *Ticholeptus* and the wide range in values for the genus suggest that *Ticholeptus* was consuming a range of plant-food resources. These findings are consistent with mesowear patterns that have suggested that this Oreodont was a mixed feeder and still had browsing tendencies like the rest of its family (Mihlbachler and Solounias 2006). Maguire (2015) found that in Oregon *Archaeohippus* had a narrow diet and suggested that this contributed to its extinction in the region shortly after the mid-Miocene Climatic Optimum. In contrast, *Ticholeptus* has quite a large range of values, but it still might not have been able to survive in a more open landscape. Body size could have also been playing a roll in these extinctions as both *Archaeohippus* and *Ticholeptus* are on the smaller size for the ungulates in the community. The changing climate might have impacted the smaller bodied ungulates not only because of their diet but because of the stresses of living in an open landscape.

In contrast to the John Day and Mascall Formations the Rattlesnake Formation samples do not show strong evidence for niche partitioning, as all the organisms have similar mean $\delta^{13}C$ values. Previous studies have shown that browser diversity fell after the mid-Miocene Climatic Optimum (Janis *et al.* 2000, 2002, 2004), and specifically in the Rattlesnake mixed feeding herbivores were more dominant in the community (Reuter Chapter IV). The Rattlesnake Formation has evidence for forested patches such as faunal presence of tapir, boreal organisms, beavers, and petrified wood fragments (Samuels and Cavin 2013). However, the isotopic evidence from the ungulates sampled in this study indicate that herbivores relied on foods found outside of closed-canopy forest environments.

5. Conclusions

Taken together, the isotopic evidence shows that during the Oligocene and mid-Miocene, ungulate niche partitioning was occurring in an ecosystem with no C_4 plants. This study shows that before and during the mid-Miocene Climatic Optimum, Oregon ungulates consumed different plant resources in a mosaic landscape. Then as the environment dried and cooled after the mid-Miocene Climatic Optimum the landscape became more homogeneous and the ungulates on the landscape were eating similar C_3

plant-food resources. A more homogeneous herbivore community arises as global temperatures decreased, and grasslands expanded.

CHAPTER VII

DISSERTATION SUMMARY

Diet and body mass are two of the most fundamental characteristics of mammals. The type of environment plays a role in determining the body mass and trophic diversity of the mammals present in an ecosystem by affecting which food sources are available. Given today's frightening, human-caused biodiversity decreases, it is important to understand how ecosystems respond to change. Paleoecological studies of past community dynamics improve our ability to navigate our current biodiversity crisis. Studying past ecological and evolutionary responses to environmental changes, such as how climate change affects mammal diet and body mass diversity, is therefore crucial for improving our predictive powers in our current human influenced environments. In this dissertation, my research expands our understanding of how mammalian diet interfaces with other ecological and evolutionary processes. I emphasize patterns of form that are important to consider when studying both extant and extinct mammals and I highlight that past community structure changes that inform how modern ecological communities might experience extinction.

In Chapter II, I investigate tooth-size variation and show that it is important variable to be aware of when investigating the fossil record. I show that a combination of factors most likely influence carnivoran tooth-size variation, such as differences in ontogeny, diet, sexual dimorphism, and evolutionary history. Patterns of carnivoran intraspecific tooth-size variation suggest a better understanding of dental size variation in extant species is essential for accurate morphological studies of fossil taxa.

In Chapter III, I show prey type is an under-appreciated but important variable for understanding mammalian omnivore ecology and evolution. Prey type was found to correlate with mammalian omnivore diversity, body mass, and evolutionary transition rates between diet types. This is critical because it provides a new insight into trends in mammalian evolution. Specifically, that prey type is an important ecological trait for mammalian evolution even in organisms that eat both prey and plant material.

In Chapter IV and V, I found that past climate change shaped extinct mammalian communities by affecting omnivore functional diversity, browser diversity, and ungulate

niche partitioning. By using measurements of functional diversity, reconstructed food webs, and isotopic evidence I found that landscape changes cause certain mammalian functional groups to be lost. The resulting communities had a lower proportion of browsers resulting in a more homogeneous community of mixed feeders. They also had a lower proportion of mid-sized and plant dependent omnivores, and a higher proportion of mid-sized carnivores. These past changes are something that could happen in mammalian communities today that experience a loss of forested habitats. If we are to understand how our actions affect the ecosystems around us, then paleoecological studies are imperative for completing our picture of how our world functions.

APPENDICES

APPENDIX A

CHAPTER II SUPPLEMENTARY INFORMATION AND FIGURES

Table 1 – Summary statistics for upper and lower tooth-type mean-percent values. IQR: inter quartile range. Upper teeth are represented with an uppercase initial letter and lower teeth with a lowercase initial letter.

	n	Median	IQR	Standard Deviation
CL	177	99.71	11.77	9.28
cL	173	100.10	12.20	9.35
PL	631	99.95	8.70	9.27
pL	519	100.11	8.38	6.87
ML	258	99.84	9.74	8.04
mL	348	99.76	8.39	7.43
CW	176	99.77	12.88	9.82
cW	173	100.44	10.27	8.88
PW	629	99.81	11.45	10.05
pW	520	100.03	8.50	7.18
MW	258	100.06	8.95	7.17
mW	347	100.03	8.98	7.01

Table 2.- Levene test results comparing upper and lower tooth-type variance.

	Df	F value	*P*.unadj	*P*.adj
Canine Length	1	0.13	0.7230	1
Premolar Length	1	8.54	0.0035	0.0212
Molar Length	1	0.36	0.5491	1
Canine Width	1	1.73	0.1893	1
Premolar Width	1	24.09	<0.00001	<0.00001
Molar Width	1	<0.001	0.9558	1

Specimens Examined for Study—All specimens used in the study are from University of Washington Burke Museum of Natural History and Culture (UWBM), Harvard University Museum of Comparative Zoology (MCZ), and the University of Oregon Museum of Natural and Cultural History (UOMNH).

Canis latrans (n = 14).—United States, Washington, King County Redmond 12053 NE 154th PI, 47.70937°, -122.13408°, female, UWBM 38275; California, Mono County, Coleville, 10 mi S, sex unknown, UWBM 76188; Nevada, Churchill County, Fallon 15 mi S, female, UWBM 73087; Oregon, Wasco County Shaniko, 6 mi S, 5 mi W, 44.917°, -120.8532°, sex unknown, UWBM 20183; Oregon, Wheeler County, Clarno, 1.5 mi N, 4 mi E, 44.9353°, -120.3907°, male, UWBM 20186; Oregon, Harney County,

Malheur National Wildlife Refuge, Sodhouse Lane, 43.2658, -118.8431, female, UWBM 38627; locality unknown, sex unknown, UOMNH 8496, UOMNH 8494, UOMNH 8474, UOMNH 8495, UOMNH 8499, UOMNH 8486, UOMNH 8478, UOMNH 8501.

Urocyon cinereoargenteus (n = 10).—United States, California, exact locality unknown, male, UWBM 13640; California, San Diego County, Escondido, 33.11888°, -117.076763°, female, UWBM 52028; California, San Diego County, Rincon Springs, 5 mi E, 33.2959184°, -116.9055871°, male, UWBM 52027; Nevada, Lyon County, Yerrington, Flying M Ranch, East Walker River, 15 mi S, 38.76838°, -119.16194°, sex unknown, UWBM 52031 and 52032; Michigan, Kalamazoo County, Comstock Township, 42.2881°, -85.4729°, male, UWBM 35221; Kalamazoo, 42.2917°, -85.5872°, male, UWBM 35222; Washington, King County, Woodland Park Zoo, Seattle, female, UWBM 6922; Texas, Palo Pinto County, near Graford, 32.938°, -98.247°, female, UWBM 41620; United States, Oregon, Douglas County, T30S R6W Sec 32, female, UWBM 77676.

Vulpes lagopus (n = 10).—United States, Alaska, St. Lawrence Island, 63.5027778°, -170.4469444°, female, UWBM 34124; St. Lawrence Island vicinity of Savoonga, 63.694139°, -170.4792408°, sex unknown, UWBM 33362-33366; St. Lawrence Island, Northeast Cape, 32 km S, 63.295°, -168.6922222°, male, UWBM 34414; Alaska, Pribilof Islands, Otter Island, 57.05°, -170.4°, male, UWBM 82375; Alaska Cape Prince of Wales, 65.5963889°, -168.0847222°, sex unknown, UWBM 31584; Russia, Poluostrov Yamal, male, UWBM 39670.

Ursus americanus (n = 10).—Canada, British Columbia, within 25-40 mi of Williams Lake, 52.1417°, -122.1417°, sex unknown, UWBM 58787; United States, Washington, Chelan County, 47.86°, -120.63°, sex known, UWBM 82196; Oregon, Lane County, sex unknown, UOMNH 9091; Oregon, Wallowa County, Wallowa, sex unknown, UOMNH 10008; locality unknown, sex unknown, UOMNH 8503, UOMNH 8471, UOMNH 8654, UOMNH 22751, UOMNH 8659, UOMNH 8653.

Ursus arctos (n = 11).—United States, Washington, King County, male, UWBM 39422; Alaska, Kodiak Archipelago, Kodiak Island, 57.3961111°, -153.4833333°, male, UWBM 6391; Alaska, Brooks Range, near Anaktuvuk Pass, 68.1333333°, -151.75°, male, UWBM 39587; Canada, British Columbia, exact locality unknown, sex unknown, UWBM 6397, male, UWBM 58757, male, UWBM 58760; Russia, Magadan Oblast, middle reaches of the Anadyr River, female, UWBM 76861; locality unknown, sex unknown, UWBM 33197, UOMNH 8656, UOMNH 8655, UOMNH 8648.

Ursus maritimus (n = 8).—United States, Washington, Pierce County, Tacoma, Point Defiance Zoo, sex unknown, UWBM 61283; Alaska, North Slope Borough, Point Barrow, ~ 75 mi NW, Bering Sea, 72.16666°, -158.66666°, male, UWBM 58803; Alaska, Nome Census Area, St. Lawrence Island, Gambell area, 63.7797222°, -171.7411111°, male, UWBM 39589; locality unknown, male, UWBM 33198; locality unknown, sex unknown, UWBM 58802, UWBM 39434, UWBM 33187, UOMNH 8658.

Mephitis mephitis (n = 11).—United States, Washington, Walla Walla County, Walla Walla; 0.5 mi W, 46.0647°, -118.3522998°, female, UWBM 41342; College Place, 46.0494°, -118.3872°, female, UWBM 41341; Washington, Whatcom County, Bellingham, 48.7597°, -122.4869°, female, UWBM 18851; Washington, Skagit County, Sedro Woolley, 48.5039°, -122.2361°, male, UWBM 41336; Washington, Kittitas County, Ellensburg, on I-90, T18N R18E Sec 33, 47.0078°, -120.5887°, female, UWBM

34275; Ellensburg, 14 km NW, on SR 10, 47.1007°, -120.6946°, male, UWBM 31871; Kittitas County, Trout Lake, 45.9975°, -121.5269°, male, UWBM 39371; locality unknown, sex unknown, UWBM 19717, UOMNH 1361/1750, UOMNH 1751, UOMNH 1344.

Gulo gulo (n = 11).—United States, Alaska, Dillingham Census Area, Dillingham, 59.0397222°, -158.4575°, sex unknown, UWBM 41384; Alaska, Aleutians East Borough, Izembek National Wildlife Refuge, Cold Bay, outer marker, 55.167°, -162.667°, male, UWBM 82394; Alaska, North Slope Borough, Anaktuvuk Pass, 68.144184°, -151.737929°, male, UWBM 82312; Alaska, North Slope Borough, Barrow, 203 km SSE, Kimmikpak Ridge, Headwaters of Aumalik River, 69.6252778°, -156.3197222°, female, UWBM 34936; Canada, British Columbia, near Nahatlatch Lake, 49.99011°, -121.79152°, female, UWBM 81885; Russia, Chukotka Autonomous Okrug, Markovo (Mapkobo) outskirts, 64.68°, 170.41°, female, UWBM 82315; locality unknown, female, UWBM 26581; United States, Alaska, sex unknown, UOMNH 8237-8239, UOMNH 8241.

Lontra canadensis (n = 12).—United States, Washington, Mason County, Coulter Creek, 47.41845°, -122.81075°, male, UWBM 32245, male, UWBM 32237; Dry Creek, female, UWBM 32233; Dewatto River, 47.4542°, -123.0472°, male, UWBM 32247; Washington, Pierce County, near Tacoma, 47.2531°, -122.4431°, female, UWBM 41397, Bay Lake, 47.2447°, -122.7567°, female, UWBM 32196; Washington, San Juan County, Jones Island, 48.615°, -123.0444°, female, UWBM 32606; Washington, Skagit County, Cypress Island, 48.575311°, -122.706605°, male, UWBM 82696; United States, Oregon, Lane County, McKenzie Bridge, sex unknown, UOMNH 4047; United States, Oregon, Lane County, sex unknown, UOMNH 8236; locality unknown, sex unknown, UOMNH 9179, UOMNH 8612.

Martes Americana (n = 11).—Canada, British Columbia, vicinity of Williams Lake, 52.1417°, -122.1417°, sex unknown, UWBM 52642, 52646, 52654, 52656, 52660, 52661, 52667, 52670, male, UWBM 52633, 52634, 52649.

Taxidea taxus (n = 8).—United States, Oregon, Wasco County, Shaniko, 2 mi S, 1.5 mi E, 44.9749°, -120.7205°, male, UWBM 20184; Shaniko, 5 mi S, 6.5 mi W, 44.9315°, -120.8838°, male, UWBM 20176; Shaniko, 3 mi N, 3 mi W, 45.0473°, -120.8123°, male, UWBM 20187; Oregon, Umatilla County, Tollgate, near our cabin, 4 mi W, 45.7806°, -118.1744°, male, UWBM 41392; Montana, Madison County, near Ennis, on Highway 287, 45.3367°, -111.74°, male, UWBM 32613; Canada, Saskatchewan, Rosthern, 1.6 km NE, Highway 11, 52.67583°, -106.31639°, female, UWBM 39646; locality unknown, sex unknown, UOMNH 93628, UOMNH 8636.

Acinonyx jubatus raineyi (n = 8).—Tanzania, Serengetti (Sarengetti) Plains, sex unknown, MCZ 27497-27499; Tanzania, Ipemi, sex unknown, MCZ 26467; Kenya, Serengetti (Sarengetti) Plains, female, MCZ 28661; Kenya, 200 miles southwest of Nairobi, male, MCZ 37678; locality unknown, male, MCZ 58142; locality unknown, sex unknown, MCZ 20047.

Leopardus pardalis (n = 10).—Panama, Canal Zone, Gamboa, sex unknown, MCZ 20326, Canal Zone, near Gamboa, sex unknown, MCZ 20210, Canal Zone, Atlantic side, sex unknown, MCZ 21502, Boquete, male, MCZ 10117; Costa Rica, Talamanca,

sex unknown, MCZ 5717, 5718, 5359; Brazil, Rio Tapajos, Tauary, female, MCZ 31822, 30728; Paraguay, Guyraungua River, male, MCZ 28099.

Lynx rufus (n = 10).—United States, New Mexico, exact locality unknown, female, UWBM 39811; Washington, Mason County, GMU 636 (Skokomish GMU), female, UWBM 31987, male, UWBM 31985; Washington, Clallam County, Hoko River, 22E Road, GMU 600 (Ozette GMU), female, UWBM 31882; Washington, Grays Harbor County, Higley Peak, near Lake Quinault, GMU 618 (Matheny GMU), 47.5103°, -123.8858°, male, UWBM 31938; Washington, Klickitat County Goldendale, GMU 588 (Grayback GMU), 6 mi N, 45.8208°, -120.8206°, male, UWBM 31982; Montana, Yellowstone County, Pompeys Pillar Creek, MT FWP Region # 5, 45.9807°, -108.2155°, female, UWBM 81357; Montana, Treasure County, Sarpy Creek, MT FWP Region # 7, 46.2443°, -107.2451°, male, UWBM 81455; Oregon, Malheur County, Malheur Lake, 43.3117°, -118.7942°, sex unknown, UWBM 52047; Nebraska, Lancaster County, Lincoln, exact locality unknown, sex unknown, UWBM 33213.

Panthera leo (n = 11).—United States, Washington, King County, Seattle, Woodland Park Zoo, male, UWBM 81888, female, UWBM 34193; locality unknown, male, UWBM 33191, female, UWBM 33192; Washington, Pierce County, Tacoma, Point Defiance Zoo, female, UWBM 6833; India, Sirsi, exact locality unknown, male, MCZ 8052; Kenya, Mara Plains, 200 miles southwest of Nairobi, sex unknown, MCZ 37751; Ethiopia, exact locality unknown, female, MCZ 5086; locality unknown, male, MCZ 9487; locality unknown, sex unknown, MCZ 9352, MCZ 1718.

Puma concolor (n = 9).—United States, Oregon, Douglas County, Sutherlin, Calapooya Drainage, 7 mi E, T25S R4W Sec 17, 43.3967°, -123.1981°, female, UWBM 51188; I-5 NE, NE of Yoncalla, Cox Creek Drainage, 3 mi E, T22S R4W Sec 23, 43.6463°, -123.1359°, male, UWBM 51197; Milo, St. Johns Creek Drainage, 2 mi N, T30S R3W Sec 15, 42.9634°, -123.0438°, female, UWBM 51198; Oregon, Wallowa County, Bear Creek, male, UWBM 51182; Oregon, Lane County, Goshen, 5 mi W, 43.9956°, -123.1106°, female, UWBM 51180; Oregon, Curry County, ~0.5 mi from Panthu Mountain, off road 3302 in N fork of Lobster Creek, T33S R13W Sec 35, 42.6743°, -124.2124°, male, UWBM 51186; Washington, Jefferson County, lower Hoh River, sex unknown, UWBM 12518; Washington, Chelan County, Cashmere, Trip Canyon, GMU 251, 47.488°, -120.485°, UWBM 82204; locality unknown, sex unknown, UWBM 19676.

Ichneumia albicauda ibeana (n = 10).—Kenya, Kaimosi, Kakamega, female, MCZ 32258, male, MCZ 31601, sex unknown, MCZ 32252; Mount Elgon, Kirui, female, MCZ 32255; upper Ura River, Female, MCZ 16118; Tana River, male, MCZ 16124-16125; Kenya, -2.41083°, 37.964183°, male, MCZ 31958; Tanzania, Tanganyika T., Kilosa, female, MCZ 22714; Lake Natron, male, MCZ 28759.

Suricata suricatta suricatta (n = 10).—South Africa, exact locality unknown, sex unknown, MCZ 5115; Namaqualand, Ezelfontein, North Leliefontein, male, MCZ 35396-35397; North Transvaal, Pietersburg, male, MCZ 33971, female, MCZ 33972; near Lamberts Bay, sex unknown, MCZ 6218; Kolmanskop, sex unknown, MCZ 20078; Western Cape, Kamiesberg, Witwater Plateau, male, MCZ 35395; Botswana, near Rakops, exact locality unknown, female, MCZ 62928, sex undetermined, MCZ 62927.

Crocuta crocuta (n = 2).—Kenya, Kapiti Plains, female, MCZ 13232; East Africa, exact locality unknown, sex unknown, MCZ 8518.

Crocuta crocuta habessynica (n = 1).—Somalia, exact locality unknown, MCZ 18623.

Crocuta crocuta germinans. (n = 5).—Tanzania, Tanganyika Territory, Izikisia, near Tabora, 6ºS, 35ºE [WGS84 alt: 4º54'S, 33º06'E], male, MCZ 23098; Tanganyika Territory, Mwanza, female, MCZ 23097; Loita Plains, male MCZ 21173; Mara, male, MCZ 21174; Kapiti Plains, female, MCZ 13232; locality unknown, sex unknown, MCZ 5213.

Crocuta crocuta crocuta (n=1)—South Africa, Cape of Good Hope, sex unknown, MCZ 20968.

Table 3 – Measurement means and standard deviations.

Measurement	*Canis latrans*	*Urocyon cinereoargenteus*	*Vulpes lagopus*	*Mephitis mephitis*	*Gulo gulo*	*Lontra canadensis*	*Martes americana*	*Taxidea taxus*	*Ursus americanus*
C^1L	9.21±0.62	4.62±0.48	6.30±0.47	4.40±0.53	10.52±0.74	6.41±0.64	3.96±0.38	8.24±0.41	16.60±1.80
P^1L	5.56±0.58	3.36±0.31	4.74±0.24		3.73±0.34	1.93±0.32	2.01±0.17		5.98±1.70
P^2L	11.13±0.76	5.46±0.37	7.65±0.48	1.88±0.17	6.63±0.39	4.85±0.35	4.17±0.22	3.90±0.31	3.93±.068
P^3L	12.32±0.78	6.11±0.39	8.48±0.52	3.51±0.25	9.91±0.62	7.20±0.33	4.81±0.21	6.52±0.34	4.88±1.10
P^4L	19.29±1.20	10.36±0.45	12.12±0.61	7.36±0.40	20.08±1.04	11.93±0.57	7.43±0.41	11.97±0.53	11.15±0.78
M^1L	12.50±0.75	8.32±0.46	8.32±0.41	7.44±0.39	7.31±0.67	8.81±0.40	4.29±0.33	10.99±0.66	17.29±0.80
M^2L	7.09±0.41	5.61±0.25	4.69±0.21						24.23±1.47
C_1L	9.03±0.81	4.62±0.44	7.07±0.65	4.54±0.62	10.81±0.93	7.57±0.57	4.87±0.44	8.29±0.35	14.85±1.90
P_1L	4.67±0.39	2.95±0.29	3.60±0.27		3.75±0.31		2.10±0.18		5.87±0.37
P_2L	9.35±1.24	5.34±0.33	7.36±0.53	2.55±0.25	6.18±0.45	5.09±0.22	4.13±0.12	3.82±0.23	
P_3L	10.65±0.93	6.04±0.43	8.35±0.41	3.41±0.21	8.23±0.48	6.07±0.40	4.80±0.18	5.76±0.31	3.80±0.85
P_4L	11.89±0.80	7.30±0.42	9.14±0.49	4.23±0.23	11.25±0.61	8.39±0.43	5.24±0.19	8.15±0.31	9.46±0.52
M_1L	20.77±1.76	11.91±0.54	13.51±0.51	10.22±0.60	20.94±1.27	13.79±0.63	8.37±0.44	13.67±0.29	17.89±0.85
M_2L	9.11±0.94	6.36±0.66	6.00±0.46	4.15±0.58	6.01±0.44	5.53±0.32	3.00±0.34	4.53±0.52	18.68±0.63
M_3L	4.54±0.61	2.97±0.32	2.72±0.34						14.32±0.93
C^1W	5.36±0.43	3.21±0.27	3.96±0.23	3.23±0.56	8.13±0.66	5.43±0.35	2.89±0.26	5.99±0.43	11.65±1.91
P^1W	3.68±0.51	2.18±0.13	2.94±0.22		3.94±0.34	2.15±0.44	1.74±0.18		3.96±0.92

P^2W	3.93±0.42	2.41±0.20	3.23±0.31	1.35±0.19	4.43±0.37	3.62±0.26	2.05±0.14	2.63±0.08	2.40±0.24
P^3W	4.29±0.36	2.73±0.16	3.50±0.28	2.53±0.22	6.08±0.48	4.87±0.29	2.43±0.17	4.53±0.30	3.56±0.71
P^4W	9.37±0.68	5.35±0.34	6.71±0.58	5.85±0.41	11.38±0.76	9.82±0.86	4.52±0.33	10.13±0.41	8.23±0.84
M^1W	15.97±1.10	10.43±0.80	11.03±0.45	8.30±0.72	13.14±0.48	10.77±0.68	7.18±0.38	10.46±0.48	12.67±0.51
M^2W	10.96±0.73	7.38±0.78	7.16±0.44						14.35±0.74
C_1W	6.12±0.62	3.17±0.27	4.12±0.23	3.55±0.59	8.71±0.86	5.53±0.35	3.51±0.25	6.11±0.29	10.46±0.99
P_1W	3.25±0.33	1.94±0.12	2.72±0.23		3.22±0.31		1.77±0.10		3.58±0.44
P_2W	4.18±0.41	2.37±0.13	3.25±0.21	1.71±0.11	4.16±0.22	3.31±0.20	2.16±0.10	2.55±0.13	
P_3W	4.41±0.48	2.48±0.15	3.41±0.27	2.52±0.14	5.48±0.38	3.77±0.22	2.29±0.18	3.11±0.13	2.96±0.48
P_4W	5.63±0.40	3.34±0.22	4.21±0.22	3.23±0.22	7.23±0.64	5.02±0.32	2.56±0.15	4.39±0.21	5.23±0.26
M_1W	8.23±0.68	4.91±0.41	5.42±0.28	4.98±0.44	9.28±0.53	7.97±0.38	3.45±0.25	5.88±0.45	8.47±0.49
M_2W	6.58±0.68	4.61±0.41	4.18±0.27	3.810.35	4.94±0.33	6.08±0.18	2.87±0.14	4.65±0.43	11.34±0.74
M_3W	4.00±0.34	2.69±0.30	2.44±0.22						11.09±0.67

Table 3: measurement means and standard deviations continued.

Measurement	*Ursus arctos*	*Ursus maritimus*	*Acinonyx jubatus*	*Leopardus pardalis*	*Lynx rufus*	*Panthera leo*	*Puma concolor*	*Ichneumia albicauda*	*Suricata suricatta*	*Crocuta crocuta*
C^1L	22.17±3.82	22.70±4.24	10.21±0.69	8.32±0.72	6.85±0.60	23.90±3.01	13.24±0.94	4.77±0.32	3.46±0.30	15.91±0.94
P^1L	6.19±0.56	5.71±0.65						2.98±0.23		7.02±0.65
P^2L	4.68±2.32		2.67±0.25	3.98±0.59		9.14±0.58	4.26±1.27	5.69±0.47	3.44±0.20	14.36±0.99
P^3L	6.17±1.63	5.51±0.74	13.66±0.80	9.73±0.38	9.11±0.55	24.62±1.56	15.61±0.75	6.14±0.36	3.68±0.19	21.49±0.92
P^4L	16.31±1.24	15.12±1.08	22.50±0.97	15.77±0.57	14.25±0.80	36.15±2.21	22.72±0.87	7.97±0.42	4.54±0.22	34.84±0.82
M^1L	22.29±1.28	19.23±1.62	4.33±0.51	2.60±0.18	2.59±0.17	6.34±1.36	3.28±0.44	6.33±0.30	3.39±0.24	3.09±0.04
M^2L	35.15±3.90	24.84±3.55						4.80±0.22	2.30±0.19	
C_1L	22.10±3.76	20.09±2.25	8.76±0.58	7.83±0.78	6.60±0.57	22.10±2.97	12.19±0.87	5.20±0.30	3.69±0.37	14.85±0.01
P_1L	6.92±0.77	5.911.38						2.86±0.22		
P_2L								5.25±0.33	3.26±0.17	14.16±0.76
P_3L			12.37±0.53	8.51±0.35	7.15±0.54	17.76±1.09	12.98±0.58	6.05±0.22	3.42±0.20	20.23±1.15
P_4L	13.01±1.64	12.52±0.88	15.69±0.79	11.06±0.51	9.09±0.49	26.25±1.87	15.52±0.74	7.44±0.47	4.33±0.28	21.07±1.04
M_1L	24.47±1.43	20.49±1.33	17.47±0.64	11.43±1.26	11.06±0.75	27.30±1.84	16.79±0.67	8.26±0.40	4.52±0.28	26.82±1.04
M_2L	24.29±1.80	19.40±1.39						7.57±0.22	3.73±0.14	
M_3L	19.80±1.46	13.72±2.25								
C^1W	15.60±2.31	16.76±3.73	7.87±0.55	6.20±0.54	5.70±0.60	17.44±2.00	10.71±0.74	3.43±0.28	2.43±0.19	11.83±0.50
P^1W	4.83±0.67	4.19±0.59						2.22±0.21		6.44±0.43

P^2W	4.09±2.54		3.17±0.45	2.95±0.37		7.28±0.68	3.52±0.81	2.85±0.42	2.13±0.18	10.83±0.88
P^3W	4.82±0.90	4.58±0.43	6.24±0.31	5.59±0.37	5.10±0.46	12.79±1.13	8.52±0.64	4.74±0.34	3.12±0.28	15.84±0.78
P^4W	12.60±1.18	9.04±1.55	9.20±0.67	8.14±0.66	7.11±0.61	17.58±1.71	11.38±0.45	6.80±0.46	4.80±0.21	19.20±0.92
M^1W	17.31±1.22	15.55±1.42	6.38±0.70	4.49±0.58	4.83±0.48	12.03±0.92	5.73±0.75	8.60±0.40	5.70±0.22	4.17±0.55
M^2W	19.21±1.14	15.02±1.17						7.10±0.38	4.40±0.33	
C_1W	15.67±2.27	15.60±2.79	7.13±0.45	5.83±0.44	5.21±0.48	15.73±1.77	9.04±0.73	3.49±0.28	2.74±0.18	12.16±0.35
P_1W	4.82±0.70	4.46±0.76						2.13±0.16		
P_2W								2.73±0.29	1.99±0.10	9.80±0.44
P_3W			5.60±0.30	4.36±0.26	3.99±0.29	9.45±0.90	6.62±0.48	2.93±0.26	2.26±0.13	13.92±0.66
P_4W	7.99±0.80	6.86±0.63	6.56±0.58	5.10±0.28	4.73±0.31	13.33±1.21	7.76±0.35	4.00±0.24	2.83±0.16	12.59±0.60
M_1W	12.26±0.98	9.19±0.87	7.54±0.45	5.28±0.40	5.15±0.44	14.25±0.95	8.19±0.41	4.87±0.10	3.22±0.13	11.46±0.63
M_2W	15.96±1.49	11.19±1.11						4.60±0.21	2.82±0.15	
M_3W	15.41±1.34	10.77±1.34								

APPENDIX B

CHAPTER III SUPPLEMENTARY INFORMATION AND FIGURES

Supplemental data 1– Results of the Levene's test for homogeneity of variance across groups run before the phylANOVA function was performed.

Table 1- Levene's test for homogeneity of variance results

	Degrees of Freedom	F value	P value
Invert/Vertebrate group	2	1.1475	0.3184
Veggie group	2	1.1375	0.3216

Supplemental data 2–transition rates effective sample sizes for tree 1

Transitions	Effective sample sizes hyperprior 0.2	Effective sample sizes hyperprior 0.10
qAB	3333	3333
qAC	2756.487	3087.514
qAD	3333	3333
qAE	2805.129	2546.116
qAF	3333	3333
qAG	3333	3333
qBA	3668.059	3333
qBC	3080.237	2876.289
qBD	3333	3162.536
qBE	3333	3333
qBF	2891.871	3107.687
qBG	3354.32	3333
qCA	2622.843	2706.104
qCB	2638.767	2461.535
qCD	3333	3333
qCE	3333	3333
qCF	2839.062	3333
qCG	2927.649	3333
qDA	3333	3333
qDB	3333	3165.016
qDC	3544.303	3333

qDE	2636.889	2547.677
qDF	2152.615	2001.353
qDG	2073.621	2235.48
qEA	2899.243	2667.834
qEB	3333	2938.502
qEC	2200.061	2093.321
qED	3061.576	3333
qEF	3090.382	3333
qEG	3140.279	3333
qFA	3333	3333
qFB	2873.448	2491.538
qFC	1598.724	1691.908
qFD	1894.588	2052.868
qFE	3333	3333
qFG	1486.625	1362.926
qGA	3060.198	3333
qGB	3076.393	3154.185
qGC	1335.459	1317.369
qGD	2209.682	2219.774
qGE	1872.227	1937.016
qGF	2131.27	1899.535

Supplemental data 3– Results of using the phylo.d function over 10 randomly selected trees for both diet categories defined by prey type and diet categories defined by plant material. Pval1 and Pval0 represent the p values for the phylo.d test of if the phylogenetic signal was different from a value of 1 (represents a random distribution) or different from a value of 0 (indicating clustering).

Results of using the phylo.d function for diet categories defined by prey type			
Diet Category	D Estimate	Pval1	Pval0
Herbivore	0.029	0.000	0.369
Herbivore	0.034	0.000	0.347
Herbivore	0.028	0.000	0.375
Herbivore	0.026	0.000	0.391
Herbivore	0.031	0.000	0.362

Herbivore	0.035	0.000	0.343
Herbivore	0.021	0.000	0.413
Herbivore	0.038	0.000	0.325
Herbivore	0.029	0.000	0.368
Herbivore	0.026	0.000	0.384
Invert	-0.075	0.000	0.747
Invert	-0.066	0.000	0.724
Invert	-0.073	0.000	0.736
Invert	-0.079	0.000	0.754
Invert	-0.070	0.000	0.733
Invert	-0.061	0.000	0.711
Invert	-0.083	0.000	0.764
Invert	-0.065	0.000	0.720
Invert	-0.069	0.000	0.733
Invert	-0.078	0.000	0.754
Invert.Omnivore	0.462	0.000	0.000
Invert.Omnivore	0.459	0.000	0.000
Invert.Omnivore	0.467	0.000	0.000
Invert.Omnivore	0.458	0.000	0.000
Invert.Omnivore	0.460	0.000	0.000
Invert.Omnivore	0.463	0.000	0.000
Invert.Omnivore	0.457	0.000	0.000
Invert.Omnivore	0.463	0.000	0.000
Invert.Omnivore	0.460	0.000	0.000
Invert.Omnivore	0.461	0.000	0.000
Vert	0.072	0.000	0.404
Vert	0.099	0.000	0.358
Vert	0.109	0.000	0.344
Vert	0.086	0.000	0.390
Vert	0.105	0.000	0.355
Vert	0.122	0.000	0.328
Vert	0.101	0.000	0.366
Vert	0.093	0.000	0.367
Vert	0.084	0.000	0.392
Vert	0.091	0.000	0.387
Vert.Omnivore	0.798	0.019	0.004
Vert.Omnivore	0.815	0.026	0.003
Vert.Omnivore	0.828	0.033	0.003
Vert.Omnivore	0.825	0.035	0.003
Vert.Omnivore	0.819	0.030	0.003
Vert.Omnivore	0.785	0.016	0.004
Vert.Omnivore	0.780	0.016	0.005

Vert.Omnivore	0.853	0.053	0.001
Vert.Omnivore	0.844	0.047	0.002
Vert.Omnivore	0.783	0.015	0.006
Vert.Invert	0.437	0.000	0.001
Vert.Invert	0.439	0.000	0.001
Vert.Invert	0.443	0.000	0.001
Vert.Invert	0.438	0.000	0.002
Vert.Invert	0.442	0.000	0.001
Vert.Invert	0.442	0.000	0.001
Vert.Invert	0.442	0.000	0.001
Vert.Invert	0.448	0.000	0.001
Vert.Invert	0.435	0.000	0.002
Vert.Invert	0.436	0.000	0.002
Vert.Invert.Omnivore	0.510	0.000	0.000
Vert.Invert.Omnivore	0.512	0.000	0.000
Vert.Invert.Omnivore	0.505	0.000	0.000
Vert.Invert.Omnivore	0.502	0.000	0.000
Vert.Invert.Omnivore	0.504	0.000	0.000
Vert.Invert.Omnivore	0.506	0.000	0.000
Vert.Invert.Omnivore	0.499	0.000	0.000
Vert.Invert.Omnivore	0.507	0.000	0.000
Vert.Invert.Omnivore	0.507	0.000	0.000
Vert.Invert.Omnivore	0.501	0.000	0.000

Results of using the phylo.d function for diet categories defined by plant material

Diet Category	D Estimate	Pval1	Pval0
Carnivore	-0.111	0.000	0.875
Carnivore	-0.105	0.000	0.866
Carnivore	-0.114	0.000	0.880
Carnivore	-0.120	0.000	0.889
Carnivore	-0.115	0.000	0.887
Carnivore	-0.104	0.000	0.861
Carnivore	-0.122	0.000	0.891
Carnivore	-0.105	0.000	0.867
Carnivore	-0.109	0.000	0.873
Carnivore	-0.120	0.000	0.897
Fibrous.Omnivore	1.012	0.543	0.000
Fibrous.Omnivore	0.969	0.327	0.000
Fibrous.Omnivore	1.037	0.679	0.000
Fibrous.Omnivore	1.006	0.507	0.000

Fibrous.Omnivore	1.013	0.540	0.000
Fibrous.Omnivore	0.969	0.333	0.000
Fibrous.Omnivore	0.985	0.400	0.000
Fibrous.Omnivore	1.022	0.594	0.000
Fibrous.Omnivore	0.976	0.361	0.000
Fibrous.Omnivore	0.988	0.418	0.000
Nonfibrous.Omnivore	0.520	0.000	0.000
Nonfibrous.Omnivore	0.518	0.000	0.000
Nonfibrous.Omnivore	0.514	0.000	0.000
Nonfibrous.Omnivore	0.510	0.000	0.000
Nonfibrous.Omnivore	0.517	0.000	0.000
Nonfibrous.Omnivore	0.521	0.000	0.000
Nonfibrous.Omnivore	0.510	0.000	0.000
Nonfibrous.Omnivore	0.522	0.000	0.000
Nonfibrous.Omnivore	0.516	0.000	0.000
Nonfibrous.Omnivore	0.513	0.000	0.000
Fibrous.Nonfibrous.Omnivore	0.576	0.000	0.000
Fibrous.Nonfibrous.Omnivore	0.582	0.000	0.000
Fibrous.Nonfibrous.Omnivore	0.594	0.000	0.000
Fibrous.Nonfibrous.Omnivore	0.577	0.000	0.000
Fibrous.Nonfibrous.Omnivore	0.592	0.000	0.000
Fibrous.Nonfibrous.Omnivore	0.575	0.000	0.000
Fibrous.Nonfibrous.Omnivore	0.589	0.000	0.000
Fibrous.Nonfibrous.Omnivore	0.592	0.000	0.000
Fibrous.Nonfibrous.Omnivore	0.577	0.000	0.000
Fibrous.Nonfibrous.Omnivore	0.578	0.000	0.000
Fibrous	0.164	0.000	0.127
Fibrous	0.163	0.000	0.126
Fibrous	0.154	0.000	0.148
Fibrous	0.146	0.000	0.159
Fibrous	0.154	0.000	0.141
Fibrous	0.164	0.000	0.116
Fibrous	0.150	0.000	0.156
Fibrous	0.157	0.000	0.134
Fibrous	0.159	0.000	0.133
Fibrous	0.158	0.000	0.136
Nonfibrous	0.282	0.000	0.012
Nonfibrous	0.278	0.000	0.015
Nonfibrous	0.276	0.000	0.018
Nonfibrous	0.281	0.000	0.015
Nonfibrous	0.283	0.000	0.010

Nonfibrous	0.288	0.000	0.011
Nonfibrous	0.282	0.000	0.015
Nonfibrous	0.278	0.000	0.014
Nonfibrous	0.278	0.000	0.014
Nonfibrous	0.282	0.000	0.012
Nonfibrous.Fibrous	0.332	0.000	0.000
Nonfibrous.Fibrous	0.334	0.000	0.000
Nonfibrous.Fibrous	0.330	0.000	0.000
Nonfibrous.Fibrous	0.332	0.000	0.000
Nonfibrous.Fibrous	0.331	0.000	0.000
Nonfibrous.Fibrous	0.335	0.000	0.000
Nonfibrous.Fibrous	0.325	0.000	0.000
Nonfibrous.Fibrous	0.334	0.000	0.000
Nonfibrous.Fibrous	0.321	0.000	0.000
Nonfibrous.Fibrous	0.329	0.000	0.000

Supplemental data 4- Summary of the transition rate estimated by chains run using an exponential (0, 10) hyperprior. Percent Z is the percentage the transition rate was estimated as zero.

Transitions	median.transition	Interquartile	percent.Z
qAB	0.000	0.000	97.163
qAC	0.722	0.136	0.000
qAD	0.000	0.000	98.042
qAE	0.082	0.061	0.136
qAF	0.000	0.000	97.872
qAG	0.000	0.000	91.666
qBA	0.000	0.000	94.176
qBC	0.082	0.066	5.155
qBD	0.000	0.000	91.247
qBE	0.000	0.000	93.107
qBF	0.699	0.138	0.000
qBG	0.000	0.000	78.475
qCA	2.346	0.381	0.000
qCB	0.682	0.158	0.002
qCD	0.000	0.000	87.787
qCE	0.040	0.072	42.114

qCF	0.000	0.047	67.405
qCG	0.722	0.136	0.000
qDA	0.000	0.060	62.581
qDB	0.000	0.080	53.884
qDC	0.000	0.081	53.609
qDE	0.522	0.649	19.104
qDF	2.289	0.444	0.216
qDG	2.198	0.779	0.116
qEA	0.093	0.739	29.891
qEB	0.051	0.157	42.099
qEC	0.093	0.814	30.030
qED	0.644	0.827	20.779
qEF	0.068	0.615	36.383
qEG	2.285	0.462	0.833
qFA	0.000	0.042	70.286
qFB	2.325	0.393	0.000
qFC	0.699	0.186	6.479
qFD	0.745	0.193	0.078
qFE	0.000	0.057	63.944
qFG	1.533	1.546	0.001
qGA	0.089	0.121	14.395
qGB	0.041	0.093	44.853
qGC	2.181	1.485	0.001
qGD	0.138	0.591	9.486
qGE	0.058	0.167	39.081
qGF	0.747	0.192	0.014

Supplemental data 5- Summary of the transition rate estimated by chains run using an exponential (0, 10) hyperprior. Percent Z is the percentage the transition rate was estimated as zero.

Transitions	median.transition	Interquartile	percent.Z
qAB	12.648	20.540	17.781
qAC	16.005	32.670	3.986

qAD	0.000	0.998	72.071
qAE	0.000	0.000	83.243
qAF	8.764	9.976	10.158
qAG	3.103	10.880	43.441
qBA	45.925	15.065	0.001
qBC	19.674	31.018	8.906
qBD	0.000	5.426	57.307
qBE	0.000	0.000	86.764
qBF	11.062	16.152	18.567
qBG	14.579	28.266	15.049
qCA	44.396	13.767	0.034
qCB	25.763	33.385	6.418
qCD	0.000	8.593	54.695
qCE	0.000	0.000	83.421
qCF	0.998	10.880	49.395
qCG	16.005	32.062	18.441
qDA	45.146	13.920	4.999
qDB	39.785	33.347	8.632
qDC	40.620	33.638	7.439
qDE	10.762	43.683	37.746
qDF	16.005	47.201	27.085
qDG	25.635	42.087	16.782
qEA	40.620	42.407	10.661
qEB	37.731	43.586	18.146
qEC	43.373	33.868	11.488
qED	12.648	41.843	22.899
qEF	12.016	43.139	29.989
qEG	19.797	42.571	19.159
qFA	46.823	12.812	0.011
qFB	44.396	13.769	6.634
qFC	44.396	14.048	8.910
qFD	11.062	39.732	25.948
qFE	0.000	8.764	62.045

qFG	38.566	38.963	12.534
qGA	46.541	13.930	2.410
qGB	44.505	18.210	3.637
qGC	44.149	17.968	3.893
qGD	0.532	16.354	49.853
qGE	0.000	3.722	68.361
qGF	13.244	42.432	25.875

Supplementary data 6-Mammal diet data used to run BayesTraits

Species	**Diet**
Macrotis_lagotis	C
Isoodon_auratus	G
Isoodon_macrourus	G
Perameles_gunnii	C
Perameles_nasuta	C
Perameles_bougainville	C
Antechinus_swainsonii	C
Antechinus_minimus	B
Antechinus_flavipes	D
Antechinus_bellus	B
Antechinus_leo	B
Antechinus_stuartii	C
Antechinus_godmani	F
Phascogale_tapoatafa	F
Dasycercus_cristicauda	B
Dasykaluta_rosamondae	F
Pseudantechinus_macdonnellensis	B
Dasyurus_hallucatus	F
Dasyurus_maculatus	F
Dasyurus_geoffroii	F
Dasyurus_viverrinus	F
Sarcophilus_harrisii	D
Parantechinus_apicalis	F
Dasyuroides_byrnei	F
Sminthopsis_ooldea	B
Sminthopsis_psammophila	B
Sminthopsis_hirtipes	F
Sminthopsis_gilberti	B

Sminthopsis_dolichura	F
Sminthopsis_leucopus	B
Sminthopsis_murina	B
Sminthopsis_griseoventer	B
Sminthopsis_granulipes	B
Ningaui_ridei	B
Ningaui_timealeyi	B
Sminthopsis_macroura	B
Sminthopsis_crassicaudata	B
Sminthopsis_longicaudata	B
Antechinomys_laniger	B
Planigale_gilesi	F
Planigale_tenuirostris	B
Planigale_ingrami	F
Planigale_maculata	F
Myrmecobius_fasciatus	B
Notoryctes_typhlops	B
Lasiorhinus_krefftii	A
Lasiorhinus_latifrons	A
Vombatus_ursinus	A
Phascolarctos_cinereus	A
Burramys_parvus	C
Cercartetus_nanus	C
Cercartetus_lepidus	C
Cercartetus_caudatus	C
Phalanger_gymnotis	A
Phalanger_orientalis	A
Wyulda_squamicaudata	A
Trichosurus_caninus	A
Trichosurus_vulpecula	A
Lagostrophus_fasciatus	A
Dendrolagus_lumholtzi	A
Dendrolagus_bennettianus	A
Petrogale_concinna	A
Petrogale_brachyotis	A
Petrogale_burbidgei	A
Petrogale_lateralis	A
Petrogale_godmani	A
Petrogale_rothschildi	A
Petrogale_assimilis	A
Petrogale_penicillata	A

Petrogale_xanthopus	A
Petrogale_persephone	A
Thylogale_stigmatica	A
Thylogale_thetis	A
Thylogale_billardierii	A
Onychogalea_fraenata	A
Onychogalea_unguifera	A
Setonix_brachyurus	A
Lagorchestes_hirsutus	A
Lagorchestes_conspicillatus	A
Macropus_irma	A
Macropus_rufogriseus	A
Macropus_parma	A
Macropus_dorsalis	A
Macropus_parryi	A
Macropus_agilis	A
Macropus_eugenii	A
Macropus_antilopinus	A
Macropus_robustus	A
Macropus_rufus	A
Macropus_bernardus	A
Wallabia_bicolor	A
Macropus_giganteus	A
Macropus_fuliginosus	A
Potorous_tridactylus	C
Potorous_longipes	C
Bettongia_lesueur	A
Bettongia_gaimardi	C
Bettongia_penicillata	A
Aepyprymnus_rufescens	A
Hypsiprymnodon_moschatus	C
Gymnobelideus_leadbeateri	C
Dactylopsila_trivirgata	G
Petaurus_breviceps	G
Petaurus_norfolcensis	C
Petaurus_australis	C
Petropseudes_dahli	A
Pseudochirulus_forbesi	A
Pseudochirulus_herbertensis	A
Pseudocheirus_peregrinus	A
Hemibelideus_lemuroides	A

Petauroides_volans	A
Tarsipes_rostratus	A
Acrobates_pygmaeus	C
Thylamys_pusillus	C
Thylamys_elegans	C
Marmosops_incanus	G
Chironectes_minimus	F
Philander_opossum	G
Didelphis_virginiana	G
Didelphis_aurita	G
Didelphis_marsupialis	C
Didelphis_albiventris	G
Monodelphis_domestica	G
Marmosa_mexicana	G
Marmosa_robinsoni	G
Marmosa_murina	C
Micoureus_demerarae	C
Tlacuatzin_canescens	G
Caluromys_derbianus	C
Caluromys_lanatus	G
Caluromysiops_irrupta	A
Rhyncholestes_raphanurus	C
Fossa_fossana	F
Eupleres_goudotii	B
Cryptoprocta_ferox	D
Salanoia_concolor	F
Mungotictis_decemlineata	F
Herpestes_ichneumon	F
Bdeogale_nigripes	G
Bdeogale_jacksoni	F
Bdeogale_crassicauda	F
Cynictis_penicillata	F
Rhynchogale_melleri	B
Ichneumia_albicauda	F
Herpestes_vitticollis	G
Herpestes_smithii	F
Herpestes_naso	F
Atilax_paludinosus	F
Helogale_parvula	B
Crossarchus_obscurus	G
Crossarchus_ansorgei	F

Suricata_suricatta	F
Mungos_mungo	G
Liberiictis_kuhni	B
Hyaena_hyaena	G
Hyaena_brunnea	G
Proteles_cristata	B
Crocuta_crocuta	D
Hemigalus_derbyanus	B
Arctogalidia_trivirgata	G
Paradoxurus_jerdoni	G
Paradoxurus_zeylonensis	A
Paradoxurus_hermaphroditus	G
Paguma_larvata	G
Arctictis_binturong	G
Genetta_servalina	F
Genetta_piscivora	G
Genetta_maculata	G
Genetta_tigrina	G
Genetta_genetta	G
Genetta_abyssinica	G
Viverricula_indica	G
Civettictis_civetta	G
Prionodon_linsang	F
Prionailurus_bengalensis	F
Prionailurus_viverrinus	G
Felis_chaus	F
Felis_nigripes	F
Felis_margarita	D
Felis_silvestris	G
Puma_yagouaroundi	D
Lynx_rufus	D
Lynx_canadensis	D
Lynx_pardinus	D
Leopardus_geoffroyi	F
Leopardus_pardalis	D
Leopardus_wiedii	D
Caracal_caracal	D
Neofelis_nebulosa	D
Panthera_pardus	D
Panthera_onca	D
Panthera_leo	D

Panthera_tigris	D
Nandinia_binotata	G
Cuon_alpinus	D
Lycaon_pictus	D
Canis_lupus	D
Canis_simensis	D
Canis_latrans	G
Canis_aureus	G
Canis_mesomelas	D
Chrysocyon_brachyurus	E
Cerdocyon_thous	G
Urocyon_cinereoargenteus	G
Urocyon_littoralis	G
Vulpes_zerda	G
Vulpes_cana	C
Vulpes_macrotis	D
Alopex_lagopus	F
Vulpes_velox	G
Vulpes_chama	F
Vulpes_vulpes	G
Vulpes_rueppellii	G
Nyctereutes_procyonoides	G
Taxidea_taxus	F
Mellivora_capensis	G
Meles_meles	G
Arctonyx_collaris	G
Martes_pennanti	D
Gulo_gulo	D
Martes_flavigula	C
Martes_foina	G
Martes_melampus	G
Martes_martes	G
Martes_americana	F
Martes_zibellina	G
Eira_barbara	E
Aonyx_cinerea	F
Aonyx_capensis	F
Enhydra_lutris	B
Lontra_provocax	F
Lontra_felina	F
Lontra_longicaudis	F

Lontra_canadensis	F
Pteronura_brasiliensis	D
Mustela_erminea	G
Mustela_putorius	F
Mustela_eversmanii	D
Mustela_lutreola	F
Mustela_lutreolina	F
Mustela_nivalis	D
Mustela_altaica	D
Neovison_vison	F
Galictis_cuja	F
Lyncodon_patagonicus	D
Vormela_peregusna	G
Ictonyx_striatus	F
Poecilogale_albinucha	D
Melogale_moschata	G
Potos_flavus	G
Procyon_cancrivorus	G
Procyon_pygmaeus	C
Procyon_lotor	G
Bassariscus_astutus	F
Bassariscus_sumichrasti	G
Bassaricyon_gabbii	A
Nasua_narica	G
Ailurus_fulgens	E
Mephitis_mephitis	G
Mephitis_macroura	G
Spilogale_pygmaea	F
Conepatus_leuconotus	G
Conepatus_chinga	F
Conepatus_humboldtii	F
Conepatus_semistriatus	F
Ailuropoda_melanoleuca	E
Melursus_ursinus	C
Ursus_americanus	G
Ursus_maritimus	D
Ursus_arctos	G
Ursus_thibetanus	G
Helarctos_malayanus	E
Tremarctos_ornatus	G
Manis_pentadactyla	B

Manis_crassicaudata	B
Tapirus_bairdii	A
Tapirus_terrestris	A
Tapirus_pinchaque	A
Tapirus_indicus	A
Diceros_bicornis	A
Ceratotherium_simum	A
Dicerorhinus_sumatrensis	A
Rhinoceros_unicornis	A
Equus_grevyi	A
Syncerus_caffer	A
Bison_bison	A
Bison_bonasus	A
Bos_sauveli	A
Bos_javanicus	A
Tragelaphus_strepsiceros	A
Tragelaphus_spekii	A
Tragelaphus_scriptus	A
Tragelaphus_imberbis	A
Tragelaphus_eurycerus	A
Tragelaphus_buxtoni	A
Tragelaphus_angasii	A
Tetracerus_quadricornis	A
Boselaphus_tragocamelus	A
Ourebia_ourebi	A
Procapra_gutturosa	A
Saiga_tatarica	A
Antidorcas_marsupialis	A
Litocranius_walleri	A
Antilope_cervicapra	A
Nanger_soemmerringii	A
Nanger_granti	A
Nanger_dama	A
Gazella_gazella	A
Gazella_dorcas	A
Gazella_spekei	A
Gazella_leptoceros	A
Gazella_cuvieri	A
Eudorcas_thomsonii	A
Eudorcas_rufifrons	A
Ammodorcas_clarkei	A

Dorcatragus_megalotis	A
Madoqua_guentheri	A
Madoqua_kirkii	A
Madoqua_saltiana	A
Madoqua_piacentinii	A
Raphicerus_melanotis	A
Raphicerus_sharpei	A
Raphicerus_campestris	A
Redunca_fulvorufula	A
Redunca_redunca	A
Redunca_arundinum	A
Kobus_megaceros	A
Kobus_leche	A
Kobus_kob	A
Kobus_vardonii	A
Kobus_ellipsiprymnus	A
Pelea_capreolus	A
Oreotragus_oreotragus	A
Pantholops_hodgsonii	A
Oreamnos_americanus	A
Rupicapra_rupicapra	A
Budorcas_taxicolor	A
Ovis_canadensis	A
Ovis_dalli	A
Ovis_ammon	A
Capra_ibex	A
Ammotragus_lervia	A
Ovibos_moschatus	A
Capricornis_sumatraensis	A
Naemorhedus_goral	A
Oryx_gazella	A
Oryx_dammah	A
Oryx_leucoryx	A
Addax_nasomaculatus	A
Hippotragus_equinus	A
Hippotragus_niger	A
Connochaetes_taurinus	A
Connochaetes_gnou	A
Beatragus_hunteri	A
Alcelaphus_buselaphus	A
Damaliscus_lunatus	A

Damaliscus_pygargus	A
Philantomba_maxwellii	A
Philantomba_monticola	E
Sylvicapra_grimmia	A
Cephalophus_zebra	A
Cephalophus_jentinki	A
Cephalophus_silvicultor	A
Cephalophus_spadix	A
Cephalophus_dorsalis	E
Cephalophus_niger	A
Cephalophus_leucogaster	A
Cephalophus_natalensis	A
Cephalophus_rufilatus	A
Cephalophus_nigrifrons	A
Cephalophus_callipygus	A
Cephalophus_ogilbyi	A
Cephalophus_adersi	A
Aepyceros_melampus	A
Neotragus_batesi	A
Neotragus_pygmaeus	A
Mazama_rufina	A
Mazama_chunyi	A
Mazama_americana	A
Mazama_bricenii	A
Mazama_nana	A
Odocoileus_virginianus	A
Odocoileus_hemionus	A
Pudu_puda	A
Pudu_mephistophiles	A
Mazama_gouazoubira	A
Blastocerus_dichotomus	A
Ozotoceros_bezoarticus	A
Hippocamelus_antisensis	A
Hippocamelus_bisulcus	A
Rangifer_tarandus	A
Alces_alces	A
Hydropotes_inermis	A
Capreolus_capreolus	A
Elaphodus_cephalophus	A
Muntiacus_reevesi	A
Muntiacus_muntjak	A

Muntiacus_atherodes	A
Muntiacus_crinifrons	A
Muntiacus_feae	A
Dama_dama	A
Rusa_unicolor	A
Rusa_timorensis	A
Cervus_nippon	A
Cervus_elaphus	A
Elaphurus_davidianus	A
Rucervus_eldii	A
Rucervus_duvaucelii	A
Axis_axis	A
Axis_calamianensis	A
Axis_porcinus	A
Axis_kuhlii	A
Moschus_fuscus	A
Moschus_chrysogaster	A
Moschus_moschiferus	A
Antilocapra_americana	A
Giraffa_camelopardalis	A
Okapia_johnstoni	A
Tragulus_javanicus	A
Hyemoschus_aquaticus	A
Moschiola_meminna	A
Hippopotamus_amphibius	A
Sus_scrofa	G
Hylochoerus_meinertzhageni	A
Phacochoerus_aethiopicus	A
Phacochoerus_africanus	A
Potamochoerus_porcus	E
Tayassu_pecari	G
Catagonus_wagneri	A
Pecari_tajacu	G
Camelus_dromedarius	A
Vicugna_vicugna	A
Scotophilus_leucogaster	B
Rhogeessa_genowaysi	B
Myotis_nigricans	B
Myotis_albescens	B
Myotis_velifer	B
Myotis_grisescens	B

Myotis_simus	B
Myotis_ruber	B
Myotis_volans	B
Myotis_sodalis	B
Myotis_auriculus	B
Myotis_lucifugus	B
Myotis_evotis	B
Myotis_thysanodes	B
Myotis_keenii	B
Myotis_californicus	B
Myotis_leibii	B
Myotis_vivesi	G
Myotis_emarginatus	B
Myotis_capaccinii	B
Myotis_adversus	F
Myotis_nattereri	B
Myotis_myotis	B
Myotis_blythii	B
Myotis_daubentonii	B
Myotis_bechsteinii	B
Myotis_mystacinus	B
Phoniscus_papuensis	B
Murina_florium	B
Nyctalus_leisleri	B
Nyctalus_noctula	B
Nyctalus_lasiopterus	F
Nyctophilus_gouldi	B
Nyctophilus_timoriensis	B
Pipistrellus_nathusii	B
Pipistrellus_coromandra	B
Pipistrellus_kuhlii	B
Vespertilio_murinus	B
Mimetillus_moloneyi	B
Philetor_brachypterus	B
Laephotis_wintoni	B
Scotorepens_sanborni	B
Chalinolobus_nigrogriseus	B
Eptesicus_nilssonii	B
Eptesicus_serotinus	B
Eptesicus_diminutus	B
Eptesicus_brasiliensis	B

Eptesicus_furinalis	B
Eptesicus_fuscus	B
Histiotus_macrotus	B
Scoteanax_rueppellii	B
Lasionycteris_noctivagans	B
Pipistrellus_subflavus	B
Euderma_maculatum	B
Lasiurus_intermedius	B
Lasiurus_ega	B
Lasiurus_cinereus	B
Lasiurus_borealis	B
Lasiurus_seminolus	B
Antrozous_pallidus	B
Bauerus_dubiaquercus	B
Barbastella_barbastellus	B
Corynorhinus_rafinesquii	B
Corynorhinus_townsendii	B
Otonycteris_hemprichii	B
Plecotus_auritus	B
Plecotus_austriacus	B
Idionycteris_phyllotis	B
Miniopterus_tristis	B
Miniopterus_fuscus	B
Miniopterus_australis	B
Miniopterus_pusillus	B
Miniopterus_magnater	B
Miniopterus_schreibersii	B
Mormopterus_planiceps	B
Mormopterus_beccarii	B
Tadarida_brasiliensis	B
Tadarida_teniotis	B
Tadarida_australis	B
Sauromys_petrophilus	B
Eumops_glaucinus	B
Eumops_dabbenei	B
Eumops_perotis	B
Eumops_hansae	B
Eumops_underwoodi	B
Eumops_auripendulus	B
Eumops_bonariensis	B
Molossus_sinaloae	B

Molossus_currentium	B
Molossus_rufus	B
Molossus_pretiosus	B
Molossus_molossus	B
Promops_centralis	B
Promops_nasutus	B
Nyctinomops_femorosaccus	B
Nyctinomops_laticaudatus	B
Nyctinomops_macrotis	B
Otomops_papuensis	B
Molossops_mattogrossensis	B
Molossops_temminckii	B
Cynomops_planirostris	B
Cynomops_abrasus	B
Cheiromeles_torquatus	B
Natalus_stramineus	B
Saccolaimus_saccolaimus	B
Saccolaimus_flaviventris	B
Saccolaimus_mixtus	B
Taphozous_hildegardeae	B
Taphozous_melanopogon	B
Taphozous_mauritianus	B
Taphozous_perforatus	B
Taphozous_australis	B
Saccopteryx_bilineata	B
Saccopteryx_leptura	B
Rhynchonycteris_naso	B
Centronycteris_maximiliani	B
Peropteryx_kappleri	B
Peropteryx_macrotis	B
Cormura_brevirostris	B
Diclidurus_albus	B
Balantiopteryx_plicata	B
Mosia_nigrescens	B
Emballonura_raffrayana	B
Emballonura_beccarii	B
Coleura_seychellensis	B
Nycteris_thebaica	B
Nycteris_macrotis	B
Nycteris_grandis	F
Nycteris_woodi	B

Noctilio_leporinus	F
Noctilio_albiventris	C
Pteronotus_parnellii	B
Pteronotus_quadridens	B
Pteronotus_davyi	B
Mormoops_megalophylla	B
Mormoops_blainvillei	B
Vampyrum_spectrum	D
Trachops_cirrhosus	G
Macrophyllum_macrophyllum	B
Phyllostomus_hastatus	C
Phyllostomus_elongatus	B
Mimon_bennettii	C
Mimon_crenulatum	F
Phylloderma_stenops	C
Lophostoma_evotis	B
Lophostoma_silvicolum	C
Lophostoma_carrikeri	B
Phyllostomus_discolor	C
Lionycteris_spurrelli	A
Carollia_perspicillata	C
Carollia_castanea	A
Carollia_brevicauda	A
Trinycteris_nicefori	C
Uroderma_bilobatum	A
Vampyressa_pusilla	A
Mesophylla_macconnelli	A
Vampyrodes_caraccioli	A
Platyrrhinus_helleri	C
Platyrrhinus_lineatus	A
Vampyressa_nymphaea	A
Chiroderma_doriae	A
Chiroderma_villosum	A
Enchisthenes_hartii	A
Ectophylla_alba	A
Artibeus_jamaicensis	A
Artibeus_fimbriatus	A
Artibeus_lituratus	A
Artibeus_glaucus	A
Artibeus_phaeotis	A
Ariteus_flavescens	A

Pygoderma_bilabiatum	A
Centurio_senex	A
Sturnira_lilium	C
Sturnira_erythromos	A
Sturnira_aratathomasi	A
Sturnira_bidens	A
Glossophaga_commissarisi	C
Glossophaga_soricina	C
Leptonycteris_curasoae	A
Leptonycteris_nivalis	C
Monophyllus_redmani	C
Erophylla_sezekorni	C
Brachyphylla_cavernarum	C
Brachyphylla_nana	C
Anoura_geoffroyi	B
Anoura_cultrata	C
Hylonycteris_underwoodi	A
Musonycteris_harrisoni	A
Choeronycteris_mexicana	A
Lonchorhina_aurita	B
Lonchorhina_marinkellei	B
Diaemus_youngi	D
Desmodus_rotundus	D
Diphylla_ecaudata	D
Lampronycteris_brachyotis	C
Micronycteris_schmidtorum	B
Micronycteris_minuta	C
Micronycteris_megalotis	C
Mystacina_tuberculata	C
Pteralopex_anceps	A
Melonycteris_melanops	A
Melonycteris_woodfordi	A
Acerodon_jubatus	A
Pteropus_temminckii	A
Pteropus_rayneri	A
Pteropus_samoensis	A
Pteropus_dasymallus	C
Pteropus_vampyrus	A
Pteropus_rufus	A
Pteropus_scapulatus	A
Pteropus_gilliardorum	A

Pteropus_tonganus	A
Pteropus_conspicillatus	A
Pteropus_macrotis	A
Pteropus_alecto	A
Pteropus_hypomelanus	A
Pteropus_neohibernicus	A
Penthetor_lucasi	A
Chironax_melanocephalus	A
Aethalops_alecto	A
Cynopterus_sphinx	A
Micropteropus_pusillus	A
Epomophorus_wahlbergi	C
Epomophorus_gambianus	A
Nanonycteris_veldkampii	A
Hypsignathus_monstrosus	A
Lissonycteris_angolensis	A
Rousettus_aegyptiacus	A
Rousettus_amplexicaudatus	A
Aproteles_bulmerae	A
Dobsonia_inermis	A
Dobsonia_praedatrix	A
Dobsonia_moluccensis	A
Dobsonia_minor	A
Syconycteris_australis	A
Macroglossus_minimus	C
Nyctimene_cephalotes	A
Nyctimene_cyclotis	A
Nyctimene_robinsoni	A
Nyctimene_major	A
Nyctimene_aello	A
Nyctimene_albiventer	C
Nyctimene_vizcaccia	A
Paranyctimene_raptor	B
Eidolon_helvum	A
Eidolon_dupreanum	A
Hipposideros_dinops	B
Hipposideros_diadema	B
Hipposideros_cervinus	B
Hipposideros_speoris	B
Hipposideros_ater	B
Hipposideros_maggietaylorae	B

Hipposideros_caffer	B
Hipposideros_semoni	B
Cloeotis_percivali	B
Rhinolophus_hipposideros	B
Rhinolophus_arcuatus	B
Rhinolophus_philippinensis	B
Rhinolophus_megaphyllus	B
Rhinolophus_blasii	B
Rhinolophus_simulator	B
Rhinolophus_swinnyi	B
Rhinolophus_ferrumequinum	B
Rhinolophus_mehelyi	B
Craseonycteris_thonglongyai	B
Cardioderma_cor	F
Macroderma_gigas	F
Megaderma_lyra	F
Megaderma_spasma	F
Lavia_frons	B
Rhinopoma_microphyllum	B
Rhinopoma_muscatellum	B
Rhinopoma_hardwickii	B
Hemiechinus_auritus	C
Hemiechinus_collaris	F
Atelerix_algirus	G
Atelerix_frontalis	F
Erinaceus_europaeus	C
Erinaceus_concolor	B
Paraechinus_micropus	F
Paraechinus_hypomelas	B
Podogymnura_truei	B
Echinosorex_gymnura	F
Hylomys_suillus	C
Myosorex_varius	B
Myosorex_cafer	C
Surdisorex_norae	B
Surdisorex_polulus	B
Crocidura_mariquensis	B
Crocidura_cyanea	B
Crocidura_montis	C
Crocidura_flavescens	B
Crocidura_suaveolens	B

Crocidura_grayi	B
Crocidura_dsinezumi	B
Diplomesodon_pulchellum	F
Crocidura_fumosa	B
Blarina_carolinensis	G
Blarina_hylophaga	F
Cryptotis_meridensis	F
Neomys_fodiens	F
Neomys_anomalus	B
Notiosorex_crawfordi	F
Sorex_trowbridgii	C
Sorex_merriami	B
Sorex_tenellus	F
Sorex_fumeus	B
Sorex_monticolus	C
Sorex_palustris	C
Sorex_pacificus	G
Sorex_bendirii	B
Sorex_vagrans	C
Sorex_ornatus	B
Sorex_nanus	F
Sorex_cinereus	F
Sorex_hoyi	F
Sorex_dispar	B
Sorex_alpinus	B
Sorex_isodon	B
Sorex_caecutiens	B
Sorex_minutissimus	B
Sorex_minutus	B
Sorex_arcticus	B
Sorex_araneus	B
Neurotrichus_gibbsii	C
Urotrichus_talpoides	B
Talpa_romana	B
Talpa_europaea	B
Condylura_cristata	B
Galemys_pyrenaicus	B
Parascalops_breweri	B
Scalopus_aquaticus	B
Scapanus_latimanus	B
Scapanus_orarius	B

Scapanus_townsendii	C
Solenodon_cubanus	F
Lepilemur_leucopus	A
Lepilemur_ruficaudatus	A
Lepilemur_mustelinus	A
Cheirogaleus_major	C
Cheirogaleus_medius	C
Microcebus_murinus	C
Mirza_coquereli	C
Phaner_furcifer	C
Propithecus_diadema	A
Propithecus_tattersalli	A
Propithecus_verreauxi	A
Avahi_laniger	A
Indri_indri	A
Prolemur_simus	A
Hapalemur_griseus	A
Hapalemur_aureus	A
Lemur_catta	A
Eulemur_rubriventer	A
Eulemur_coronatus	A
Eulemur_macaco	A
Eulemur_fulvus	A
Eulemur_mongoz	A
Varecia_variegata	A
Daubentonia_madagascariensis	C
Galago_moholi	C
Galago_senegalensis	C
Euoticus_elegantulus	C
Otolemur_crassicaudatus	C
Otolemur_garnettii	C
Arctocebus_calabarensis	C
Perodicticus_potto	G
Nycticebus_coucang	G
Nycticebus_pygmaeus	G
Loris_tardigradus	G
Pithecia_pithecia	A
Pithecia_albicans	A
Cacajao_calvus	C
Cacajao_melanocephalus	A
Chiropotes_albinasus	A

Chiropotes_satanas	A
Callicebus_moloch	A
Callicebus_cupreus	C
Callicebus_torquatus	C
Callicebus_personatus	A
Ateles_chamek	A
Ateles_paniscus	A
Ateles_geoffroyi	A
Ateles_belzebuth	A
Lagothrix_lagotricha	C
Oreonax_flavicauda	A
Brachyteles_arachnoides	A
Alouatta_pigra	A
Alouatta_palliata	A
Alouatta_belzebul	A
Alouatta_guariba	A
Alouatta_caraya	A
Alouatta_seniculus	A
Aotus_trivirgatus	C
Saguinus_fuscicollis	C
Saguinus_tripartitus	C
Saguinus_imperator	C
Saguinus_labiatus	A
Saguinus_mystax	C
Saguinus_geoffroyi	C
Saguinus_oedipus	G
Saguinus_midas	C
Callimico_goeldii	C
Callithrix_kuhlii	C
Callithrix_jacchus	E
Leontopithecus_chrysomelas	G
Leontopithecus_rosalia	G
Cebus_olivaceus	C
Cebus_albifrons	C
Cebus_capucinus	G
Cebus_apella	C
Saimiri_sciureus	C
Saimiri_oerstedii	C
Saimiri_vanzolinii	C
Homo_sapiens	G
Pan_paniscus	A

Pan_troglodytes	G
Gorilla_gorilla	A
Pongo_pygmaeus	G
Nomascus_concolor	A
Symphalangus_syndactylus	C
Hylobates_lar	C
Hylobates_agilis	A
Hylobates_muelleri	A
Hylobates_moloch	A
Miopithecus_talapoin	G
Cercopithecus_campbelli	C
Cercopithecus_mona	C
Cercopithecus_pogonias	G
Cercopithecus_neglectus	C
Cercopithecus_diana	A
Cercopithecus_mitis	C
Cercopithecus_nictitans	C
Cercopithecus_ascanius	C
Cercopithecus_cephus	G
Cercopithecus_erythrotis	A
Cercopithecus_petaurista	A
Erythrocebus_patas	C
Chlorocebus_aethiops	C
Cercopithecus_lhoesti	A
Cercopithecus_preussi	A
Allenopithecus_nigroviridis	C
Mandrillus_sphinx	C
Mandrillus_leucophaeus	C
Cercocebus_torquatus	G
Cercocebus_agilis	C
Cercocebus_galeritus	G
Theropithecus_gelada	C
Papio_hamadryas	A
Macaca_sylvanus	C
Macaca_nemestrina	C
Macaca_silenus	C
Macaca_maura	C
Macaca_fascicularis	A
Macaca_mulatta	C
Macaca_cyclopis	C
Macaca_fuscata	C

Macaca_arctoides	G
Macaca_sinica	G
Macaca_radiata	C
Macaca_assamensis	G
Presbytis_comata	A
Presbytis_rubicunda	A
Presbytis_melalophos	A
Presbytis_potenziani	A
Presbytis_thomasi	A
Trachypithecus_obscurus	A
Trachypithecus_phayrei	A
Trachypithecus_cristatus	A
Trachypithecus_johnii	A
Trachypithecus_vetulus	A
Trachypithecus_geei	A
Trachypithecus_pileatus	A
Semnopithecus_entellus	A
Nasalis_larvatus	A
Rhinopithecus_roxellana	A
Rhinopithecus_bieti	A
Colobus_polykomos	A
Colobus_guereza	A
Colobus_angolensis	A
Colobus_satanas	A
Procolobus_verus	A
Tarsius_bancanus	G
Ratufa_affinis	A
Ratufa_bicolor	A
Sciurillus_pusillus	A
Petaurista_leucogenys	A
Petaurista_petaurista	A
Pteromys_volans	A
Eupetaurus_cinereus	A
Aeromys_thomasi	A
Glaucomys_volans	G
Glaucomys_sabrinus	E
Tamiasciurus_hudsonicus	A
Tamiasciurus_douglasii	A
Sciurus_igniventris	A
Sciurus_spadiceus	A
Sciurus_griseus	A

Sciurus_alleni	C
Sciurus_colliaei	A
Sciurus_aureogaster	A
Sciurus_aestuans	A
Sciurus_vulgaris	C
Sciurus_yucatanensis	A
Sciurus_nayaritensis	A
Sciurus_deppei	A
Microsciurus_flaviventer	C
Microsciurus_alfari	C
Sciurus_niger	A
Sciurus_granatensis	A
Sciurus_variegatoides	A
Sciurus_anomalus	A
Rheithrosciurus_macrotis	A
Dremomys_everetti	C
Rhinosciurus_laticaudatus	B
Sundasciurus_tenuis	C
Sundasciurus_lowii	C
Sundasciurus_hippurus	C
Callosciurus_prevostii	C
Lariscus_insignis	C
Callosciurus_orestes	C
Callosciurus_notatus	C
Nannosciurus_melanotis	C
Exilisciurus_whiteheadi	A
Atlantoxerus_getulus	A
Xerus_inauris	C
Xerus_rutilus	C
Xerus_erythropus	A
Spermophilopsis_leptodactylus	A
Epixerus_ebii	A
Protoxerus_stangeri	A
Paraxerus_cepapi	C
Paraxerus_poensis	C
Funisciurus_pyrropus	C
Funisciurus_congicus	C
Funisciurus_carruthersi	A
Funisciurus_lemniscatus	C
Funisciurus_anerythrus	C
Funisciurus_isabella	C

Myosciurus_pumilio	C
Heliosciurus_rufobrachium	C
Tamias_amoenus	C
Tamias_ruficaudus	A
Tamias_ochrogenys	A
Tamias_striatus	C
Tamias_townsendii	C
Tamias_senex	C
Tamias_obscurus	A
Tamias_durangae	A
Tamias_bulleri	A
Tamias_canipes	C
Tamias_rufus	C
Tamias_quadrivittatus	C
Tamias_cinereicollis	A
Tamias_alpinus	A
Tamias_panamintinus	G
Tamias_speciosus	C
Tamias_quadrimaculatus	G
Tamias_minimus	C
Ammospermophilus_interpres	C
Ammospermophilus_harrisii	A
Ammospermophilus_leucurus	G
Ammospermophilus_nelsoni	C
Spermophilus_beldingi	C
Spermophilus_armatus	A
Spermophilus_columbianus	C
Spermophilus_richardsonii	C
Spermophilus_elegans	G
Spermophilus_brunneus	A
Spermophilus_washingtoni	C
Spermophilus_townsendii	A
Spermophilus_spilosoma	C
Spermophilus_tereticaudus	C
Spermophilus_mohavensis	C
Spermophilus_mexicanus	G
Spermophilus_tridecemlineatus	C
Spermophilus_annulatus	A
Spermophilus_adocetus	A
Cynomys_parvidens	A
Cynomys_leucurus	A

Cynomys_gunnisoni	C
Cynomys_ludovicianus	A
Marmota_flaviventris	A
Marmota_olympus	A
Marmota_monax	C
Spermophilus_variegatus	C
Spermophilus_saturatus	A
Spermophilus_lateralis	C
Aplodontia_rufa	A
Eliomys_quercinus	G
Eliomys_melanurus	C
Muscardinus_avellanarius	G
Glis_glis	A
Graphiurus_murinus	A
Myocastor_coypus	A
Makalata_didelphoides	A
Phyllomys_blainvillii	A
Echimys_chrysurus	A
Kannabateomys_amblyonyx	A
Dactylomys_dactylinus	A
Dactylomys_boliviensis	A
Mesomys_hispidus	C
Hoplomys_gymnurus	C
Proechimys_semispinosus	C
Geocapromys_brownii	A
Octodon_degus	A
Spalacopus_cyanus	A
Tympanoctomys_barrerae	A
Ctenomys_mendocinus	A
Ctenomys_torquatus	A
Ctenomys_talarum	A
Chinchilla_lanigera	A
Lagostomus_maximus	A
Dinomys_branickii	A
Cavia_aperea	A
Microcavia_australis	A
Hydrochoerus_hydrochaeris	A
Dolichotis_patagonum	A
Dasyprocta_fuliginosa	A
Dasyprocta_punctata	A
Dasyprocta_leporina	A

Myoprocta_acouchy	A
Cuniculus_paca	A
Erethizon_dorsatum	A
Sphiggurus_mexicanus	A
Coendou_rothschildi	A
Coendou_prehensilis	A
Petromus_typicus	A
Thryonomys_swinderianus	A
Thryonomys_gregorianus	A
Heliophobius_argenteocinereus	A
Cryptomys_mechowi	G
Cryptomys_zechi	C
Cryptomys_damarensis	A
Cryptomys_hottentotus	A
Georychus_capensis	A
Bathyergus_suillus	A
Bathyergus_janetta	A
Heterocephalus_glaber	A
Atherurus_africanus	A
Hystrix_brachyura	A
Hystrix_africaeaustralis	A
Hystrix_cristata	E
Trichys_fasciculata	A
Ctenodactylus_vali	A
Pectinator_spekei	A
Massoutiera_mzabi	A
Felovia_vae	A
Lophiomys_imhausi	C
Deomys_ferrugineus	C
Lophuromys_sikapusi	B
Acomys_cahirinus	C
Pachyuromys_duprasi	A
Taterillus_gracilis	C
Psammomys_obesus	A
Meriones_hurrianae	C
Meriones_shawi	A
Meriones_unguiculatus	A
Meriones_meridianus	G
Meriones_libycus	A
Meriones_crassus	C
Meriones_persicus	C

Meriones_tamariscinus	G
Sekeetamys_calurus	C
Gerbillus_pyramidum	A
Gerbillus_cheesmani	A
Gerbillus_andersoni	A
Gerbillus_henleyi	A
Desmodillus_auricularis	A
Gerbillurus_paeba	C
Gerbillurus_tytonis	C
Gerbilliscus_leucogaster	C
Gerbilliscus_validus	C
Gerbillurus_vallinus	C
Gerbillurus_setzeri	C
Tatera_indica	C
Maxomys_whiteheadi	B
Maxomys_alticola	B
Sundamys_muelleri	C
Bandicota_bengalensis	A
Rattus_villosissimus	C
Rattus_lutreolus	C
Rattus_fuscipes	C
Rattus_tiomanicus	C
Rattus_rattus	A
Rattus_everetti	C
Apodemus_sylvaticus	C
Mus_musculus	C
Mus_setulosus	A
Mus_minutoides	C
Malacomys_longipes	A
Zelotomys_woosnami	C
Colomys_goslingi	B
Mastomys_natalensis	A
Praomys_tullbergi	A
Heimyscus_fumosus	A
Hylomyscus_stella	A
Hylomyscus_aeta	A
Otomys_angoniensis	A
Otomys_irroratus	A
Oenomys_hypoxanthus	A
Hybomys_univittatus	A
Stochomys_longicaudatus	A

Aethomys_chrysophilus	C
Desmomys_harringtoni	A
Rhabdomys_pumilio	C
Lemniscomys_rosalia	A
Arvicanthis_niloticus	C
Mylomys_dybowskii	A
Archboldomys_luzonensis	B
Chrotomys_gonzalesi	B
Rhynchomys_isarogensis	B
Apomys_musculus	C
Leporillus_conditor	A
Zyzomys_pedunculatus	A
Notomys_alexis	C
Notomys_cervinus	C
Notomys_mitchellii	C
Notomys_fuscus	A
Pseudomys_occidentalis	A
Pseudomys_oralis	C
Pseudomys_bolami	C
Pseudomys_pilligaensis	A
Pseudomys_desertor	C
Pseudomys_apodemoides	C
Pseudomys_albocinereus	C
Pseudomys_gracilicaudatus	C
Pseudomys_hermannsburgensis	C
Pseudomys_australis	C
Pseudomys_fieldi	A
Pseudomys_higginsi	C
Leggadina_forresti	C
Leggadina_lakedownensis	C
Xenomys_nelsoni	A
Neotoma_albigula	A
Neotoma_stephensi	A
Neotoma_lepida	A
Neotoma_fuscipes	A
Neotoma_phenax	A
Neotoma_micropus	A
Neotoma_floridana	A
Neotoma_mexicana	A
Neotoma_cinerea	A
Onychomys_leucogaster	G

Onychomys_torridus	F
Peromyscus_boylii	C
Peromyscus_levipes	C
Peromyscus_truei	G
Peromyscus_attwateri	C
Peromyscus_pectoralis	A
Peromyscus_mexicanus	C
Peromyscus_aztecus	C
Peromyscus_melanophrys	A
Podomys_floridanus	C
Peromyscus_maniculatus	C
Peromyscus_polionotus	C
Peromyscus_melanotis	C
Peromyscus_leucopus	C
Peromyscus_eremicus	C
Peromyscus_californicus	C
Peromyscus_crinitus	C
Reithrodontomys_fulvescens	C
Reithrodontomys_megalotis	C
Reithrodontomys_mexicanus	A
Reithrodontomys_gracilis	C
Reithrodontomys_humulis	C
Reithrodontomys_montanus	C
Scotinomys_xerampelinus	B
Scotinomys_teguina	C
Baiomys_musculus	A
Baiomys_taylori	C
Ochrotomys_nuttalli	C
Scapteromys_tumidus	C
Deltamys_kempi	B
Akodon_cursor	C
Wilfredomys_oenax	A
Reithrodon_auritus	A
Irenomys_tarsalis	A
Oecomys_trinitatis	C
Oryzomys_couesi	C
Oryzomys_palustris	G
Melanomys_caliginosus	C
Nectomys_squamipes	G
Holochilus_sciureus	A
Oligoryzomys_flavescens	C

Oligoryzomys_nigripes	C
Neacomys_guianae	C
Zygodontomys_brevicauda	A
Phyllotis_xanthopygus	C
Abrothrix_olivaceus	C
Delomys_dorsalis	C
Anotomys_leander	B
Ichthyomys_tweedii	B
Ichthyomys_pittieri	B
Ichthyomys_hydrobates	B
Ichthyomys_stolzmanni	F
Neusticomys_monticolus	B
Neusticomys_venezuelae	B
Sigmodon_leucotis	A
Sigmodon_ochrognathus	A
Sigmodon_hispidus	C
Rheomys_mexicanus	F
Rheomys_thomasi	F
Rheomys_raptor	B
Chibchanomys_trichotis	B
Ototylomys_phyllotis	A
Nyctomys_sumichrasti	C
Lemmus_sibiricus	A
Synaptomys_cooperi	A
Dicrostonyx_torquatus	A
Phenacomys_intermedius	A
Arborimus_longicaudus	A
Arborimus_albipes	A
Arborimus_pomo	A
Myodes_rutilus	A
Myodes_californicus	A
Myodes_gapperi	C
Alticola_strelzowi	A
Alticola_argentatus	A
Myodes_rufocanus	A
Ellobius_talpinus	A
Lemmiscus_curtatus	A
Microtus_socialis	A
Microtus_arvalis	A
Microtus_multiplex	A
Microtus_ochrogaster	C

Microtus_oaxacensis	A
Microtus_pinetorum	A
Microtus_chrotorrhinus	A
Microtus_oregoni	A
Microtus_longicaudus	A
Microtus_pennsylvanicus	C
Microtus_breweri	A
Microtus_montanus	A
Microtus_townsendii	A
Microtus_xanthognathus	A
Microtus_richardsoni	C
Microtus_agrestis	A
Lasiopodomys_brandtii	A
Dinaromys_bogdanovi	A
Arvicola_amphibius	A
Arvicola_sapidus	A
Neofiber_alleni	A
Ondatra_zibethicus	A
Phodopus_sungorus	C
Phodopus_campbelli	A
Phodopus_roborovskii	C
Cricetulus_barabensis	C
Cricetulus_migratorius	C
Cricetus_cricetus	C
Dendromus_mystacalis	C
Dendromus_mesomelas	A
Steatomys_pratensis	A
Malacothrix_typica	A
Saccostomus_campestris	A
Saccostomus_mearnsi	C
Cricetomys_emini	A
Beamys_hindei	A
Delanymys_brooksi	A
Mystromys_albicaudatus	C
Eliurus_webbi	A
Tachyoryctes_splendens	A
Tachyoryctes_macrocephalus	A
Spalax_microphthalmus	A
Spalax_ehrenbergi	A
Allactaga_euphratica	C
Allactaga_elater	C

Allactaga_tetradactyla	A
Stylodipus_telum	A
Dipus_sagitta	A
Paradipus_ctenodactylus	A
Napaeozapus_insignis	C
Zapus_trinotatus	C
Zapus_princeps	C
Zapus_hudsonius	C
Pygeretmus_pumilio	A
Sicista_betulina	C
Anomalurus_derbianus	C
Anomalurus_beecrofti	A
Anomalurus_pelii	A
Anomalurus_pusillus	A
Idiurus_zenkeri	A
Pedetes_capensis	A
Thomomys_talpoides	A
Thomomys_mazama	A
Thomomys_bottae	A
Thomomys_townsendii	A
Thomomys_bulbivorus	A
Cratogeomys_castanops	A
Geomys_bursarius	A
Geomys_personatus	A
Microdipodops_megacephalus	C
Microdipodops_pallidus	C
Dipodomys_phillipsii	A
Dipodomys_elator	A
Dipodomys_nitratoides	A
Dipodomys_californicus	A
Dipodomys_microps	A
Dipodomys_heermanni	A
Dipodomys_panamintinus	A
Dipodomys_ingens	C
Dipodomys_venustus	A
Dipodomys_spectabilis	E
Dipodomys_nelsoni	A
Dipodomys_ordii	A
Dipodomys_deserti	A
Perognathus_inornatus	A
Perognathus_flavus	A

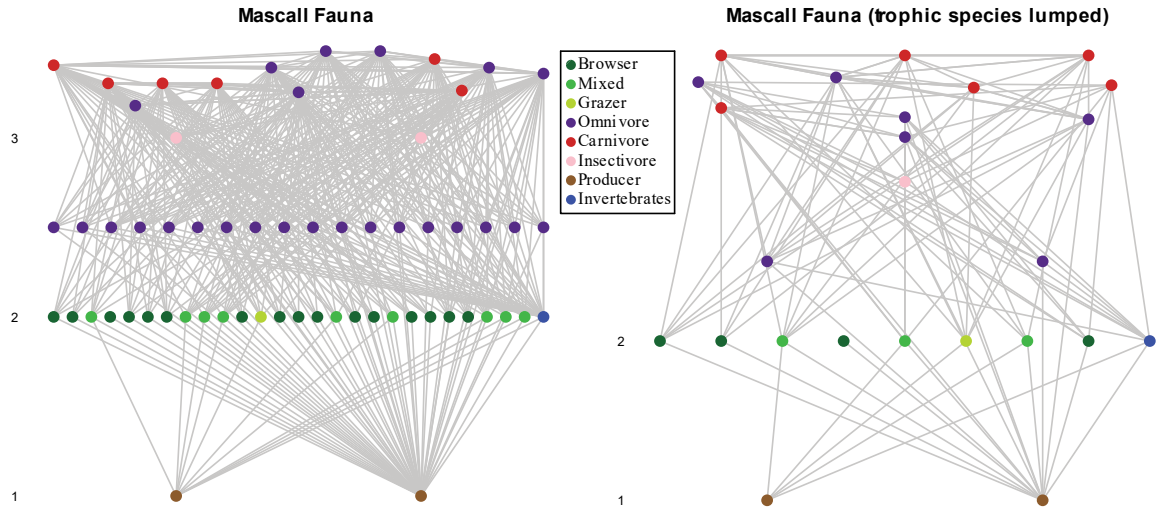
Perognathus_merriami	C
Perognathus_alticolus	A
Perognathus_parvus	C
Perognathus_flavescens	A
Chaetodipus_hispidus	C
Chaetodipus_pernix	A
Chaetodipus_penicillatus	C
Chaetodipus_fallax	A
Chaetodipus_californicus	A
Chaetodipus_nelsoni	C
Chaetodipus_baileyi	C
Liomys_salvini	C
Liomys_adspersus	C
Heteromys_oresterus	A
Heteromys_desmarestianus	E
Heteromys_anomalus	A
Liomys_pictus	C
Castor_canadensis	A
Ochotona_rufescens	A
Ochotona_dauurica	A
Ochotona_princeps	A
Ochotona_collaris	A
Ochotona_alpina	A
Ochotona_hyperborea	A
Oryctolagus_cuniculus	A
Bunolagus_monticularis	A
Sylvilagus_aquaticus	A
Sylvilagus_brasiliensis	A
Sylvilagus_bachmani	A
Sylvilagus_palustris	A
Sylvilagus_transitionalis	A
Sylvilagus_floridanus	A
Sylvilagus_cunicularius	A
Sylvilagus_audubonii	A
Sylvilagus_nuttallii	A
Brachylagus_idahoensis	A
Poelagus_marjorita	A
Pronolagus_crassicaudatus	A
Pronolagus_randensis	A
Pronolagus_rupestris	A
Romerolagus_diazi	A

Lepus_flavigularis	A
Lepus_alleni	A
Lepus_californicus	A
Lepus_callotis	A
Lepus_townsendii	A
Lepus_othus	A
Lepus_arcticus	A
Lepus_timidus	A
Lepus_capensis	A
Lepus_saxatilis	A
Lepus_microtis	A
Lepus_americanus	A
Lepus_europaeus	A
Anathana_ellioti	C
Urogale_everetti	G
Tupaia_glis	G
Tupaia_minor	G
Tupaia_montana	C
Dendrogale_melanura	B
Ptilocercus_lowii	F
Dasypus_sabanicola	B
Dasypus_kappleri	F
Dasypus_novemcinctus	G
Chaetophractus_vellerosus	G
Chaetophractus_villosus	G
Euphractus_sexcinctus	G
Priodontes_maximus	C
Tolypeutes_matacus	B
Cyclopes_didactylus	B
Tamandua_mexicana	B
Tamandua_tetradactyla	B
Myrmecophaga_tridactyla	B
Bradypus_torquatus	A
Choloepus_hoffmanni	A
Elephas_maximus	A
Loxodonta_africana	A
Procavia_capensis	A
Heterohyrax_brucei	A
Dendrohyrax_dorsalis	A
Orycteropus_afer	C
Elephantulus_rufescens	B

Elephantulus_brachyrhynchus	C
Elephantulus_myurus	C
Petrodromus_tetradactylus	B
Macroscelides_proboscideus	C
Rhynchocyon_chrysopygus	B
Rhynchocyon_cirnei	B
Setifer_setosus	B
Echinops_telfairi	B
Tenrec_ecaudatus	F
Hemicentetes_semispinosus	B
Limnogale_mergulus	F
Amblysomus_hottentotus	B
Chrysochloris_stuhlmanni	B
Ornithorhynchus_anatinus	B
Tachyglossus_aculeatus	B

APPENDIX C

CHAPTER IV SUPPLEMENTARY INFORMATION AND FIGURES



Chapter IV Supplementary figure 1 - Example of Mascall original web and "Trophic Species Web". Trophic species are calculated by collapsing all nodes that have identical relationships in the food web into a "trophic species" that represents a node in a new web.

Chapter IV Supplementary data 1 -Species and references used in this study

Formation	Occurrence	Body Mass kilograms	Diet Category1	Diet Category2	Body Mass references	Diet references
Juntura	*Ammospermophilus junturensis*	0.0401	Mixed	Omnivore	Korth 1998, Shotwell and Russell 1963	Fossilworks
Juntura	*Anouroneomys minimus*	0.0174	Insectivore	Omnivore	Fossilworks	Fossilworks
Juntura	*Aphelops megalodus*	1032.4991	Browser	Browser	Prothero and Manning 1987	Fossilworks
Juntura	Caninae	9.5502	Omnivore	Omnivore	Alroy 2000, Galbreath 1953, Henshaw 1942, Merriam 1919, Nelson and Madsen 1987, Storer 1975, Webb 1969	Fossilworks
Juntura	*Carpocyon*	53.2216	Omnivore	Omnivore	Wang et al. 1999	Fossilworks
Juntura	*Cupidinimus*	0.0073	Omnivore	Omnivore	Lindsay 1972, Sutton and Korth 1995	Fossilworks
Juntura	*Epicyon haydeni*	223.7332	Omnivore	Omnivore	Wang et al. 1999	Fossilworks
Juntura	*Epicyon saevus*	106.1058	Omnivore	Omnivore	Wang et al. 1999	Fossilworks
Juntura	*Eucastor malheurensis*	0.7003	Browser	Browser	Storer 1975	Fossilworks
Juntura	*Eurybelodon shoshanii*	25537.9156	Browser	Browser	Lambert 2016	Fossilworks
Juntura	*Hesperolagomys galbreathi*	0.0769	Mixed	Mixed	Shotwell 1970, Tedrow and Robison 1999	Fossilworks
Juntura	*Hesperosorex*	0.0070	Insectivore	Omnivore	Size was assumed from modern species	Fossilworks
Juntura	*Hipparion*	101.5396	Mixed	Mixed	Shotwell and Russell 1963; Drescher 1941; MacFadden and Hulbert 1990	Fossilworks
Juntura	*Hypolagus fontinalis*	0.1764	Mixed	Mixed	Dawson 1958, Kelly 1995	Fossilworks
Juntura	*Hystricops*	8.7857	Browser	Browser	Korth 1997, Korth 1998, Stirton 1935	Fossilworks

Juntura	*Leptodontomys*	0.0032	Mixed	Mixed	Burke 1934, Korth and Bailey 1992	Fossilworks
Juntura	*Macrognathomys nanus*	0.0050	Omnivore	Omnivore	Green 1977, Shotwell 1970	Fossilworks
Juntura	*Mammut furlongi*	18890.8186	Browser	Browser	Shotwell and Russell 1963	Fossilworks
Juntura	*Marmotini*	0.1331	Mixed	Omnivore	Black 1962	Fossilworks
Juntura	*Martes*	0.7900	Carnivore	Carnivore	Size was assumed from modern species	Fossilworks
Juntura	*Megatylopus gigas*	969.0159	Mixed	Mixed	Gustafson 1978, Hibbard and Riggs 1949	Semprebon and Rivals 2010
Juntura	*Merychyus*	24.2687	Mixed	Mixed	Dougherty 1940, Thorpe 1937	Mihlbachler and Solounias 2006
Juntura	*Mystipterus*	0.0161	Insectivore	Insectivore	Hutchison 1968	Fossilworks
Juntura	*Perognathinae indet.*	0.0073	Omnivore	Omnivore	Alroy 2000, Barnosky 1986, Evander 1999, James 1963, Lindsay 1972	Fossilworks
Juntura	*Peromyscus cf. esmeraldensis*	0.0179	Omnivore	Omnivore	Clark et al. 1964, Lindsay 1972, Shotwell 1967	Fossilworks
Juntura	*Peromyscus dentalis*	0.0085	Omnivore	Omnivore	Alroy 2000, Clark et al. 1964, Shotwell 1967, Shotwell and Russell 1963	Fossilworks
Juntura	*Plesiosorex*	0.2251	Insectivore	Omnivore	Meade 1941	Fossilworks
Juntura	*Pliosaccomys*	0.0217	Mixed	Mixed	Dalquest and Patrick 1989	Fossilworks
Juntura	*Pliotaxidea nevadensis*	6.9342	Carnivore	Carnivore	Alroy 2000, Becker and McDonald 1998, Butterworth 1916, Cook and Macdonald 1962	Fossilworks
Juntura	*Procamelus grandis*	368.1204	Browser	Browser	Cassiliano 1980, MacFadden and Hulbert 1990, Shotwell and Russell 1963	Semprebon and Rivals 2010
Juntura	*Pseudaelurus*	31.0651	Carnivore	Carnivore	Storer 1975	Fossilworks

Juntura	*Scalopoides*	0.0483	Insectivore	Insectivore	Hutchison 1968	Fossilworks
Juntura	*Scapanus shultzi*	0.0841	Insectivore	Insectivore	Hutchison 1968, Tedrow 1997	Fossilworks
Juntura	*Spermophilus*	0.1331	Mixed	Omnivore	Black 1963	Fossilworks
Juntura	*Sthenictis junturensis*	10.8332	Carnivore	Carnivore	Shotwell and Russell 1963	Fossilworks
Juntura	Tapiridae indet	150.0000	Browser	Browser	Size was assumed from modern species	Fossilworks
Juntura	*Tardontia occidentale*	0.1199	Mixed	Mixed	Shotwell 1958	Fossilworks
Juntura	Tayassuinae	88.3949	Omnivore	Omnivore	Colbert 1935, Colbert 1938, Dalquest 1983, Hulbert and Whitmore 2006, Schultz et al. 1975	Fossilworks
Lower Turtle Cove	*Agriochoerus guyotianus*	34.8855	Mixed	Mixed	Wilson 1971	Boardman and Secord 2013
Lower Turtle Cove	*Allocyon loganensis*	12.8620	Omnivore	Omnivore	Finarelli and Flynn 2006	Fossilworks
Lower Turtle Cove	*Allomys*	0.0700	Browser	Browser	Tedrow and Korth 1997	Fossilworks
Lower Turtle Cove	*Archaeotherium caninus*	202.0228	Omnivore	Omnivore	Sinclair 1922	Fossilworks
Lower Turtle Cove	*Cormocyon copei*	9.5191	Omnivore	Omnivore	Strganac 2011, Wang et al. 1999	Fossilworks
Lower Turtle Cove	*Corumictis wolsani*	0.5878	Carnivore	Carnivore	Paterson et al. 2020	Fossilworks
Lower Turtle Cove	*Cynarctoides lemur*	2.2043	Omnivore	Omnivore	Wang et al. 1999	Fossilworks
Lower Turtle Cove	*Cynorca sociale*	25.4214	Omnivore	Omnivore	Woodburne 1969, Wright and Eshelman 1987	Fossilworks
Lower Turtle Cove	*Daphoenus*	22.5852	Omnivore	Omnivore	Hunt 1996, Stock 1932	Fossilworks
Lower Turtle Cove	*Diceratherium annectens*	488.9741	Browser	Browser	Prothero 2008	Fossilworks

Lower Turtle Cove	*Diceratherium armatum*	575.9156	Browser	Browser	Green 1958	Fossilworks
Lower Turtle Cove	*Dinictis cyclops*	67.0179	Carnivore	Carnivore	JODA 4314	Fossilworks
Lower Turtle Cove	*Enhydrocyon stenocephalus*	103.1593	Omnivore	Omnivore	Wang 1994	Fossilworks
Lower Turtle Cove	*Eporeodon occidentalis*	61.4577	Mixed	Mixed	Fossilworks	Mihlbachler and Solounias 2006
Lower Turtle Cove	*Eporeodon trigonocephalus*	44.4885	Mixed	Mixed	Fossilworks	Mihlbachler and Solounias 2006
Lower Turtle Cove	*Haplomys liolophus*	0.0280	Browser	Browser	Tedrow and Korth 1997	Fossilworks
Lower Turtle Cove	*Herpetotherium merriami*	0.0258	Omnivore	Omnivore	Korth 1994	Fossilworks
Lower Turtle Cove	*Hoplophoneus cerebralis*	23.5606	Carnivore	Carnivore	Macdonald 1963	Fossilworks
Lower Turtle Cove	*Hoplophoneus strigidens*	120.3179	Carnivore	Carnivore	Peigne et al. 2000	Fossilworks
Lower Turtle Cove	*Hypertragulus hesperius*	2.1564	Browser	Browser	Stevens et al. 1968	Fossilworks
Lower Turtle Cove	*Leptocyon mollis*	9.5502	Omnivore	Omnivore	Alroy 2000, Galbreath 1953, Henshaw 1942, Merriam 1919, Nelson and Madsen 1987, Storer 1975, Webb 1969	Fossilworks
Lower Turtle Cove	*Lepus ennisianus*	0.1517	Mixed	Mixed	Dawson 1958	Fossilworks
Lower Turtle Cove	*Merycoidodon bullatus*	46.1911	Browser	Browser	Clark and Beerbower 1967, Thorpe 1937	Mihlbachler and Solounias 2006
Lower Turtle Cove	*Mesocyon brachyops*	24.6981	Omnivore	Omnivore	Wang 1994	Fossilworks
Lower Turtle Cove	*Mesocyon coryphaeus*	40.2693	Omnivore	Omnivore	Wang 1994	Fossilworks
Lower Turtle Cove	*Mesohippus*	22.8158	Browser	Browser	Forsten 1970, Prothero and Shubin 1989, White 1954	Fossilworks
Lower Turtle Cove	*Micropternodus morgani*	0.1073	Insectivore	Insectivore	Ostrander 1983	Fossilworks

Lower Turtle Cove	*Miohippus annectens*	55.6188	Browser	Browser	Prothero and Shubin 1989	Fossilworks
Lower Turtle Cove	*Miosciurus ballovianus*	0.0258	Browser	Omnivore	Black 1963	Fossilworks
Lower Turtle Cove	*Nanotragulus planiceps*	2.1564	Browser	Browser	Stevens et al. 1968	Fossilworks
Lower Turtle Cove	*Nimravus brachyops*	123.9720	Carnivore	Carnivore	Peigne et al. 2000	Fossilworks
Lower Turtle Cove	*Osbornodon sesnoni*	26.4498	Omnivore	Omnivore	Wang 1994	Fossilworks
Lower Turtle Cove	*Palaeocastor peninsulatus*	0.5063	Browser	Browser	Stefen 2014	Fossilworks
Lower Turtle Cove	*Paraenhydrocyon josephi*	23.1403	Omnivore	Omnivore	Strganac 2011, Wang 1994	Fossilworks
Lower Turtle Cove	*Perchoerus probus*	32.1362	Omnivore	Omnivore	Albright 1999, Macdonald 1970, Pearson 1923, Peterson 1906	Fossilworks
Lower Turtle Cove	*Phlaocyon latidens*	3.7967	Omnivore	Omnivore	Wang et al. 1999	Fossilworks
Lower Turtle Cove	*Pogonodon platycopis*	123.9720	Carnivore	Carnivore	Barret 2016	Fossilworks
Lower Turtle Cove	*Rhizocyon oregonensis*	3.7762	Omnivore	Omnivore	Wang et al. 1999	Fossilworks
Lower Turtle Cove	*Temnocyon altigenis*	77.9425	Carnivore	Carnivore	Alroy 2002, Stock 1933	Fossilworks
Lower Turtle Cove	*Thinohyus lentus*	26.3017	Omnivore	Omnivore	Fossilworks	Fossilworks
Mascall	*"Cynorca" hesperia*	24.8901	Omnivore	Omnivore	Woodburne 1969	Schmidt 2008
Mascall	*"Cynorca" sp.*	20.7950	Omnivore	Omnivore	Maguire et al 2018	Schmidt 2008
Mascall	*Acritohippus isonesus*	101.1917	Grazer	Grazer	Gazin 1932, Scharf 1935, Storer 1975	Maguire, 2013
Mascall	*Alphagaulus vetus*	1.1000	Mixed	Mixed	Hopkins 2007, Hopkins 2008	Calede, 2010
Mascall	*Amphicyon cf. frendens*	792.8805	Carnivore	Carnivore	Wallace 1946	Sorkin, 2006

Mascall	*Anchitheriomys sp.*	18.1244	Browser	Browser	Assumbed from modern beavers	Fossilworks
Mascall	*Aphelops megalodus*	1032.4991	Browser	Browser	Prothero and Manning 1987	Fossilworks
Mascall	*Archaeohippus ultimus*	35.0947	Browser	Browser	Downs 1956	Maguire, 2013
Mascall	*Archaeolagus sp.*	0.2149	Mixed	Mixed	Green 1972, Korth 1992, Storer 2002	Fossilworks
Mascall	*Balantiomys oregonensis*	0.0206	Omnivore	Omnivore	Korth 1997; Downs 1956	Tapaltsyan et al, 2012
Mascall	*Bassariscus lycopotamicus*	2.1090	Omnivore	Omnivore	Gustafson 2015	Fossilworks
Mascall	*Blackia sp.*	0.0289	Browser	Omnivore	Biedron 2016	Black 2012
Mascall	*Blastomeryx gemmifer*	5.4778	Browser	Browser	Patton 1969, Storer 1975, Voorhies 1990	Janis et al., 2004; Prothero, 2007
Mascall	*cf. Domnina sp.*	0.0388	Omnivore	Omnivore	Hutchison 1972; Storer 2002; Galbreath 1953, Krishtalka and Setoguchi 1977, Ostrander 1987, Patterson and McGrew 1937, Setoguchi 1978, Storer 1994, Storer 1995; Simpson 1941	Fossilworks
Mascall	*cf. Kalobatippus sp.*	152.9437	Browser	Browser	Fossilworks	Fossilworks
Mascall	*cf. Miopetaurista sp.*	0.5000	Browser	Omnivore	Size was assumed from modern squirrels	Black, 2012
Mascall	*cf. Moropus sp.*	344.9073	Browser	Browser	Peterson 1907; Coombs et al. 2001	Janis et al., 2004; Semprebon et al., 2010
Mascall	*Copemys sp.*	0.0156	Omnivore	Omnivore	Lindsay 1972; Clark et al. 1964; Lindsay 1972; Shotwell 1967; Sutton and Korth 1995; James 1963; Klingener 1968; Voorhies 1990; Wood 1936; Dalquest et al. 1996; Korth 1998; Alroy 2000; Korth 1997; Dalquest et al. 1996	Tapaltsyan et al, 2012
Mascall	*Cryptailurus tinaynakti*	1.5001	Carnivore	Carnivore	Barret et al. 2020	Barret et al. 2020

Mascall	*Cynarctoides acridens*	3.4995	Omnivore	Omnivore	Wang et al. 1999	Wang et al. 2008
Mascall	*Cynelos sinapius*	678.3104	Carnivore	Carnivore	Hunt 1998, Stock, 1930	Fossilworks
Mascall	*Desmatippus avus*	142.9598	Browser	Browser	Bode 1934, Scharf 1935	Maguire, 2013
Mascall	*Dromomeryx borealis*	149.0843	Browser	Browser	Gazin 1932, Scharf 1935	Semprebon, et al. 2004
Mascall	*Euroxenomys sp.*	0.3551	Browser	Browser	Sutton and Korth 1995	Fossilworks
Mascall	*Gomphotherium sp.*	17777.8950	Browser	Browser	UCMP 22511	Janis et al. 2004; Fox and Fisher 2003
Mascall	*Herpetotherium sp.*	0.0212	Omnivore	Omnivore	Gunnell 1998, Krishtalka and Stucky 1983, Krishtalka and Stucky 1984, Rothecker and Storer 1996, Strait 2001, Zonneveld et al. 2000, Korth 1994, Bown 1982, Lillegraven 1976, McGrew and Sullivan 1971, Rothecker and Storer 1996, Setoguchi 1975, Eberle and Storer 1995, Green and Martin 1976, Korth 1992, Macdonald 1970, Macdonald 1972, Setoguchi 1978, Storer 2002	Fossilworks
Mascall	*Hesperogaulus gazini*	1.4884	Mixed	Mixed	Hopkins 2007, Hopkins 2008	Calede, 2010
Mascall	*Hypolagus fontinalis*	0.1777	Mixed	Mixed	Dawson 1958, Kelly 1995	Fossilworks
Mascall	*Hypolagus parviplicatus*	0.2542	Mixed	Mixed	Dawson 1958	Fossilworks
Mascall	*Leptarctus oregonensis*	7.3409	Omnivore	Omnivore	JODA 3335	Calede, 2018
Mascall	*Leptocyon cf. leidyi*	8.2532	Omnivore	Omnivore	Alroy 2000, Galbreath 1953, Henshaw 1942, Merriam 1919, Nelson and Madsen 1987, Storer 1975, Webb 1969	Wang et al. 2008

Mascall	*Limnoecus niobrarensis*	0.0081	Omnivore	Omnivore	Green and Holman 1977, James 1963	Fossilworks
Mascall	*Limnoecus tricuspis*	0.0055	Omnivore	Omnivore	James 1963, Lindsay 1972	Fossilworks
Mascall	*Merychippus relictus*	47.5482	Mixed	Mixed	Downs 1956	Janis et al., 2004; Hayek et al, 1991
Mascall	*Miolabis transmontanus*	85.9141	Browser	Browser	Maguire et al 2018	Janis et al. 2004; Semprebon and Rivals 2010
Mascall	*Mioscalops cf. ripafodiator*	0.1000	Insectivore	Insectivore	Size was assumed from modern species	Fossilworks
Mascall	*Miospermophilus sp.*	0.0565	Mixed	Omnivore	Biedron 2016	Black 2012
Mascall	*Monosaulax sp.*	0.4997	Browser	Browser	Korth2000, Shotwell 1968, Lindsay 1972	Tapaltsyan et al, 2012
Mascall	*Nototamias sp.*	0.0049	Browser	Omnivore	Biedron 2016	Black 2012
Mascall	*Parablastomeryx sp.*	10.7241	Browser	Browser	Maguire et al 2018	Janis et al., 2004; Prothero, 2007
Mascall	*Paradomnina cf. relictus*	0.0308	Insectivore	Omnivore	Hutchison 1966, Lindsay 1972	Fossilworks
Mascall	*Parahippus sp.*	67.9184	Browser	Browser	Dingus 1990, Emry and Eshelman 1998, Forsten 1975	Janis et al., 2004; Maguire, 2013
Mascall	*Paratomarctus temperarius*	43.4354	Omnivore	Omnivore	Wang et al. 1999	Wang et al. 2008
Mascall	*Petauristodon sp.*	0.2208	Browser	Omnivore	Pratt and Morgan 1989; James 1963	Black, 2012
Mascall	*Pliocyon ossifragus*	475.2792	Carnivore	Carnivore	Berta and Galiano 1984, Macdonald 1960	Fossilworks
Mascall	*Procamelus sp.*	242.4700	Browser	Browser	Cassiliano 1980, MacFadden and Hulbert 1990, Shotwell and Russell 1963, Alroy 2000	Dompierre and Churcher 1996
Mascall	*Prodipodomys mascallensis*	0.2441	Omnivore	Omnivore	CIT 1869	Assumed from other Herteromyids
Mascall	*Protospermophilus oregonensis*	0.3579	Mixed	Omnivore	Black 1963	Black, 2012

Mascall	*Protospermophilus malheurensis*	0.0766	Mixed	Omnivore	Gazin 1932, Shotwell 1968	Black, 2012
Mascall	*Pseudaelurus skinneri*	31.0651	Carnivore	Carnivore	Storer 1975	Fossilworks
Mascall	*Pseudotrimylus mawbyi*	0.2286	Omnivore	Omnivore	Mawby 1960	Fossilworks
Mascall	*Rakomeryx sinclairi*	108.7612	Browser	Browser	Maguire et al 2018	Semprebon, et al. 2004
Mascall	*Tamias sp.*	0.0180	Browser	Omnivore	Biedron 2016	Black 2012
Mascall	*Teleoceras medicornutum*	2219.7188	Mixed	Mixed	Prothero and Manning 1987	Janis et al., 2004; MacFadden, 1998
Mascall	*Tephrocyon rurestris*	48.5192	Omnivore	Omnivore	Wang et al. 1999	Wang et al. 2008
Mascall	*Ticholeptus zygomaticus*	40.8487	Mixed	Mixed	Maguire et al 2018	Janis et al. 2004; Mihlbachler and Solounias 2006
Mascall	*Undentified gopher*	0.0138	Mixed	Mixed	JODA 3770	Tapaltsyan et al, 2012
Mascall	*Unknown genus and species*	0.1064	Insectivore	Insectivore	Barnosky 1981; Alroy 2000; Setoguchi 1978; Korth 1992; Macdonald 1972; Storer 2002; Alroy 2000; Reed 1961	Fossilworks
Mascall	*Watay tabutsigwii*	3.0000	Carnivore	Carnivore	Mclaughlin et al., 2016	Mclaughlin et al., 2016
McKay	*Antecalomys valensis*	0.0073	Omnivore	Omnivore	Shotwell 1967	Fossilworks
McKay	*Basirepomys pliocenicus*	0.0541	Omnivore	Omnivore	Wilson 1937	Fossilworks
McKay	Castor	12.0000	Browser	Browser	Size was assumed from modern species	Fossilworks
McKay	*Copemys esmeraldensis*	0.0179	Omnivore	Omnivore	Clark et al. 1964, Lindsay 1972, Shotwell 1967	Fossilworks
McKay	*Dipoides smithi*	3.5540	Browser	Browser	Green 1977	Fossilworks
McKay	*Epicyon saevus*	106.1058	Omnivore	Omnivore	Wang et al. 1999	Fossilworks

McKay	*Eucyon davisi*	33.0595	Omnivore	Omnivore	Alroy 2000, Gustafson 1978, Harrison 1983, Shotwell 1970	Fossilworks
McKay	*Gaillardia thomsoni*	0.1033	Insectivore	Insectivore	Hutchison 1968	Fossilworks
McKay	*Hipparionini indet*	101.5396	Mixed	Mixed	Shotwell and Russell 1963; Drescher 1941; MacFadden and Hulbert 1990	Fossilworks
McKay	*Hypolagus oregonensis*	0.4028	Mixed	Mixed	Shotwell 1956	Fossilworks
McKay	*Leptodontomys oregonensis*	0.0032	Mixed	Mixed	Burke 1934, Korth and Bailey 1992	Fossilworks
McKay	Liodontia	0.2309	Browser	Browser	Gazin 1932	Fossilworks
McKay	*Lynx longignathus*	6.3745	Carnivore	Carnivore	Pantheria	Pantheria
McKay	*Machairodus*	332.0616	Carnivore	Carnivore	Antón et al. 2013; Savage 1941; Martin 1998	Fossilworks
McKay	Mammutidae	18890.8186	Browser	Browser	Shotwell and Russell 1963	Fossilworks
McKay	*Mustela*	0.7900	Carnivore	Carnivore	Size was assumed from modern species	Fossilworks
McKay	*Neotamias*	0.0179	Browser	Omnivore	Martin 1998	Fossilworks
McKay	*Neurotrichus columbianus*	0.0350	Insectivore	Insectivore	Hutchison 1968	Fossilworks
McKay	*Ochotona spanglei*	0.0375	Mixed	Mixed	Guilday 1979	Fossilworks
McKay	*Oregonomys sargenti*	0.0179	Omnivore	Omnivore	Alroy 2000, Shotwell 1956	Fossilworks
McKay	*Parapaenemarmota oregonensis*	1.8198	Mixed	Omnivore	Nelson and Miller 1990	Fossilworks
McKay	*Parapliosaccomys oregonensis*	0.0179	Mixed	Mixed	Kelly 2000	Fossilworks
McKay	*Perognathinae indet.*	0.0073	Omnivore	Omnivore	Alroy 2000, Barnosky 1986, Evander 1999, James 1963, Lindsay 1972	Fossilworks

McKay	*Peromyscus antiquus*	0.0197	Omnivore	Omnivore	Hoffmeister 1945	Fossilworks
McKay	*Platygonus brachirostris*	66.5718	Omnivore	Omnivore	Prothero and Grenader 2012	Fossilworks
McKay	*Plesiogulo marshalli*	59.8392	Carnivore	Carnivore	Harrison 1981	Fossilworks
McKay	*Pliotaxidea nevadensis*	6.9342	Carnivore	Carnivore	Alroy 2000, Becker and McDonald 1998, Butterworth 1916, Cook and Macdonald 1962	Fossilworks
McKay	*Pliozapus solus*	0.2000	Omnivore	Omnivore	Size was assumed from modern species	Fossilworks
McKay	*Procamelus* or *Pliauchenia*	354.7263	Browser	Browser	Cassiliano 1980, MacFadden and Hulbert 1990, Shotwell and Russell 1963	Semprebon and Rivals 2011
McKay	*Prosomys mimus*	0.0237	Omnivore	Omnivore	Shotwell 1956	Fossilworks
McKay	*Scalopoides*	0.0483	Insectivore	Insectivore	Hutchison 1968	Fossilworks
McKay	*Scapanus proceridens*	0.0841	Insectivore	Insectivore	Hutchison 1968, Tedrow 1997	Fossilworks
McKay	*Spermophilus mckayensis*	0.1331	Mixed	Omnivore	Black 1963	Fossilworks
McKay	*Spermophilus wilsoni*	0.1920	Mixed	Omnivore	Black 1963, Shotwell 1970	Fossilworks
McKay	*Teleoceras hicksi*	2000.0193	Mixed	Mixed	Dalquest and Mooser 1980, Tanner 1975	Fossilworks
Modern John Day Basin	*Alces alces*	461.9008	Browser	Browser	Pantheria	Franzmann, A. (1981). Alces alces. *Mammalian Species,* (154), 1-7. doi:10.2307/3503876
Modern John Day Basin	*Callospermophilus lateralis*	0.1751	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Canis latrans*	11.9891	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Canis lupus*	31.7565	Carnivore	Carnivore	Pantheria	Pantheria

Modern John Day Basin	*Castor canadensis*	18.1244	Browser	Browser	Pantheria	Pantheria
Modern John Day Basin	*Cervus canadensis*	240.8671	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Didelphis virginiana*	2.4421	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Dipodomys ordii*	0.0504	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Erethizon dorsatum*	7.4195	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Glaucomys sabrinus*	0.1375	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Gulo gulo*	12.7925	Carnivore	Carnivore	Pantheria	Pantheria
Modern John Day Basin	*Lemmiscus curtatus*	0.0283	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Lepus americanus*	1.5684	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Lepus californicus*	2.4225	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Lepus townsendii*	3.3716	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Lontra canadensis*	8.0874	Carnivore	Carnivore	Pantheria	Pantheria
Modern John Day Basin	*Lynx rufus*	6.3745	Carnivore	Carnivore	Pantheria	Pantheria
Modern John Day Basin	*Marmota flaviventris*	3.7097	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Martes americana*	0.8737	Carnivore	Carnivore	Pantheria	Pantheria
Modern John Day Basin	*Mephitis mephitis*	2.4000	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Microdipodops megacephalus*	0.0123	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Microtus longicaudus*	0.0448	Mixed	Mixed	Pantheria	Pantheria

Modern John Day Basin	*Microtus montanus*	0.0429	Mixed	Mixed	Pantheria	Sera, W., C. Early. 2003. Microtus montanus. Mammalian Species, 716: 1-10.
Modern John Day Basin	*Microtus richardsoni*	0.0855	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Mustela erminea*	0.2845	Carnivore	Carnivore	Pantheria	Pantheria
Modern John Day Basin	*Mustela frenata*	0.1900	Carnivore	Carnivore	Pantheria	Pantheria
Modern John Day Basin	*Myodes gapperi*	0.0198	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Neotamias amoenus*	0.0506	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Neotamias minimus*	0.0429	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Neotoma cinerea*	0.2859	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Neovison vison*	1.0000	Carnivore	Carnivore	Larivière, 1999 https://doi.org/10.2307/3504420	Larivière, 1999 https://doi.org/10.2307/3504420
Modern John Day Basin	*Ochotona princeps*	0.1576	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Odocoileus hemionus*	84.5606	Mixed	Mixed	Pantheria	Anderson 1984. doi:10.2307/3504024
Modern John Day Basin	*Odocoileus virginianus*	75.9013	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Ondatra zibethicus*	0.9913	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Onychomys leucogaster*	0.0279	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Oreamnos americanus*	72.1054	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Ovis canadensis*	74.6449	Mixed	Mixed	Pantheria	Shackleton, D. (1985). Ovis canadensis. *Mammalian Species,* (230), 1-9. doi:10.2307/3504034

Modern John Day Basin	*Perognathus parvus*	0.0216	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Peromyscus crinitus*	0.0163	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Peromyscus maniculatus*	0.0200	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Peromyscus truei*	0.0270	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Procyon lotor*	6.3737	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Puma concolor*	53.9541	Carnivore	Carnivore	Pantheria	Pantheria
Modern John Day Basin	*Reithrodontomys megalotis*	0.0107	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Scapanus orarius*	0.0621	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Sciurus griseus*	0.7039	Browser	Browser	Pantheria	Carraway 1994 doi:10.2307/3504097
Modern John Day Basin	*Sorex merriami*	0.0060	Carnivore	Carnivore	Pantheria	Pantheria
Modern John Day Basin	*Sorex monticolus*	0.0069	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Sorex pacificus*	0.0106	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Sorex palustris*	0.0131	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Sorex preblei*	0.0031	Omnivore	Omnivore	Pantheria	Cornely, 1992, https://doi.org/10.2307/3504115
Modern John Day Basin	*Sorex vagrans*	0.0060	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Spilogale gracilis*	0.3500	Omnivore	Omnivore	Verts, B.J., Carraway, L.N. and Kinlaw, A., 2001. Spilogale gracilis. Mammalian species, 2001(674), pp.1-10.	Verts, B.J., Carraway, L.N. and Kinlaw, A. 2001. Spilogale gracilis. Mammalian species, 2001(674), pp.1-10.
Modern John Day Basin	*Sylvilagus nuttallii*	0.8015	Mixed	Mixed	Pantheria	Pantheria

Modern John Day Basin	*Tamiasciurus douglasii*	0.2250	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Tamiasciurus hudsonicus*	0.2002	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Taxidea taxus*	7.8422	Carnivore	Carnivore	Pantheria	Long, C. (1973). Taxidea taxus. *Mammalian Species,* (26), 1-4. doi:10.2307/3504047
Modern John Day Basin	*Thomomys talpoides*	0.1046	Mixed	Mixed	Pantheria	Pantheria
Modern John Day Basin	*Urocitellus beldingi*	0.2725	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Urocitellus canus*	0.1800	Omnivore	Omnivore	Cole and Wilson 2009 https://doi.org/10.1644/834.1	Cole and Wilson 2009 https://doi.org/10.1644/834.1
Modern John Day Basin	*Urocitellus columbianus*	0.4709	Omnivore	Omnivore	Pantheria	Elliott and Flinders 1991 doi:10.2307/3504178
Modern John Day Basin	*Urocitellus washingtoni*	0.2151	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Urocyon cinereoargenteus*	3.8337	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Ursus americanus*	110.5000	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Ursus arctos*	196.2875	Omnivore	Omnivore	Pantheria	Pantheria
Modern John Day Basin	*Zapus princeps*	0.0272	Omnivore	Omnivore	Pantheria	Pantheria
Rattlesnake	*Amebelodon sp.*	23058.9320	Browser	Browser	Alroy 2000	Lambert. 1992
Rattlesnake	*Castor californicus*	11.3533	Browser	Browser	Shotwell 1970, Wilson 1933	Samuels, 2009; Samuels and Zancanella, 2011
Rattlesnake	*Dipoides stirtoni*	2.1867	Browser	Browser	Wilson 1934	Samuels, 2009; Samuels and Zancanella, 2011
Rattlesnake	*Eucyon davisi*	33.0595	Omnivore	Omnivore	Alroy 2000, Gustafson 1978, Harrison 1983, Shotwell 1970	Fossilworks
Rattlesnake	*Hesperogaulus wilsoni*	0.5030	Mixed	Mixed	Hopkins 2007, Hopkins 2008	Calede, 2010

Rattlesnake	*Hipparion sp.*	101.5396	Mixed	Mixed	Shotwell and Russell 1963; Drescher 1941; MacFadden and Hulbert 1990	Janis et al., 2004; Hayek et al 1991; Famoso et al, 2013
Rattlesnake	*Hypolagus vetus*	0.3857	Mixed	Mixed	Dawson 1958	Fossilworks
Rattlesnake	*Ilingoceras or Sphenophalos*	14.9469	Mixed	Mixed	JODA 10763	Semprebon and Rivals 2007
Rattlesnake	*Indarctos oregonensis*	1332.7664	Omnivore	Omnivore	Schultz and Martin 1975	Fossilworks
Rattlesnake	*Lutravus halli*	18.5842	Carnivore	Omnivore	Furlong 1932	Fossilworks
Rattlesnake	*Lynx sp.*	6.3745	Carnivore	Carnivore	Pantheria	Pantheria
Rattlesnake	*Machairodus sp.*	332.0616	Carnivore	Carnivore	Antón et al. 2013; Savage 1941; Martin 1998	Fossilworks
Rattlesnake	*Martes sp.*	0.7900	Carnivore	Carnivore	Size was assumed from modern species	Pantheria
Rattlesnake	*Megalonyx sp.*	291.6332	Browser	Browser	Gazin 1935, Mills 1975, Schubert et al. 2004, Dalquest 1975, Meade 1945, Hirschfeld and Webb 1968	Fields, 2009
Rattlesnake	*Megatylopus sp.*	870.2882	Mixed	Mixed	Alroy 2000, Kelly 2000	Semprebon and Rivals 2010
Rattlesnake	*Metalopex merriami*	20.2026	Omnivore	Omnivore	Tedford and Wang, 2008	Wang and Tedford, 2008
Rattlesnake	*Mustela sp.*	0.7900	Carnivore	Carnivore	Size was assumed from modern species	Pantheria
Rattlesnake	*Mylohyus longirostris*	100.9143	Omnivore	Omnivore	JODA 10827	Schmidt, 2008
Rattlesnake	*Neohipparion leptode*	180.2588	Mixed	Mixed	Merriam and Stock 1928, Stock 1951	Janis et al., 2004; MacFadden, 1998; Famoso et al, 2013
Rattlesnake	*Pekania occulta*	3.5000	Carnivore	Carnivore	Size was assumed from modern species	Assumed from modern species
Rattlesnake	*Peromyscus antiquus*	0.0197	Mixed	Omnivore	Hoffmeister 1945	Fossilworks
Rattlesnake	*Platygonus oregonensis*	81.8784	Omnivore	Omnivore	Fossilworks	Schmidt, 2008

Rattlesnake	*Pleiolama cf. vera*	237.6394	Mixed	Mixed	JODA 1342, 1346	Dompierre and Churcher 1996; Yann et al 2016
Rattlesnake	*Pliohippus spectans*	163.4324	Mixed	Mixed	Leite 1990; Drescher 1941; Gazin 1930	Janis et al., 2004; MacFadden, 2008; Famoso et al, 2013
Rattlesnake	*Plionarctos edensis*	116.4329	Omnivore	Omnivore	Tedford and Martin 2001, Hunt 1998	Fossilworks
Rattlesnake	*Scapanus sp.*	0.0956	Insectivore	Insectivore	Hutchison 1968, Tedrow 1997	Fossilworks
Rattlesnake	*Simocyon primigenius*	150.8073	Omnivore	Omnivore	Tedrow et al. 1999, Wang 1997	Salesa et al., 2007
Rattlesnake	*Sorex edwardsi*	0.0086	Omnivore	Omnivore	Eshelman and Hager 1984, Storer 2004, Paulson 1961, Hibbard and Bjork 1971	Fossilworks
Rattlesnake	*Spermophilus gidleyi*	0.0509	Mixed	Omnivore	JODA 11501	Fossilworks
Rattlesnake	*Teleoceras cf. fossiger*	2584.5504	Mixed	Mixed	Cast of CIT 18/1154	Janis et al., 2004; MacFadden, 1998; Famoso et al, 2013
Rattlesnake	*Thomomys sp.*	0.0298	Mixed	Mixed	Kelly 1994; Albright 1999; Wilson 1933; Zakrzewski 1969; Alroy 2000	Loeb, 1990
Rattlesnake	*Unidentified tapir*	150.0000	Browser	Browser	Size was assumed from modern species	Fossilworks
Rattlesnake	*Vulpes stenognathus*	15.9699	Omnivore	Omnivore	Leite 1990, Savage 1941	Van Valkenburgh, 1988
Upper Turtle Cove	*Allomys simplicidens*	0.0700	Browser	Browser	Tedrow and Korth 1997	Fossilworks
Upper Turtle Cove	*Alwoodia magna*	0.1764	Browser	Browser	Korth 1992, Macdonald 1970, Macdonald 1972	Fossilworks
Upper Turtle Cove	*Archaeotherium caninus*	202.0228	Omnivore	Omnivore	Sinclair 1922	Fossilworks
Upper Turtle Cove	*Capacikala gradatus*	0.4287	Browser	Browser	Stefen 2014	Fossilworks
Upper Turtle Cove	*Cormocyon copei*	9.5191	Omnivore	Omnivore	Strganac 2011, Wang et al. 1999	Fossilworks
Upper Turtle Cove	*Daphoenus socialis*	22.5852	Omnivore	Omnivore	Hunt 1996, Stock 1932	Fossilworks

Upper Turtle Cove	*Desmatolagus*	0.1974	Mixed	Mixed	Dawson 1965	Fossilworks
Upper Turtle Cove	*Desmocyon thomsoni*	17.0475	Omnivore	Omnivore	Wang et al. 1999	Fossilworks
Upper Turtle Cove	*Diceratherium annectens*	488.9741	Browser	Browser	Prothero 2008	Fossilworks
Upper Turtle Cove	*Diceratherium armatum*	575.9156	Browser	Browser	Green 1958	Fossilworks
Upper Turtle Cove	*Domnina*	0.0375	Omnivore	Omnivore	Hutchison 1972, Storer 2002	Fossilworks
Upper Turtle Cove	*Ekgmowechashala zancanellai*	0.9240	Omnivore	Omnivore	Samuels et al. 2015	Fossilworks
Upper Turtle Cove	*Enhydrocyon stenocephalus*	103.1593	Omnivore	Omnivore	Wang 1994	Fossilworks
Upper Turtle Cove	*Entoptychus planifrons*	0.0916	Browser	Browser	Wood 1936	Fossilworks
Upper Turtle Cove	*Eporeodon occidentalis*	61.4577	Mixed	Mixed	Fossilworks	Mihlbachler and Solounias 2006
Upper Turtle Cove	*Gentilicamelus sternbergi*	33.7183	Browser	Browser	Prothero 1996	Fossilworks
Upper Turtle Cove	*Herpetotherium merriami*	0.0258	Omnivore	Omnivore	Korth 1994	Fossilworks
Upper Turtle Cove	*Hypertragulus calcaratus*	2.1564	Browser	Browser	Stevens et al. 1968	Fossilworks
Upper Turtle Cove	*Hypertragulus hesperius*	2.1564	Browser	Browser	Stevens et al. 1968	Fossilworks
Upper Turtle Cove	*Hypsiops*	120.2198	Mixed	Mixed	Thorpe 1937	Mihlbachler and Solounias 2006
Upper Turtle Cove	*Jimomys lulli*	0.0197	Mixed	Mixed	Alroy 2000	Assumed from other Geomyids
Upper Turtle Cove	*Leidymys lockingtonianus*	0.0326	Omnivore	Omnivore	Williams and Storer 1998	Assumed from other Cricetids
Upper Turtle Cove	*Leidymys nematodon*	0.0326	Omnivore	Omnivore	Williams and Storer 1998	Assumed from other Cricetids
Upper Turtle Cove	*Meniscomys uhtoffi*	0.0603	Mixed	Mixed	Macdonald 1963, Nichols 1976, Rensberger 1980	Assumed from other Aplodontidae

Upper Turtle Cove	*Merycoides*	32.7867	Mixed	Mixed	Fossilworks	Mihlbachler and Solounias 2006
Upper Turtle Cove	*Mesocyon brachyops*	24.6981	Omnivore	Omnivore	Wang 1994	Fossilworks
Upper Turtle Cove	*Miohippus intermedius*	55.6188	Browser	Browser	Prothero and Shubin 1989	Fossilworks
Upper Turtle Cove	*Nanotragulus planiceps*	2.1564	Browser	Browser	Stevens et al. 1968	Fossilworks
Upper Turtle Cove	*Nimravus brachyops*	123.9720	Carnivore	Carnivore	Peigne et al. 2000	Fossilworks
Upper Turtle Cove	*Ocajila*	0.8000	Insectivore	Omnivore	Size was assumed from modern species	Fossilworks
Upper Turtle Cove	*Oreodontoides oregonensis*	16.3653	Browser	Browser	Thorpe 1937	NOW database
Upper Turtle Cove	*Paciculus insolitus*	0.0603	Omnivore	Omnivore	Alker 1969, Korth 1992, Williams and Storer 1998	Assumed from other Cricetids
Upper Turtle Cove	*Palaeolagus haydeni*	0.1114	Mixed	Mixed	Dawson 1958	Fossilworks
Upper Turtle Cove	*Paradaphoenus cuspigerus*	7.3162	Carnivore	Carnivore	Hunt 2001	Fossilworks
Upper Turtle Cove	*Paraenhydrocyon wallovianus*	75.1450	Omnivore	Omnivore	Stevens 1991, Wang 1994	Fossilworks
Upper Turtle Cove	*Paratylopus*	18.0736	Browser	Browser	Galbreath 1953, Prothero 1996	Fossilworks
Upper Turtle Cove	*Paroreodon*	16.3653	Browser	Browser	Thorpe 1937	NOW database
Upper Turtle Cove	*Philotrox condoni*	56.0346	Omnivore	Omnivore	Wang 1994	Fossilworks
Upper Turtle Cove	*Pleurolicus sulcifrons*	0.0769	Browser	Browser	Macdonald 1963, Rensberger 1973, Wood 1936	Fossilworks
Upper Turtle Cove	*Pogonodon*	123.9720	Carnivore	Carnivore	Barret 2016	Fossilworks
Upper Turtle Cove	*Promerycochoerus superbus*	210.6624	Mixed	Mixed	Thorpe 1937	Mihlbachler and Solounias 2006
Upper Turtle Cove	*Proscalops*	0.1073	Insectivore	Insectivore	Korth 1992, Macdonald 1972, Storer 2002	Fossilworks

Upper Turtle Cove	*Protosciurus rachelae*	0.2485	Browser	Omnivore	Black 1963, Korth 1987	Fossilworks
Upper Turtle Cove	*Protospermophilus vortmani*	0.1764	Mixed	Omnivore	Black 1963	Fossilworks
Upper Turtle Cove	*Rhizocyon oregonensis*	3.7762	Omnivore	Omnivore	Wang et al. 1999	Fossilworks

APPENDIX D

CHAPTER V SUPPLEMENTARY INFORMATION AND FIGURES

Supplemental data 1- Environmental cutoffs and enrichment values used to past estimate plant $\delta^{13}C$ values. See Passey et al. 2002 for further examples.

Environment	$\delta^{13}C$ C3 Vegetation cutoffs from Kohn 2010	ε∗PLANT−CO2
closed canopy	-31.5	-23.68951613
global average	-28.5	-20.66532258
dry environment	-25.5	-17.64112903
upper c3 limit	-23	-15.12096774

Supplemental data 2- Estimates of past plant $\delta^{13}C$ value calculated from past atmospheric estimates and enrichment values from Supplemental data 1. Past enamel values were calculated using -14.1 enrichment value from Cerling and Harris (1999).

Age (Ma)		27	15	7
$\delta^{13}C$ atmos.	3 million year average Tipple et al. 2010	-6.27	-5.27	-6.1
$\delta^{13}C$ plant	closed canopy. C_3	-29.3	-28.3	-29.1
$\delta^{13}C$ plant	average. C_3	-26.4	-25.4	-26.2
$\delta^{13}C$ plant	water stressed	-23.5	-22.5	-23.3
$\delta^{13}C$ plant	max. C_3	-21.1	-20.1	-20.9
$\delta^{13}C$ enamel	closed canopy. C_3	-15.4	-14.4	-15.2
$\delta^{13}C$ enamel	average. C_3	-12.5	-11.5	-12.3
$\delta^{13}C$ enamel	water stressed	-9.5	-8.5	-9.4
$\delta^{13}C$ enamel	max. C_3	-7.1	-6.1	-6.9

Supplemental data 3- Individual $\delta^{13}C$ values, $\delta^{18}O$ values and stratigraphic assignment for each specimen in this study. JODA= John Day Fossil Beds National Monument specimen, UOMNH = University of Oregon Museum of Natural and Cultural History specimen.

Specimen	Group	Formation	$\delta^{13}C$ VPDB	$\delta^{13}C$ stdev	$\delta^{18}O$ VPDB	$\delta^{18}O$ stdev
UOMNH 72348	*Archeohippus*	Mascall	-7.1	0.1	-2.6	0.1
UOMNH 17045	*Archeohippus*	Mascall	-9.9	0.1	-9	0.1
JODA 15598	*Blastomeryx* sp.	Mascall	-9.5	0.03	-10	0.09
JODA 16563	*Desmatippus* sp.	Mascall	-10.4	0.1	-3.5	0
UOMNH 17601	*Dromomeryx*	Mascall	-11	0.1	-6.3	0.1
UOMNH 36120	*Dromomeryx*	Mascall	-10.7	0	-6.9	0.1
UOMNH 4844	*Dromomeryx*	Mascall	-11.9	0	-8.6	0.1
JODA 15293	*Dromomeryx* sp.	Mascall	-10	0.04	-3.5	0.07
JODA 7686	*Dromomeryx* sp.	Mascall	-9.8	0.1	-5.8	0

JODA 16124	Rhinocerotidae	Mascall	-10.4	0.1	-5.9	0.1
JODA 10314	Rhinocerotidae	Mascall	-9.4	0	-4	0.1
UOMNH 75068	Rhinocerotidae	Mascall	-9.6	0.1	-7.3	0
JODA 15631	Rhinocerotidae	Mascall	-11.7	0.03	-6.5	0.1
JODA 15326	Rhinocerotidae	Mascall	-9.6	0.06	-4.4	0.11
JODA 15792	Rhinocerotidae	Mascall	-9.6	0.05	-7.9	0.12
UOMNH 36408	*Ticholeptus*	Mascall	-13	0.1	-4.7	0
UOMNH 36407	*Ticholeptus*	Mascall	-9.8	0	-5.3	0.1
JODA 15930	*Ticholeptus* cf.	Mascall	-13.1	0.1	-7.8	0.1
JODA 6450	*Ticholeptus* cf.	Mascall	-9.9	0.11	-5.4	0.1
JODA 6604	*Ticholeptus* sp.	Mascall	-12.3	0.1	-6.1	0.1
UOMNH BKM 07201503 C	Tayassuidae	Mascall	-8.3	0.1	-9.8	0.1
JODA 16317	Antilocapridae	Rattlesnake	-11.5	0.1	-2.1	0.1
JODA 1117	Antilocapridae	Rattlesnake	-9	0	-10	0.1
JODA 14022	Antilocapridae	Rattlesnake	-10.9	0.09	-7.1	0.1
JODA 1127	Antilocapridae	Rattlesnake	-11.4	0	-9.7	0.1
JODA 7926	*Aphelops* sp.	Rattlesnake	-11.3	0	-10.1	0
UOMNH 16753	*Hipparion*	Rattlesnake	-10.5	0	-9.7	0.1
UOMNH 16806	*Hipparion*	Rattlesnake	-10.4	0	-6	0.1
JODA 559	*Hipparion* sp.	Rattlesnake	-11.5	0.1	-8	0
JODA 300	*Hipparion* sp.	Rattlesnake	-9.4	0	-7.9	0.1
UOMNH 30992	*Ilingocerus* or *Sphenophalos*	Rattlesnake	-8.9	0	-7.2	0
UOMNH 30991	*Ilingocerus* or *Sphenophalos*	Rattlesnake	-9.8	0	-4.5	1.5
JODA 561	*Neohipparion* sp.	Rattlesnake	-9.9	0.1	-7.1	0.1
JODA 17762	*Platygonus oregonensis*	Rattlesnake	-9.5	0	-7.2	0.1
JODA 17760	*Platygonus oregonensis*	Rattlesnake	-11.2	0.04	-7.1	0.06
JODA 13774	*Pliohippus*	Rattlesnake	-11.3	0.04	-8.1	0.07
UOMNH 188	*Pliohippus*	Rattlesnake	-10.2	0	-7.7	0
JODA 15956	*Pliohippus* cf.	Rattlesnake	-10.9	0	-7.6	0.1
JODA 6750	*Prosthennops* cf.	Rattlesnake	-11.1	0.08	-8	0.13
JODA 11479	*Prosthennops* sp.	Rattlesnake	-10.4	0.11	-6.9	0.05
JODA 16141	Rhinocerotidae	Rattlesnake	-10.7	0.1	-9.2	0.1
JODA 16322	Tayassuidae	Rattlesnake	-10.9	0.1	-3.5	0.1
JODA 16177	Tayassuidae	Rattlesnake	-11.9	0.05	-7.5	0.13
JODA 7511	Tayassuidae	Rattlesnake	-11.2	0.1	-5.5	0.1
JODA 1278	*Agriochoerus antiquus*	Turtle Cove	-11.6	0.1	-7.3	0.1
JODA 14954	*Agriochoerus antiquus*	Turtle Cove	-10.1	0	-5.3	0.1
JODA 6978	*Agriochoerus antiquus*	Turtle Cove	-10.5	0.1	-1.5	0
JODA 10261	*Agriochoerus antiquus*	Turtle Cove	-10.9	0.1	-4.4	0.1
JODA 1421	*Agriochoerus antiquus*	Turtle Cove	-10.3	0.05	-1	0.14

JODA 16261	*Archaeotherium* sp.	Turtle Cove	-12.5	0.1	-6.9	0
JODA 16397	*Archaeotherium* sp.	Turtle Cove	-11.6	0.06	-6.6	0.06
JODA 330	*Archaeotherium* cf. *caninus*	Turtle Cove	-12.1	0.1	-5.4	0.1
JODA 8758	*Archaeotherium* cf. *caninus*	Turtle Cove	-11.8	0.04	-6.5	0.06
JODA 15437a	*Archaeotherium* cf. *caninus*	Turtle Cove	-9.3	0.11	-8.4	0.13
JODA 10028	*Archaeotherium* cf. *caninus*	Turtle Cove	-9.9	0.1	-7.1	0.1
JODA 6253	*Archaeotherium caninus*	Turtle Cove	-13	0.07	-6.5	0.06
JODA 11604	*Archaeotherium* cf. *caninus*	Turtle Cove	-10.8	0.06	-7.7	0.11
JODA 4599	*Diceratherium*	Turtle Cove	-10.4	0.06	-6.8	0.06
JODA 1961	*Diceratherium annectens*	Turtle Cove	-10.1	0.07	-8	0.06
JODA 12915	*Diceratherium annectens*	Turtle Cove	-9.3	0.11	-8.4	0.13
JODA 7383	*Diceratherium armatum*	Turtle Cove	-10.9	0.09	-7.1	0.1
JODA 10247	*Diceratherium annectens*	Turtle Cove	-11.5	0.13	-7.1	0.13
JODA 17447	*Diceratherium annectens*	Turtle Cove	-10.5	0.04	-9.7	0.12
JODA 14070	*Diceratherium armatum*	Turtle Cove	-10.2	0.1	-9.4	0.02
JODA 14103	*Diceratherium armatum*	Turtle Cove	-9	0.09	-8.5	0.05
UOMNH 58664	*Eporeodon*	Turtle Cove	-13.1	0.1	-8.7	0.1
UOMNH 64649	*Eporeodon*	Turtle Cove	-12.5	0	-8.7	0.1
JODA 16675	*Eporeodon occidentalis*	Turtle Cove	-13.4	0	-10.3	0
UOMNH 58658	*Hypertragulus*	Turtle Cove	-11.2	0.1	-3.6	0.1
UOMNH 69550	*Hypertragulus*	Turtle Cove	-10.2	0.1	-3.7	0.1
JODA 17624	*Mesohippus*	Turtle Cove	-10.3	0	-7.7	0.1
JODA 17633	*Mesohippus*	Turtle Cove	-11.5	0.1	-3.5	0.1
JODA 14172	*Mesohippus* cf.	Turtle Cove	-10.7	0.06	-5.5	0.12
JODA 12340	*Miohippus*	Turtle Cove	-9.6	0.06	-6	0.09
UOMNH 58687	*Miohippus*	Turtle Cove	-9.7	0.1	-6.9	0.1
UOMNH 58592	*Miohippus*	Turtle Cove	-8.7	0.1	-8.8	0.1
JODA 6363	*Miohippus* cf. *annectens*	Turtle Cove	-11.8	0.03	-8.3	0.14
JODA 13014	*Miohippus* cf. *annectens*	Turtle Cove	-10.5	0.09	-9	0.03
JODA 13004	*Miohippus* cf. *annectens*	Turtle Cove	-9.2	0	-6.6	0.1
JODA 15427b	*Miohippus* cf. *annectens*	Turtle Cove	-9.7	0.06	-3.2	0.06
JODA 796	*Nanotragulus planiceps*	Turtle Cove	-11	0.2	-3	0.1
JODA 17771	*Nanotragulus planiceps*	Turtle Cove	-10.5	0.1	-5	0.09
JODA 16109	*Nanotragulus planiceps*	Turtle Cove	-11.1	0.1	-6.2	0.1

JODA 1889	*Paroreodon* sp.	Turtle Cove	-11.9	0.1	-6.3	0.07
JODA 8686	*Paroreodon* sp.	Turtle Cove	-10.5	0.05	-5	0.06
JODA 1592	*Perchoerus probus*	Turtle Cove	-10.2	0	-8.4	0.1
JODA 1154	*Perchoerus probus*	Turtle Cove	-8.3	0.02	-8.3	0.08
JODA 3655	*Perchoerus probus*	Turtle Cove	-9.5	0.04	-8.3	0.13
JODA 3504	Tayassuidae	Turtle Cove	-8.7	0.07	-5.6	0.06
JODA 7738	Tayassuidae	Turtle Cove	-11.2	0.02	-5.7	0.05
UOMNH 56075	*Thinohyus*	Turtle Cove	-10	0.1	-7.6	0.1

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